

The Turnover of Organic Carbon and Nitrogen in Soil [and Discussion]

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The turnover of organic carbon and nitrogen in soil

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SUMMARY

Although the decomposition of plant material in soil is an extremely complex process, relatively simple models can give good fits to the decay process. Thus a two-compartment model gives a close representation, over the first few years, of the decay of ^{14}C -labelled plant material in soil. A model containing a single homogeneous humus compartment decomposing by a first-order process is surprisingly useful for soil organic nitrogen over periods measured in decades. More sophisticated multicompartmental models are now widely used to represent turnover in soil. One of these, the Rothamsted turnover model, is described in detail and shown to give a useful representation of data from the Rothamsted long-term field experiments.

1. INTRODUCTION

This paper is about modelling the turnover of organic matter in soil over the 'years-to-centuries' timespan. It is based mainly on Rothamsted work, not because of parochialism, but because the long-term field experiments on Rothamsted and Woburn experimental farms provide unique material for studying the dynamics of organic matter in soils. In several of these experiments manuring and cropping have remained substantially unchanged since the beginning, nearly 150 years ago.

2. MODELS FOR THE TURNOVER OF ORGANIC MATTER IN SOILS

(a) *Single homogeneous compartment*

The simplest turnover model (Jenny 1941; Woodruff 1949) postulates that all the organic nitrogen in soil occupies a single compartment. If N is the quantity of nitrogen in this compartment, A the annual input of fresh organic nitrogen and k the rate constant (i.e. the fraction of the soil organic nitrogen decomposed each year), then

$$dN/dT = A - kN. \quad (1)$$

The solution of this differential equation is

$$N = N_E + (N_O - N_E) e^{-kt}, \quad (2)$$

where N_O is the initial nitrogen content of the soil and N_E the equilibrium content. For this model the 'turnover time' is $1/k$ and the average age when equilibrium has been attained is also $1/k$ (Bartholomew & Kirkham 1960). This model has been repeatedly fitted to data (Nye & Greenland 1960; Bartholomew & Kirkham 1960; Jenkinson & Johnston 1977; Bjarnason 1989) from measurements of the changes in soil organic nitrogen brought about by agriculture. Table 1 shows some typical calculated values of k , ranging from 0.028 to 0.055 a^{-1} , the corresponding turnover times varying from 18 to 36 years. The rate constant for organic

nitrogen in the farmyard manure plot of the Hoosfield continuous barley experiment at Rothamsted is 0.031 a^{-1} (table 1). From equation 2 it can be shown that the time required to attain 95% of a new equilibrium content after a change in annual input of organic nitrogen is approximately $3/k$ years, or 97 years in the Hoosfield farmyard manure plot. Because of this timescale, longer than most human lives, experiments are hardly ever specifically designed to follow turnover; data on turnover processes are usually taken from experiments set up for quite different purposes.

(b) *Two-compartment model*

Curves showing the decay of plant material in soil are L-shaped, with a rapid loss of carbon over the first few months, followed by a much slower loss (Jenkinson 1977; Gonzalez & Sauerbeck 1982; Ladd *et al.* 1985). Thus the two compartment model

$$C = 71 e^{-2.83t} + 29 e^{-0.087t}, \quad (3)$$

gave a very good representation of the decay of ^{14}C -labelled ryegrass leaves in the field over a 10-year period (Jenkinson 1977). In this model the incoming plant carbon is split into two compartments, each

Table 1. *The turnover time of organic nitrogen in soil organic matter*

land use	soil layer (cm)	period studied (years)	rate constant (a^{-1})	turnover time (years)
pasture ^a	0-5	39	0.029	34
arable ^b	0-18	60	0.055	18
grassland ^c	0-23	300	0.028	36
arable ^c	0-23	123	0.031	32

^a Russell (1960).

^b Bartholomew & Kirkham (1960).

