

Soil Biota and Global Change

Soil biota and global change at the ecosystem level: describing soil biota in mathematical models

PETE SMITH,* OLOF ANDRÉN,+ LIJBERT BRUSSAARD,‡ MARK DANGERFIELD,§
KLEMENS EKSCMITT,¶ PATRICK LAVELLE** and KEVIN TATE††

*Soil Science Department, IACR-Rothamsted, Harpenden, Herts AL5 2JQ, UK, †Soil Science Department, SLU, PO Box 7014, S-750 07, Uppsala, Sweden, ‡Department of Terrestrial Ecology & Nature Conservation, Wageningen Agricultural University, Bornesteeg 69, 6708 PD, Wageningen, The Netherlands, §Key Centre for Biodiversity & Bioresources, School of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia, †Department of Animal Ecology, University of Giessen, Stephanstrasse 24, 35390 Giessen, Germany, **ORSTOM, Ecologie des Sol Tropicaux, 32 avenue Varagnat, F-93143, Bondy cedex, France, ††Landcare Research, Massey University, Private Bag 11052, Palmerston North, New Zealand

Abstract

All current mathematical models of the soil system are underpinned by a wealth of research into soil biology and new research continues to improve the description of the real world by mathematical models. In this review we examine the various approaches for describing soil biology in mathematical models and discuss the use of each type of model in global change research. The approaches represented among models participating in the Global Change and Terrestrial Ecosystems (GCTE) Soil Organic Matter Network (SOMNET) are described. We examine the relative advantages and constraints of each modelling approach and, using these, suggest appropriate uses of each. We show that for predictive purposes at ecosystem scale and higher, process-orientated models (which have only an implicit description of soil organisms) are most commonly used. As a research tool at the ecosystem level, both process-orientated and organism-orientated models (in which functional or taxonomic groups of soil organisms are explicitly described) are commonly used. Because of uncertainties introduced in internal model parameter estimation and system feedbacks, the predictive use of organism-orientated models at the ecosystem scale and larger is currently less feasible than is the use of process-orientated models. In some specific circumstances, however, an explicit description of some functional groups of soil organisms within models may be required to adequately describe the effects of global change. No existing models can adequately predict the feedback between global change, a change in soil community function, and the response of the changed system to future global change. To find out if these feedbacks exist and to what extent they affect future global change, more research is urgently required into the response of soil community function to global change and its potential ecosystem-level effects.

Keywords: ecosystem, global environmental change, mathematical models, soil biota, soil organic matter network (SOMNET), soil organic matter

Received 26 June 1997; revised version received 17 August and accepted 15 August 1997

Introduction

An ecosystem is to some extent shaped by its soil biota. The soil biota are the main agents in mediation of the rate of nutrient release, which in turn influences the

growth and community structure of plants, and thereby the functioning of the whole ecosystem. The vast wealth of soil biological research, even if it not apparent from the model structure, underpins all current mathematical models of the soil system. New soil biological research continues to improve the description of the real world

Correspondence: Dr Pete Smith, tel + 44/ (0)1582 763133, fax + 44/ (0)1582 760981, e-mail pesmith@bbsrc.ac.uk

by mathematical models. In this review we examine the various approaches for incorporating soil biology into mathematical models and discuss the use of each type of model in global change research.

A number of recent reviews have dealt in some way with the role of soil biota in ecosystem models and soil organic matter (SOM) models, e.g. Paustian (1994), McGill (1996), Molina & Smith (1997), and Brussaard (1997). These reviews are collectively quite comprehensive and we will not attempt to cover the same ground here — instead we will give an overview of the types of models available for simulating and predicting the ecosystem-level effects on soil of global environmental change. We present the approaches reflected in models participating in the Global Change and Terrestrial Ecosystems (GCTE) Soil Organic Matter Network (SOMNET; Smith *et al.* 1996a,b; Powlson *et al.* 1998). We also suggest situations in which each type of model is most appropriately used to study global change considering the main advantages and constraints of each approach.

McGill (1996) presents a scheme for classifying and comparing SOM models in which he examined nine SOM models used in a model evaluation and comparison exercise (Powlson *et al.* 1996; Smith *et al.* 1997a). One aspect he examined was the biotic component of models; indeed one of his three main conclusions was that a more mechanistic treatment of soil organisms was required. He also emphasized (a) the importance of cross-scale (temporal and spatial) comparisons, links to geographical information system (GIS), and of determining an appropriate level of detail needed as a function of scale; and (b) the importance of physical fractionations of soil to relate soil structure through organism-substrate accessibility to turnover rates.

Paustian (1994) provides a review closely focused on the description of soil organisms in simulation models. He reviewed nine groups of models and emphasized the distinction between 'process-oriented' and 'organism-oriented' models. These terms are used throughout this paper and are described in greater detail below. In common with McGill (1996), Paustian emphasized the importance of relating soil structure to soil organic matter and nutrient dynamics and on reconciling measurable organic matter pools with the theoretical pools used in models. These arguments, further developed by Elliott *et al.* (1996) and Christensen (1996), have yet to be resolved. The other main area he identified for future development was a greater examination of the links between soil community structure and soil processes. He further identified a need for comprehensive model validation across a range of soil climate and management conditions and recognized experimental site networks, GIS, and adoption of modular programming methods as factors that would facilitate these developments.

Brussaard (1997) divides models into food web models (analogous to Paustian's organism-orientated models) and organic matter models (analogous to Paustian's process-orientated models). In organic matter models, he noted that apart from inclusion of the microbial biomass, soil biota were ignored. In food web models, he noted that although the soil biota were divided into functional groups, soil organic matter and litter were not specified beyond roots and detritus. He also presents examples of comparisons between process- and organism-orientated approaches and provides a thoughtful discussion of the relative advantages and limitations of food web models when used in global change research.

Two approaches — process-orientated models and organism-orientated models

Both process-orientated and organism-orientated models use information derived from soil biological research, but each uses the information in a different way. Paustian (1994) describes process-orientated models as those which focus on the processes mediating the movement and transformations of matter or energy; soil organisms are mainly implicit in the model formulations and organism components, if present, tend to represent a generic soil biomass, i.e. an undifferentiated mass of organisms in the soil. In many models, the soil microbial biomass is treated as an active (and often measurable) pool of soil organic matter (e.g. Molina *et al.* 1983; Parton *et al.* 1988; Jenkinson 1990; Arah 1996; Mueller *et al.* 1996). As McGill (1996) emphasizes, there is some justification for this approach but he suggests that this simple treatment of biomass precludes the possibility of simulating changes that occur because of changes in the activity or characteristics of the soil organisms. Process-orientated models describe fluxes of soil carbon with varying levels of complexity. Some use one-compartment (e.g. Jenny 1941), some two (e.g. Jenkinson 1977), some are noncompartmental, describing decomposition as a continuum (e.g. Bosatta & Ågren 1985), but most have more than two compartments, i.e. they are multicompartiment (see McGill 1996). Models differ in detail but an example of the structure of a multicompartiment process-orientated model, in this case DAISY, is shown in Fig. 1.

Organism-orientated models (called food web models by Brussaard 1997) are more diverse in nature than are process-based models but fewer have been developed (see below). All model the flows of matter or energy through different groups of soil organisms, which are described either by functional or taxonomic groups. Examples of organism-orientated models include a fungal growth model developed by Paustian (1985), a model of decomposition in grasslands which includes functional groups of microbial biomass but does not divide the

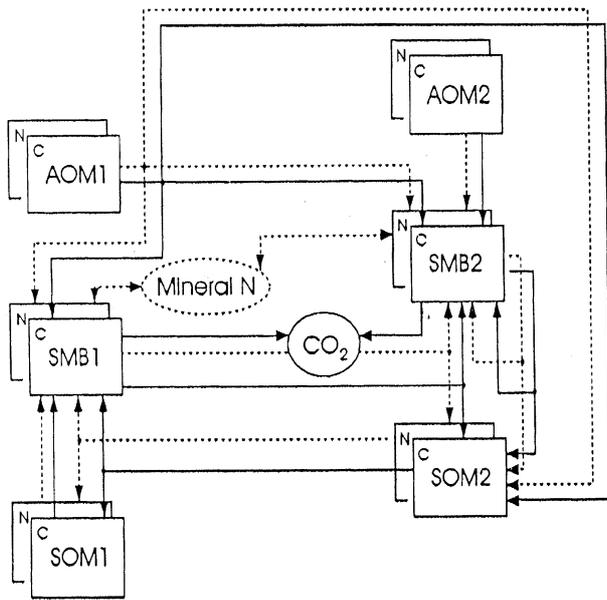


Fig. 1 Example of the structure of a multicompartamental, process-orientated model, in this case DAISY (from Mueller *et al.* 1996). AOM = Added organic matter; SMB, Soil microbial biomass; SOM, Soil organic matter.

biomass by taxonomic group (Hunt 1977), and other models of Hunt and coworkers which describe the detrital food web by taxonomic group (e.g. Hunt *et al.* 1987; see also Wardle *et al.* (1998, this volume) for further discussion of food webs). Other researchers have also used organism-orientated models extensively, notably those among the group at AB-DLO, Haren, The Netherlands. This group has used such models to explore N mineralization in arable soils (e.g. de Ruiter *et al.* 1993a), and C and N mineralization in grassland soils (e.g. Hassink *et al.* 1994). Many uses are described in a number of other studies (de Ruiter *et al.* 1993b, 1994, 1995). An example of the structure of an organism-orientated model, in this case the detrital food-web model of de Ruiter *et al.* (1993a), is shown in Fig. 2.

A few models have incorporated aspects of both process-orientated and organism-orientated approaches. Paustian *et al.* (1990), for example, use this approach in their description of C and N flows through various groups of soil organisms in agroecosystems. McGill *et al.* (1981) developed a predominantly process-orientated model but bacteria and fungi were assumed to directly control decomposition. In the model of van Veen & Frissel (1981) the rate constant for decomposition was assumed to be controlled by microbial biomass. There is no intrinsic reason why ecosystem models should not include aspects of both process- and organism-orientated approaches if required, especially if they are programmed in a modular way. The possibility of further combined approaches is discussed later.

Models represented within the GCTE Soil Organic Matter Network (SOMNET)

The models described in this section participate in the GCTE SOMNET [full details of all models can be found on the GCTE SOMNET World-Wide-Web page at URL: <http://yacorba.res.bbsrc.ac.uk/cgi-bin/somnet>; a summary of all model (and experimental) metadata can be found in Smith *et al.* (1996b)]. Models participating in SOMNET (with notes and key references) are shown in Table 1 and are categorized as either process- or organism-orientated, according to the classification of Paustian (1994). None, however, fall into the organism-orientated category which may partly reflect the way in which the network was established; it initially focused on models that could describe soil organic matter dynamics in long-term field experiments (Powelson *et al.* 1996) as historically, process-orientated models have always been deemed more appropriate for simulating SOM dynamics over long periods. The fact that no organism-orientated models are represented in SOMNET may also reflect the fact that far fewer organism-orientated models have been developed.

Many of the process-orientated models shown in Table 1 do contain some description of organisms but this is confined to generic biomass as described earlier. There are subtle differences in the way in which biomass is included in the models but elaboration of these differences would require unwarranted space in a review of this kind. Molina & Smith (1997) provide a more detailed description.

Some of the models specify microbial biomass (i.e. excluding meso- and macro-fauna; Pankhurst & Lynch 1994) but only one model, SOMM, describes larger organisms (earthworms and microarthropods) specifically. In SOMM, which was originally developed for forest soils, there are some distinctions of humus forms based on different abundances and roles of microarthropods and earthworms. These differences in turn affect the way the model treats organic matter turnover (Chertov & Komarov 1996). Despite this distinction, the model is predominantly process-orientated.

Different uses of each type of model in global change research

Models may be used for a range of purposes (Pielou 1981) and there are many possible applications of models in global change research. Among other things, models can be used as research tools to test hypotheses about the soil system, for example to examine contrasting hypotheses of nitrogen mineralization and immobilization. They can also be used predictively, for example to estimate fluxes of CO₂ and trace gases after changes in

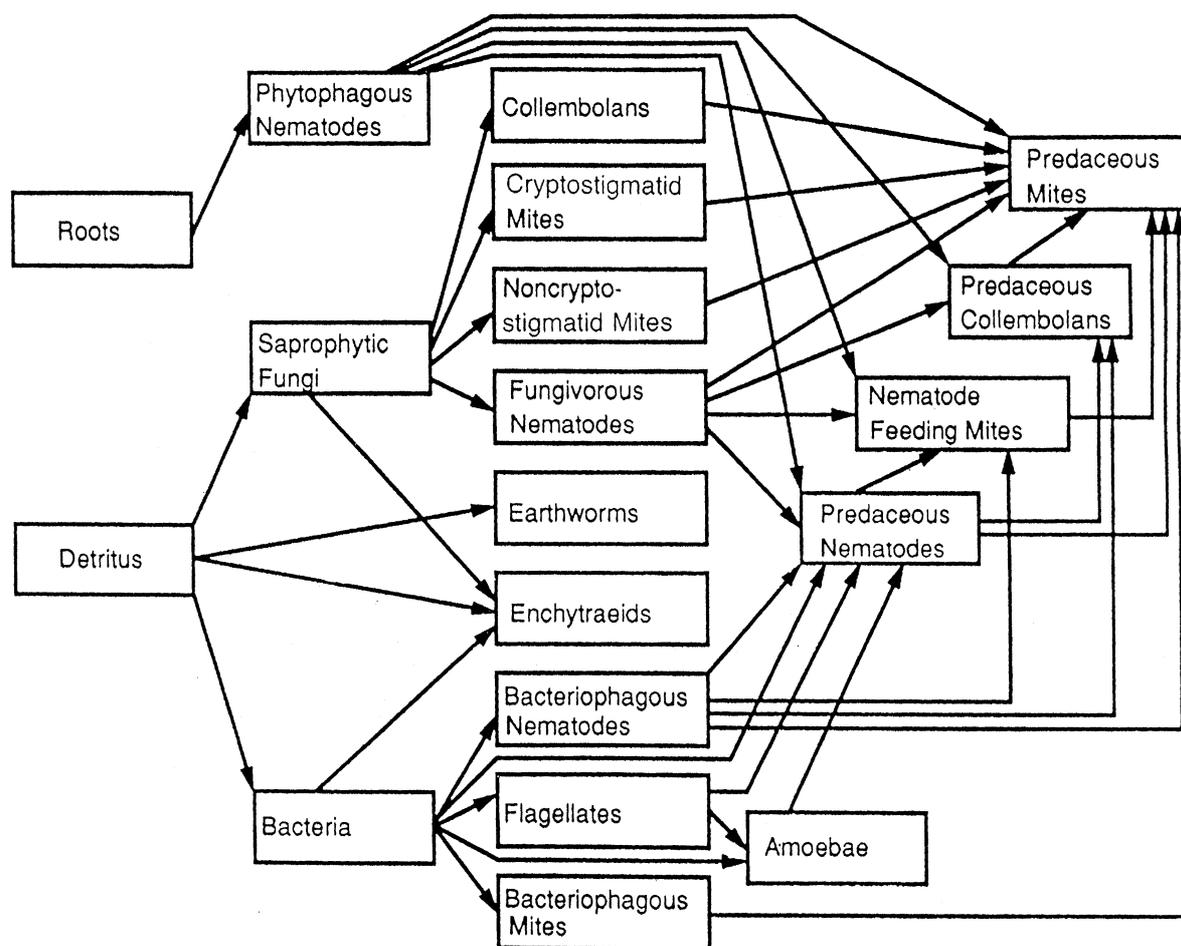


Fig. 2 Example of the structure of an organism-orientated model, in this case the detrital food-web model of de Ruiter *et al.* (1993a). The figure shows the food web at Lovinkhoeve experimental farm, Marknesse, Noordoostpolder, The Netherlands.

land-use or during climate change. As well as being used to answer different types of question, models are also used at vastly different scales. Some models are intended to be used at the microsite scale over periods of hours or days whilst others are used at the ecosystem, regional and global scales for periods of years or decades. When assessing the suitability of each type of model in global change research it is important to clearly identify the question being asked and at what scale the question is best answered. In this paper we consider both purpose and scale; in terms of scale (in line with the objectives of this volume) we consider the use of models only at the ecosystem scale and greater, whilst in terms of purpose, we consider the use of models both as research tools and predictive tools.

Use of soil ecosystem models as research tools

Both process-orientated and organism-orientated models are used as research tools. All of the process-orientated

models in Table 1 and the models given as examples of organism-orientated models above have been used to test our understanding of the soil system and its response to various environmental perturbations. Often, the different approaches have been applied to the same problem; for example the processes of nitrogen mineralization and immobilization have benefited from the application of both process-orientated models (e.g. Molina *et al.* 1983) and organism-orientated models (e.g. Hunt *et al.* 1987).

Organism-orientated models have already provided insights into the details of C and N flows through food webs (Hunt *et al.* 1984, 1987; Paustian *et al.* 1990), and particularly the role of soil biota in C and N mobilization (Paustian 1994). They have also proved to be useful tools in environmental risk assessment and in assessing the environmental effects of soil contaminants (P.C. de Ruiter, personal communication); in guiding monitoring programs and as a link to above ground food webs (O.W. Heal, personal communication); and as a tool to look at spatial variability at different scales (M. Van Noordwijk,

Table 1 Broad categorizations of the models participating in SOMNET

Model	Model type	Notes	Reference
ANIMO	Process	Biomass included	Rijtema & Kroes (1991)
Candy	Process		Franko <i>et al.</i> (1995), Franko (1996)
CENTURY	Process	Biomass included	Parton <i>et al.</i> (1988)
DAISY	Process	Biomass included	Svendsen <i>et al.</i> (1995), Mueller <i>et al.</i> (1996)
DNDC	Process	Biomass included	Li <i>et al.</i> (1994)
DSSAT	Process		Hoogenboom <i>et al.</i> (1994)
D3R	Process		Douglas & Rickman (1992)
ecosys	Process	Biomass included	Grant <i>et al.</i> (1993a,b), Grant (1995)
EPIC	Process	Biomass included	Williams (1990)
FERT	Process	Biomass included	Kan & Kan (1991)
GENDEC	Process	Biomass included	Moorhead & Reynolds (1991)
Hurley Pasture ITE(Edinburgh) Forestry Model	Process	Biomass included	Thornley & Verberne (1989) Thornley & Cannell (1992)
KLIMAT-SOIL-YIELD	Process	Biomass included	Sirotenko (1991)
McCaskill & Blair	Process		McCaskill & Blair (1990a,b)
CNSP Pasture Model	Process		Schevtsova & Mikhailov (1992)
Model of Humus Balance	Statistical *	Static model based on statistical relationships *	
MOTOR	Process	Biomass included user-defined inputs and outputs	Whitmore (1995)
NAM SOM	Process	Two differential equations	Ryzhova (1993)
NCISOIL	Process	Biomass included	Molina <i>et al.</i> (1983)
O'Leary Model	Process	Fallow-Wheat only	O'Leary (1994)
Q-Soil	Process	Non-compartmental model	Ågren & Bosatta (1987)
RothC	Process	Biomass included	Jenkinson & Rayner (1977)
SOCRATES	Process	Biomass included	Grace & Ladd (1995)
SOMM	Process	Some distinctions of humus forms based on different roles of soil fauna (microarthropods and earthworms)	Chertov & Komarov (1996)
Sundial	Process	Biomass included	Smith <i>et al.</i> (1996), Bradbury <i>et al.</i> (1993)
Verberne	Process	Biomass included	Verberne <i>et al.</i> (1990)
VOYONS	Process	Composite model using many submodels	André <i>et al.</i> (1994)
Wave	Process	Biomass included	Vanclouster <i>et al.</i> (1995)

* All other models are dynamic process-orientated models. Note that none are organism-orientated

pers. comm.). Brussaard (1997) makes a convincing case for using organism-orientated (food web) models for integrating current knowledge and for guiding research in a very complex system. Food web models are, of course, also of critical importance when assessing the stability of the below-ground food webs under global change (De Ruiter *et al.* 1995; Brussaard 1997).

The main advantage of organism-orientated models for use in global change studies at the ecosystem level is the inclusion of an explicit description of soil biota which potentially allows the simulation of changes in soil C, N, SOM or energy that occur due to changes in the activity or characteristics of those organisms. McGill (1996) also noted that without the explicit inclusion of soil organisms, process-orientated models could not include such feedback mechanisms. A note of caution is required here:

there is evidence that organism abundances rarely limit process rates at the ecosystem level (see Paustian 1994). Reasonable arguments have been made which claim that the soil organisms are there and they do their job — which is why first-order kinetics work so well in the simple models (e.g. Andrén *et al.* 1994). The ecosystem can also be viewed as a hierarchy, with processes at a high level, fairly isolated from the organisms and their interactions well below (O'Neill *et al.* 1986). This view has been modified, or to some extent challenged (Beare *et al.* 1994), but the 'importance' of species numbers, population dynamics, etc. for ecosystem processes remains an open question.

Despite the need for caution outlined above, there are probably qualitative and quantitative changes in soil community structure which occur as a result of environ-

mental perturbation that will affect ecosystem level process rates, and such feedbacks may be best simulated by an explicit description of soil organisms. Large and immediate environmental changes, for example a change in land-use from grassland or forest to arable agriculture, may be relatively easy to define in terms of changes in the soil community. Ecosystems and possible functional groups of soil organisms where this may be necessary are detailed elsewhere in this volume (e.g. Swift *et al.* 1998, this volume).

It should be noted, however, that although organism-orientated models (with some process-based components) have been used to study the effects of climate change (Hunt *et al.* 1991), much research is still required into the effects of global change on soil community function so that models can be parameterized to simulate and predict system feedbacks. The problem of defining the feedback between global change, its effects on soil community function, and the subsequent response of the system to further global change is discussed further in the last section in this paper.

Use of soil ecosystem models as predictive tools

Most mathematical models of the soil were developed as research tools; as encapsulations of a number of hypotheses of how the soil functions. However, policy-makers (and others) increasingly demand that models be used to predict how the soil system will respond to various changes in the future. For this reason we need to consider which type of model is most appropriate for use as a predictive tool at spatial scales as large as the ecosystem and larger, and at temporal scales of many years or decades. Although organism-orientated models have been used to assess the impact of global change at the ecosystem level (e.g. Hunt *et al.* 1991), process-orientated models are currently far more commonly used (e.g. Post *et al.* 1982; Jenkinson *et al.* 1991; Donigan *et al.* 1994; Schimel *et al.* 1994; Parton *et al.* 1995).

There are a number of reasons for the greater use of process-orientated models for predictive purposes compared with organism-orientated models: first, their internal parameters (such as rate constants or rate modifiers) are easier to estimate. These are often derived from field experiments (e.g. Jenkinson & Rayner 1977), and less commonly from laboratory incubations (e.g. Molina *et al.* 1983). Consequently, it is simpler to calibrate process-orientated models for a specific purpose. Site specific calibration of organism-orientated models involves more complex and labour-intensive measurements. For example, the model described by Hunt *et al.* (1987) requires that for each group of organisms, the following parameters be measured or estimated: feeding preferences, nitrogen contents, life spans, assimilation efficien-

ies, production:assimilation ratios, decomposabilities and population sizes. Since there are inevitably many functional or taxonomic groups of organisms present in the soil community, the estimation of these parameters is difficult and introduces a large degree of uncertainty into the process of model parameterization. Some authors have questioned if the organism-orientated approach can ever give insights into real systems when all possible errors are taken into account, particularly since organism populations and their preferences and activities fluctuate at varying rates (see, e.g., Andr en *et al.* 1990). The topic of uncertainty in organism-orientated models was dealt with in some depth by de Ruiter *et al.* (1993a, 1994) and Paustian (1994).

Second, and related to the problem of parameter estimation, is the problem of ecosystem specificity. Many of the most widely used process-orientated models have been applied successfully to a range of ecosystems (e.g. arable rotations, permanent grass, grass-arable rotations, forestry, natural woodland regeneration) without adjusting internal model parameters (e.g. CENTURY – Kelly *et al.* 1997; Rothamsted Carbon Model – Coleman *et al.* 1997; NCSOIL – Molina *et al.* 1997) though not all simulate plant dynamics in addition to the soil ecosystem. One factor that makes this possible is that process-orientated models are less sensitive to soil community structure. They can therefore be more easily applied to a range of soils and environments regardless of large differences in soil community structure between ecosystems. The downside of the lack of specific soil community description, is that any special features of a given ecosystem that result from its particular soil community will not be adequately simulated by process-orientated models. At least for temperate agroecosystems and forestry, however, many process-orientated models appear to work adequately (see Smith *et al.* 1997b).

Third, Brussaard (1997) considers that the main limitations of using current food web models for predictive purposes are, (a) the quality of organic matter consumed at each trophic interaction is poorly known, (b) despite seemingly working well, a number of functional groups are not included, (c) different spatially restricted habitats of the four guilds of soil animals (root herbivores, litter degraders, litter transformers and ecosystem engineers) are not acknowledged, and (d) many biological interactions in the soil are nontrophic in nature.

Finally, process-orientated models are used more frequently for predictive purposes for technical reasons which are not insurmountable. Compared to organism-orientated models, process-orientated models have a relatively simple structure and (often) a larger integration time-step (e.g. months). This means that the computer processing time is likely to be shorter than for more complex organism-orientated models making them more

suitable (from a technical point of view) for running simulations over longer periods (years, decades). Organism-orientated models are more commonly used for periods of days rather than years, decades or centuries (e.g. Hunt *et al.* 1984). The same technical reasons also make process-orientated models more suitable for use at larger scales (landscape, regional, global) since multiple runs are frequently required. Many process-orientated models have been linked to GIS systems. CANDY, for example has GIS capability (Franko 1996), CENTURY (e.g. Donigan *et al.* 1994) and RothC (e.g. Parshotam *et al.* 1995) have also been linked to GIS for regional scale calculations, and some models have been used for global calculations (e.g. with RothC – Post *et al.* 1982; Jenkinson *et al.* 1991; and with CENTURY – Schimel *et al.* 1994).

Despite their more common use for predictive purposes, process-orientated models suffer from the same problem as organism-orientated models for global change studies: they will not be able to predict adequately the effects of a global change if the change affects the way in which the soil system responds to future global change. This problem is discussed further in the final section of this paper.

Combined process- and organism-orientated models

Combined approaches using both process- and organism-orientated components within the same model (e.g. Hunt *et al.* 1991), show some promise. de Ruiter & Van Faassen (1994) used both approaches and concluded that although the food web components of models may at present play an explanatory, rather than a predictive role, there was potential for a predictive model incorporating aspects of both modelling approach. There may be some limitations in our understanding that could hinder progress towards predictive combined models (Brussaard 1997). From a logistical point of view also, combined models may be constrained by the data requirements of the organism-orientated components. A modular approach to programming (as emphasized by Paustian 1994) would facilitate the development of combined models. Some progress has been made since Paustian's review toward modular programming systems in which modellers can swap modules with each other to build custom models for a specific purpose. However, it is fair to say that modular programming remains the holy grail of ecosystem modelling.

Most combined approaches have focused on the trophic role of the soil biota in nutrient turnover; few have examined the role of soil biota as 'ecosystem engineers'. One example of combining a process-orientated approach with an explicit description of the action of soil biota as ecosystem engineers was provided by Lavelle *et al.* (1997). In this study, an attempt was made to simulate the effect

of earthworm activities on the three kinetically defined organic pools of the CENTURY model (Parton *et al.* 1988). Earthworm activity was simulated by calibrating CENTURY pool decomposition rates to those observed in worm casts. The study suggested that slow decomposition soil C may be influenced significantly by earthworm activities and it was concluded that earthworms may play an important role in stabilizing SOM, and hence maintaining the SOM stock and soil structure in the long term.

Earthworms also enhance the decomposition and turnover of soil organic matter by facilitating the transfer of surface litter to the mineral soil and its comminution; their burrowing action also speeds up the flow of water, gases and nutrients in the soil profile. O'Brien (1984) used a simple two-compartment process-orientated model to quantify the enhancement of soil C turnover rate by earthworm activity in a comparative experiment at two sites in a paddock where earthworms were present or absent. A much larger C input rate to the soil was observed where worms were present. The worm-rich soil exhibited a much shorter decomposition time of 52 years against 148 years for the wormless pasture, indicating the presence of more labile C and higher microbial activity where worms were present. The efficient transport of C down the profile was also indicated in the presence of worms, this soil having a diffusivity parameter more than twice that of wormless pasture.

These studies provide examples of how a more explicit description of the effects of soil biota can be achieved within a process-orientated model without explicitly including population descriptions and interactions of soil organisms. Some apparent conflicts between the process- and organism-orientated approach may be resolved by adjusting process-orientated models as described above, or by using even simpler approaches, e.g. Andr n & K tterer (in press).

Problems in modelling the soil biota-mediated effects of global change

The most comprehensive evaluation and comparison of SOM models to date has now been completed (Smith *et al.* 1997a). This exercise, focusing entirely on process-orientated models, reveals that many models can adequately simulate SOM dynamics in a range of ecosystems but that most still require significant site-specific calibration. Advances in modelling techniques to allow these models to be used truly predictively are still required (Smith *et al.* 1997b). Given that the relatively simple process-orientated models cannot yet be used predictively with full confidence suggests that the predictive use of organism-orientated models may still be some way off.

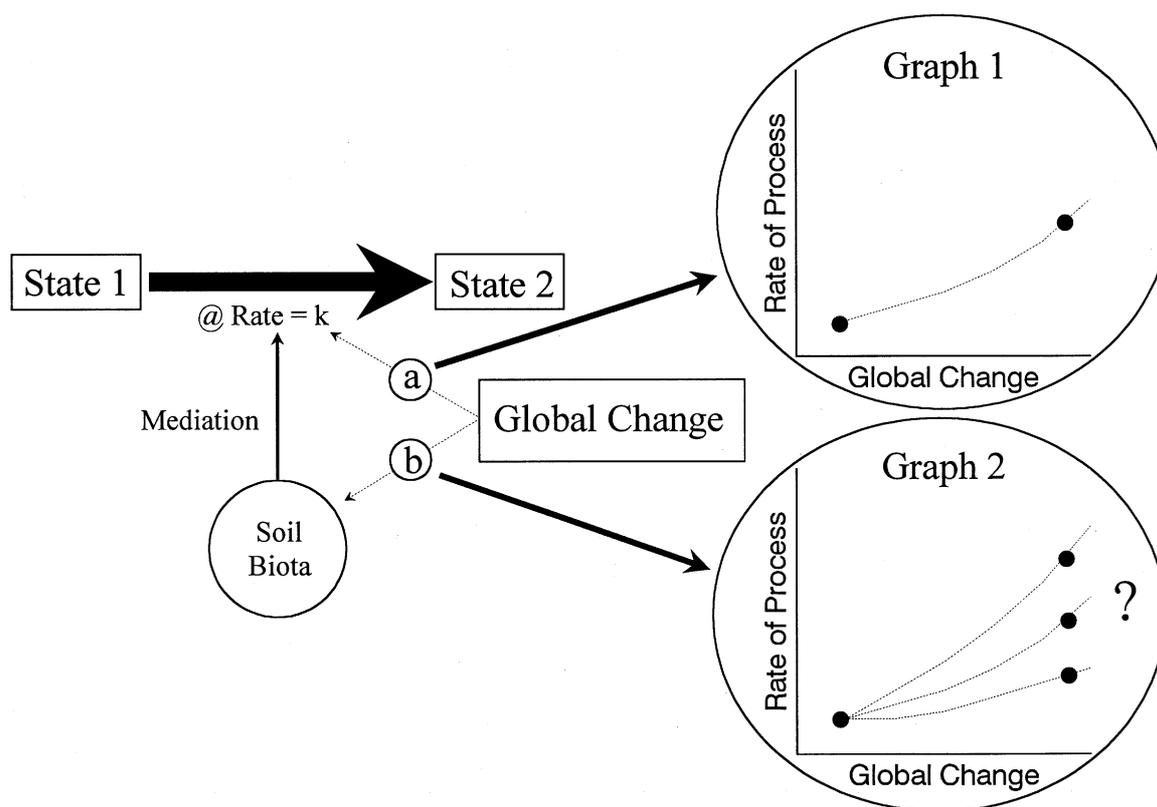


Fig. 3 Schematic diagram of a soil process covering a component from state 1 to state 2 at rate k . It is assumed that the process rate is mediated by the soil biota present. It is postulated that global change may affect the process rate directly (route 'a') or through an effect on soil community function (route 'b'). If global change acts only through route 'a', the future process rate should be predictable as long as the change is within limits of model calibration. If global change also acts through route 'b', and the mediating effect of the soil biota on the process rate is altered, the future process rate may not be predictable. For full explanation, see text.

Figure 3 presents a schematic diagram of how global change may affect a given process in the soil. Graphs 1 and 2 in the figure are developed from ideas presented by Schimel & Gullledge (this volume).

As a global change occurs, for example through a change in temperature, the process rate may simply be adjusted according to a simple relationship ('a' in Fig. 3). This may occur through a purely physico-biochemical response (e.g. a Q10 response) or may implicitly involve the soil biota (e.g. through increasing or decreasing the size of the microbial biomass). In either case, there is an assumption that the response of the system will remain predictable within calibrated limits, i.e. that the response surface remains the same (Fig. 3, Graph 1; see also Schimel & Gullledge 1998, this volume). All current models, whether process- or organism-orientated, assume a change in process rate according to Graph 1 in Fig. 3, i.e. a shift along a single response surface.

Alternatively, global change may also adjust the process rate indirectly by affecting the way in which the system responds to global change in the future ('b' in Fig. 3). As described above, route 'a' may include an implicit

description of soil biota in which the system responds predictably within the calibrated limits of the model. Route 'b' differs, however, in that the global change may affect the soil biota in such a way that the system no longer responds to future change in the predicted way, i.e. there may be a change from one response surface to another (Graph 2 in Fig. 3). Global change via route 'b' suggests that the future rate of a process may, in certain circumstances, be radically different from that predicted if only route 'a' were considered. No current models, whether process- or organism-orientated, take account of process rate adjustments via route 'b'.

Should the effects of global change on process rates mediated by changes in the soil community (route 'b') prove to affect significantly a given process in a given environment, only models that can explicitly account for this will be able to predict accurately the effects of global change. The inclusion of route 'b' is possible for either process- or for organism-orientated models. In a process-orientated model, route 'b' would take the form either of a rate-modifying factor to approximate the change, or of an internal switch in the model to move the process

response from one surface to another. In an organism-orientated model, changes in the populations of the key functional groups involved in a process would respond to global change in the model and this would subsequently change the response of the soil community to future global change.

Route 'b' is not included in any model because soil ecosystems are only part of systems of a higher order. More is known about what to expect from global change at the atmospheric level than down the chain to the soil biota — at this level the driving forces remain unknown. So although there is a considerable body of research into the effects of global change on soil biodiversity, the reason that route 'b' is not included in any model is that not enough is known about: (i) the impacts of global change on functional groups of soil organisms and how widespread these are; (ii) the significance of these impacts for function; and (iii) the likely change in response of the soil system to future global change as a result of these impacts on functional groups.

The ecosystem-level significance of route 'b' in specific circumstances remains unknown as does the extent of its occurrence for specific global changes in particular ecosystems. Some of the other papers in this volume (e.g. Swift *et al.* 1998 this volume; Schimel & Gullledge 1998, this volume) point to possible examples of where route 'b' may be critical. A further example might be land-use change leading to an increase in earthworms. This may lead to a significant quantity of the soil organic matter being sequestered within worm casts thus making SOM accessible only to anaerobic methanogens. In this case rates of methanogenesis might be radically altered. Another possible example is a switch from predominantly nitrate-N to predominantly ammonium-N in the soil following soil acidification. This may occur since nitrifiers, which convert ammonium to nitrate, are particularly sensitive to pH. Any global change resulting in a decrease in soil pH could lead to this biota-mediated change.

Only through further research into the gaps in knowledge identified above will we be able to ascertain the importance of explicitly including route 'b' in our mathematical models. Even though much of the research outlined elsewhere in this volume addresses issues (i) and (ii) above, much work is yet required to answer (iii). Route 'b' cannot be modelled until we have a mechanistic understanding of how process-response surfaces will change in the future, i.e. which line on Graph 2 of Fig. 3 will be followed. To predict with confidence the effects of global change at the ecosystem level using mathematical models, further research is urgently required to address the gaps identified here.

Acknowledgements

P.S. is grateful to the Workshop Organizing Committee for an invitation to participate by leading the modelling discussion

(from which this paper arose) and would like to thank Jo Smith and David Powlson of IACR-Rothamsted, and John Ingram of the GCTE Focus 3 Office, for helpful comments on this paper. We are also grateful to other workshop participants, especially Meine Van Noordwijk, who do not appear as coauthors but who contributed freely during plenary and workgroup discussions. IACR receives grant-aided support from the Biotechnology and Biological Sciences Research Council of the United Kingdom.

References

- Ågren GI, Bosatta E (1987) Theoretical analysis of the long-term dynamics of carbon and nitrogen in soils. *Ecology*, **68**, 1181–1189.
- André M, Thiéry J, Cournac L (1994) ECOSIMP2 model: prediction of CO₂ concentration changes and carbon status in closed ecosystems. *Advances in Space Research*, **14**, 11,323–11,326.
- Andrén O, Bengtsson J, Clarholm M (1994) Biodiversity and species redundancy among litter decomposers. In: *The Significance and Regulation of Soil Biodiversity* (eds Collins HP, Robertson GP, Klug, MJ), pp. 141–151. Kluwer, Dordrecht.
- Andrén O, Kätterer T (in press) ICBM – the Introductory Carbon Balance Model for exploration of soil carbon balances. *Ecological Applications*, **7**, 1226–1236.
- Andrén O, Lindberg T, Paustian K, Rosswall T (eds) (1990) Ecology of arable land – organisms, carbon and nitrogen cycling. *Ecological Bulletins* **40**.
- Arah JRM (1996) The soil submodel of the ITE (Edinburgh) Forest and Hurley Pasture models. In: *Evaluation of Soil Organic Matter Models Using Existing, Long-Term Datasets* (eds Powlson DS, Smith P, Smith JU), NATO ASI, I38, 225–230. Springer, Berlin.
- Beare MH, Coleman DC, Crossley DA, (Jr) Hendrix PF, Odum EP (1994) A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. In: *The Significance and Regulation of Soil Biodiversity* (eds Collins HP, Robertson GP, Klug, MJ), pp. 5–22. Kluwer, Dordrecht.
- Bosatta E, Ågren GI (1985) Theoretical analysis of decomposition of heterogeneous substrates. *Soil Biology and Biochemistry*, **17**, 601–610.
- Bradbury NJ, Whitmore AP, Hart PBS, Jenkinson DS (1993) Modelling the fate of nitrogen in crop and soil in the years following application of ¹⁵N-labelled fertilizer to winter wheat. *Journal of Agricultural Science, Cambridge*, **121**, 363–379.
- Brussaard L (1997) Soil fauna, guilds, functional groups and ecosystem processes. *Applied Soil Ecology* (in press) [Special issue of *Proceedings of XII International Soil Zoology Colloquium, Dublin, 20–27 July 1996*].
- Chertov OG, Komarov AS (1996) SOMM – a model of soil organic matter and nitrogen dynamics in terrestrial ecosystems. In: *Evaluation of Soil Organic Matter Models Using Existing, Long-Term Datasets*. (eds Powlson DS, Smith P, Smith JU), NATO ASI, I38, 231–236. Springer, Berlin.
- Christensen BT (1996) Matching measurable soil organic matter fractions with conceptual pools in simulation models of carbon turnover: Revision of model structure. In: *Evaluation of Soil Organic Matter Models Using Existing, Long-Term*

- Datasets*. (eds Powlson DS, Smith P, Smith JU), NATO ASI, I38, 143–161. Springer, Berlin.
- Coleman K, Jenkinson DS, Crocker GJ, Grace PR, Klír J, Körschens M, Poulton PR, Richter DD (1997) Simulating trends in soil organic carbon in long-term experiments using RothC-23.6. In: *Evaluation and Comparison of Soil Organic Matter Models Using Datasets from Seven Long-Term Experiments* (eds Smith P, Powlson DS, Smith JU, Elliott ET). Special Issue of *Geoderma*, **81**, 29–44.
- Donigan Jr AS, Barnwell Jr TO, Jackson IV RB, Patwardhan AS, Weinrich KB, Rowell AL, Chinnaswamy RV, Cole CV (1994) Assessment of Alternative Management Practices and Policies Affecting Soil Carbon in Agroecosystems of the Central United States. *US EPA Report EPA/600/R-94/067*, Athens, 194 pp.
- Douglas Jr CL, Rickman RW (1992) Estimating crop residue decomposition from air temperature, initial nitrogen content, and residue placement. *Soil Science Society of America Journal*, **56**, 272–278.
- Elliott ET, Paustian K, Frey SD (1996) Modeling the measurable or measuring the modelable: A hierarchical approach to isolating meaningful soil organic matter fractionations. In: *Evaluation of Soil Organic Matter Models Using Existing, Long-Term Datasets* (eds Powlson DS, Smith P, Smith JU), NATO ASI, I38, 161–180. Springer, Berlin.
- Franko U (1996) Modelling approaches of soil organic matter turnover within the CANDY system. In: *Evaluation of Soil Organic Matter Models Using Existing, Long-Term Datasets* (eds Powlson DS, Smith P, Smith JU), NATO ASI, I38, 247–254. Springer, Berlin.
- Franko U, Oelschlägel B, Schenk S (1995) Simulation of temperature-, water- and nitrogen dynamics using the model CANDY. *Ecological Modelling*, **81**, 213–222.
- Grace PR, Ladd JN (1995) *SOCRATES v2.00 User Manual*. Cooperative Research Centre for Soil and Land Management. PMB 2, Glen Osmond 5064, South Australia.
- Grant RF (1995) Dynamics of energy, water, carbon and nitrogen in agricultural ecosystems: simulation and experimental validation. *Ecological Modelling*, **81**, 169–181.
- Grant RF, Juma NG, McGill WB (1993a) Simulation of carbon and nitrogen transformations in soil: mineralisation. *Soil Biology and Biochemistry*, **25**, 1317–1329.
- Grant RF, Juma NG, McGill WB (1993a) Simulation of carbon and nitrogen transformations in soil: microbial biomass and metabolic products. *Soil Biology and Biochemistry*, **25**, 1331–1338.
- Hassink J, Neutel AM, De Ruyter PC (1994) C and N mineralization in sandy and loamy grassland soils: the role of microbes and microfauna. *Soil Biology and Biochemistry*, **26**, 1565–1571.
- Hoogenboom G, Jones JW, Hunt LA, Thornton PK, Tsuji GY (1994) An integrated decision support system for crop model applications. Paper 94–3025 presented at ASAE Meeting, Missouri, June, 1994, 23pp.
- Hunt HW (1977) A simulation model for decomposition in grasslands. *Ecology*, **58**, 469–484.
- Hunt HW, Coleman DC, Cole CV, Ingham RE, Elliott ET, Woods LE (1984) Simulation model of a food web with bacteria, amoebae, and nematodes in soil. In: *Current Perspectives in Microbial Ecology* (eds Klug MJ, Reddy CA), pp. 346–352. American Society for Microbiology, Washington, DC.
- Hunt HW, Coleman DC, Ingham ER *et al.* (1987) The detrital food web in a shortgrass prairie. *Biology and Fertility of Soils*, **3**, 57–68.
- Hunt HW, Trlica MJ, Redente EF *et al.* (1991) Simulation model for the effects of climate change on temperate grassland ecosystems. *Ecological Modelling*, **53**, 205–246.
- Jenkinson DS (1977) Studies on the decomposition of plant material in soil. V. *Journal of Soil Science*, **28**, 424–434.
- Jenkinson DS (1990) The turnover of organic carbon and nitrogen in soil. *Philosophical Transactions of the Royal Society of London B*, **329**, 361–368.
- Jenkinson DS, Adams DE, Wild A (1991) Global warming and soil organic matter. *Nature*, **351**, 304–306.
- Jenkinson DS, Rayner JH (1977) The turnover of soil organic matter in some of the Rothamsted Classical Experiments. *Soil Science*, **123**, 298–305.
- Jenny H (1941) *Factors of Soil Formation*. McGraw-Hill, New York.
- Kan NA, Kan EE (1991) Simulation model of soil fertility. *Physiology and Biochemistry of Cultivated Plants*, **23**, 3–16 (in Russian).
- Kelly RH, Parton WJ, Crocker GJ, Grace PR, Klír J, Körschens M, Poulton PR, Richter DD (1997) Simulating trends in soil organic carbon in long-term experiments using the CENTURY model. In: *Evaluation and Comparison of Soil Organic Matter Models Using Datasets from Seven Long-Term Experiments* (eds Smith P, Powlson DS, Smith JU, Elliott, ET). Special Issue of *Geoderma*, **81**, 75–90.
- Lavelle P, Pashanishi B, Charpentier FC, Rossi JP, Derouard L, André J, Ponge JF, Bernier N (1997) Large-scale effects of earthworms on soil organic matter and nutrient dynamics. In: *Proceedings of the International Symposium on Earthworm Ecology*, Columbus, Ohio, 1996, in press.
- Li C, Frolking S, Harriss R (1994) Modelling carbon biogeochemistry in agricultural soils. *Global Biogeochemical Cycles*, **8**, 237–254.
- McCaskill M, Blair GJ (1990a) A model of S, P and N uptake by a perennial pasture. I. Model construction. *Fertilizer Research*, **22**, 161–172.
- McCaskill M, Blair GJ (1990b) A model of S, P and N uptake by a perennial pasture. II. Calibration and prediction. *Fertilizer Research*, **22**, 173–179.
- McGill WB (1996) Review and classification of ten soil organic matter (SOM) models. In: *Evaluation of Soil Organic Matter Models Using Existing, Long-Term Datasets* (eds Powlson DS, Smith P, Smith JU), NATO ASI, I38, 111–133. Springer, Berlin.
- McGill WB, Hunt HW, Woodmansee RG, Reuss JO (1981) PHOENIX, a model of the dynamics of carbon and nitrogen in grassland soil. In: *Terrestrial Nitrogen Cycles. Processes, Ecosystem Strategies and Management Impacts* (eds Clark FE, Roswall T). *Ecological Bulletins*, **33**, 49–115.
- Molina JAE, Clapp CE, Shaffer MJ, Chichester FW, Larson WE (1983) NCSOIL, a model of nitrogen and carbon transformations in soil: Description, calibration and behaviour. *Soil Science Society of America Journal*, **47**, 85–91.
- Molina JAE, Crocker GJ, Grace PR, Klír J, Körschens M, Poulton

- PR, Richter DD (1997) Simulating trends in soil organic carbon in long-term experiments using the NCSOIL and NCSWAP models. In: *Evaluation and Comparison of Soil Organic Matter Models Using Datasets from Seven Long-Term Experiments* (eds Smith P, Powlson DS, Smith JU, Elliott ET). Special Issue of *Geoderma*, **81**, 91–107.
- Molina JAE, Smith P (1997) Modeling carbon and nitrogen processes in soils. *Advances in Agronomy*, **62**, 253–298.
- Moorhead DL, Reynolds JF (1991) A general model of litter decomposition in the northern Chihuahuan Desert. *Ecological Modelling*, **56**, 197–219.
- Mueller T, Jensen LS, Hansen S, Nielsen NE (1996) Simulating soil carbon and nitrogen dynamics with the soil-plant-atmosphere system model DAISY. In: *Evaluation of Soil Organic Matter Models Using Existing, Long-Term Datasets* (eds Powlson DS, Smith P, Smith JU), NATO ASI I38, pp. 275–281. Springer, Berlin.
- O'Brien BJ (1984) Soil organic carbon fluxes and turnover rates estimated from radiocarbon measurements. *Soil Biology and Biochemistry*, **16**, 115–120.
- O'Leary GJ (1994) *Soil water and nitrogen dynamics of dryland wheat in the Victorian Wimmera and Mallee*. PhD Thesis, University of Melbourne, 332pp.
- O'Neill RV, DeAngelis DL, Waide JB, Allen TFH (1986) *A hierarchical concept of ecosystems*. Monographs in Population Biology **23**, Princeton University Press, Princeton, NJ.
- Pankhurst CE, Lynch JM (1994) The role of the soil biota in sustainable agriculture. In: *Soil Biota. Management in Sustainable Farming Systems* (eds Pankhurst CE, Doube BM, Gupta VVSR, Grace PR), pp. 3–9. CSIRO Information Services, Melbourne.
- Parshotam A, Tate KR, Giltrap DJ (1995) Potential effects of climate and land-use change on soil carbon and CO₂ emissions from New Zealand's indigenous forests and unimproved grasslands. *Weather and Climate*, **15**, 47–56.
- Parton WJ, Scurlock JMO, Ojima DS, Schimel DS, Hall DO, SCOPEGRAM members (1995) Impact of climate change on grassland production and soil carbon worldwide. *Global Change Biology*, **1**, 13–22.
- Parton WJ, Stewart JWB, Cole CV (1988) Dynamics of C, N, P, and S in grassland soils: A model. *Biogeochemistry*, **5**, 109–131.
- Paustian K (1985) Influence of fungal growth pattern on decomposition and nitrogen mineralisation in a model system. In: *Ecological Interactions in Soil* (eds Fitter AH, Atkinson D, Read DJ, Usher MB), pp. 159–174. Special Publication 4 of British Ecological Society. Blackwell Scientific Publications, London.
- Paustian K (1994) Modelling soil biology and biochemical processes for sustainable agricultural research. In: *Soil Biota. Management in Sustainable Farming Systems* (eds Pankhurst CE, Doube BM, Gupta VVSR, Grace PR), pp. 182–193. CSIRO Information Services, Melbourne.
- Paustian K, Andrén O, Clarholm M *et al.* (1990) Carbon and nitrogen budgets of four agro-ecosystems with annual and perennial crops, with and without N fertilization. *Journal of Applied Ecology*, **27**, 60–84.
- Pielou EC (1981) The usefulness of ecological models: a stock taking. *Quarterly Review of Biology*, **56**, 17–31.
- Post WM, Emanuel WR, Zinke PJ, Stangenberger AG (1982) Soil carbon pools and world life zones. *Nature*, **298**, 156–159.
- Powlson DS, Smith P, Coleman K, Smith JU, Glendining MJ, Körschens M, Franko U (1998) A European network of long-term sites for studies on soil organic matter. *Soil and Tillage Research*, in press.
- Powlson DS, Smith P, Smith JU (eds) (1996) *Evaluation of Soil Organic Matter Models Using Existing, Long-Term Datasets*. NATO ASI I38. Springer, Berlin, 429pp.
- Rijtema PE, Kroes JG (1991) Some results of nitrogen simulations with the model ANIMO. *Fertilizer Research*, **27**, 189–198.
- de Ruiter PC, Moore JC, Zwart KB *et al.* (1993a) Simulation of nitrogen mineralization in the belowground food webs of two winter wheat fields. *Journal of Applied Ecology*, **30**, 95–106.
- de Ruiter PC, Neutel AM, Moore JC (1994) Modelling food webs and nutrient cycling in agro-ecosystems. *Trends Ecology and Evolution*, **9**, 378–383.
- de Ruiter PC, Neutel A-M, Moore JC (1995) Energetics and stability in belowground food webs. In: *Food Webs, Integration of Patterns and Dynamics* (eds Polis GA, Winemiller KO), pp. 201–210. Chapman & Hall, New York.
- de Ruiter PC, Van Faassen HG (1994) A comparison between an organic matter dynamics model and a food web model simulating nitrogen mineralization in agro-ecosystems. *European Journal of Agronomy*, **3**, 347–354.
- de Ruiter PC, Van Veen JA, Moore JC, Brussaard L, Hunt HW (1993b) Calculation of nitrogen mineralization in soil food webs. *Plant and Soil*, **157**, 263–273.
- Ryzhova IM (1993) Analysis of sensitivity of soil-vegetation systems to variations in carbon turnover parameters based on a mathematical model. *Eurasian Soil Science*, **25**, 43–50.
- Schevtsova LK, Mikhailov BG (1992) *Control of Soil Humus Balance Based on Statistical Analysis of Long-Term Field Experiments Database Vivo*. Moscow, 1992 (in Russian).
- Schimel DS, Braswell Jr BH, Holland EA, McKeown R, Ojima DS, Painter TH, Parton WJ, Townsend JR (1994) Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. *Global Biogeochemical Cycles*, **8**, 279–293.
- Schimel J, Gullledge J (1998) Microbial community structure and global trace gases. *Global Change Biology*, **4**, 745–758.
- Sirotenko OD (1991) The USSR climate-soil-yield simulation system. *Meteorologia i Hidrologia*, **4**, 67–73 (in Russian).
- Smith JU, Bradbury NJ, Addiscott TM (1996) SUNDIAL: A user friendly PC-based system for simulating nitrogen dynamics in arable land. *Agronomy Journal*, **88**, 38–43.
- Smith P, Powlson DS, Smith JU, Elliott ET (eds) (1997a) *Evaluation and Comparison of Soil Organic Matter Models Using Datasets from Seven Long-Term Experiments*. Special Issue of *Geoderma*, **81**, 1–225.
- Smith P, Powlson DS, Smith JU, Glendining MJ (1996a) The GCTE SOMNET: A global network and database of soil organic matter models and long-term datasets. *Soil Use and Management*, **108**, 57.
- Smith P, Smith JU, Powlson DS (eds) (1996b) *Soil Organic Matter Network (SOMNET): 1996 Model and Experimental Metadata*. GCTE Report 7, GCTE Focus 3 Office, Wallingford, U.K., 255 pp.
- Smith P, Smith JU, Powlson DS *et al.* (1997b) A comparison of

- the performance of nine soil organic matter models using datasets from seven long-term experiments. *Geoderma*, **81**, 153–225.
- Svendsen H, Hansen S, Jensen HE (1995) Simulation of crop production, water and nitrogen balances in two German agro-ecosystems using the DAISY model. *Ecological Modelling*, **81**, 197–212.
- Swift MJ, Andr n O, Brussaard L, Briones M, Couteaux M-M, Ekschmitt K, Kjoller A, Loiseau P, Smith P (1998) Global change, soil biodiversity, and nutrient cycling in terrestrial ecosystems: three case studies. *Global Change Biology*, **4**, 729–743.
- Thornley JHM, Cannell MGR (1992) Nitrogen relations in a forest plantation – soil organic matter ecosystem model. *Annals of Botany*, **70**, 137–151.
- Thornley JHM, Verberne ELJ (1989) A model of nitrogen flows in grassland. *Plant, Cell and Environment*, **12**, 863–886.
- Vanclooster M, Viaene P, Diels J, Feyen J (1995) A deterministic evaluation analysis applied to an integrated soil-crop model. *Ecological Modelling*, **81**, 183–195.
- van Veen JA, Frissel MJ (1981) Simulation model of the behaviour of N in soil. In: *Simulation of Nitrogen Behaviour of Soil-Plant Systems*. (eds Frissel MJ, van Veen JA), pp. 126–144. Pudoc, Wageningen.
- Verberne ELJ, Hassink J, de Willigen P, Groot JRR, van Veen JA (1990) Modelling soil organic matter dynamics in different soils. *Netherlands Journal of Agricultural Science*, **38**, 221–238.
- Wardle DA, Verhoeff HA, Claholm M (1998) Trophic relationships in the soil microfood web: predicting the responses to a changing global environment. *Global Change Biology*, **4**, 713–727.
- Whitmore AP (1995) Modelling the mineralization and leaching of nitrogen from crop residues during three successive growing seasons. *Ecological Modelling*, **81**, 233–241.
- Williams JR (1990) The erosion-productivity impact calculator (EPIC) model: a case history. *Philosophical Transactions of the Royal Society of London B*, **329**, 421–428.