^c Jenkinson (1988).

decomposing by a first-order process, but one much more quickly than the other. Although the model gives a very accurate representation of the initial years of the decomposition process, an annual input of 1 t of organic carbon to the soil would only give an equilibrium carbon content of 3.58 t, an order of magnitude too small. The soil must therefore contain at least one compartment with a rate constant far smaller than that of the slow compartment of equation (3).

An even simpler (and much used) two compartment model was proposed by Henin & Dupuis (1945). In it, the annual input of plant carbon (A_C) decomposes very rapidly, forming a quantity of humus carbon (fA_C) that is identical to that already in the soil. The factor f is known as the isohumic coefficient; it is commonly about 0.3 for residues from agricultural crops but much larger for materials such as peat (Janssen 1984). For this model

$$C = fA_C/k + (C_0 - fA_C/k) e^{-kt}, \quad (4)$$

where C is the organic carbon content of the soil and k is the fraction of this carbon decomposing each year. The quantity of fresh plant carbon present in the soil at any particular time is assumed to be negligible compared with the amount of 'humus' carbon. Equation 4 closely fits changes in soil organic carbon over the 10–100 year period (Jenkinson & Johnston 1977), giving values of A_C that are far more realistic than if the whole plant input is assumed to join the carbon already in the soil, as in the nitrogen model (equation 2). The reason why a single compartment model, without an isohumic coefficient, is adequate for nitrogen but not for carbon is that most plant materials entering the soil have wide carbon:nitrogen ratios. During the early stages of decomposition nitrogen is therefore retained in the soil, whereas carbon is rapidly lost as CO_2 .

(c) *Non-compartmental decay models*

Bosatta & Ågren (1985) introduced the idea that decomposition is a continuum, organic matter moving down a 'quality' scale as it decays, fresh decomposable organic matter having a high quality (set at 1), with the most resistant material present in the system being of zero quality. In this approach the problem of selecting compartments and fitting rate constants to them is replaced by the problem of establishing the decay pattern for each incoming cohort of plant material as it enters the soil and decomposes (Ågren & Bosatta 1987). Under steady-state conditions the amount of organic carbon in a soil is then the sum of the contribution from that year's input plus the fraction of the previous year's input remaining, plus the fraction remaining from the year before that, and so on. The mathematics of this approach is more complex than that of compartmental models and it has not, as yet, been applied to long runs of data from agricultural soils.

(d) *Multicompartmental models*

Many multicompartmental models for the de-

composition of organic matter in or on the soil have been described over the past 20 years. Most focus on the early days, weeks or months of decay, when the physical and chemical composition of the incoming material dominate the pattern of decomposition (Olson 1963; Minderman 1968; Hunt 1977; Smith 1979; McGill *et al.* 1981; Molina *et al.* 1983; Van Veen *et al.* 1984; Andren & Paustian 1987; Hadas *et al.* 1987; Bujanovsky *et al.* 1987; Hunt *et al.* 1987; Houot *et al.* 1989). Such models are usually validated against data from litter bag experiments, laboratory incubations, or short-term field incubations.

There are far fewer models directed towards the years-to-centuries timespan (Russell 1975; Jenkinson & Rayner 1977; Van Veen & Paul 1981; Voroney *et al.* 1981; Parton *et al.* 1983; Van Der Linden *et al.* 1987; Parton *et al.* 1987; Jenkinson *et al.* 1987; Parton *et al.* 1988; Wolf *et al.* 1989). These long-term models are usually tuned and validated using data from prolonged field incubations with ^{14}C -labelled organic matter, from long-term agronomic experiments or from measurements on the pedological scale, i.e. from the effects of climate, vegetation, land use and soil type on the amount of organic matter in soil. In all of them the material in a compartment is assumed to decay by first-order kinetics, as in equation 1, so that the rate of decomposition in a particular compartment is deemed to be a feature of the organic matter itself, and is never retarded by a lack of competent organisms. In most of these long-term models the rate constants for the various compartments are multiplied by one or more 'rate modifiers' that alter the rate constants to speed decomposition as the temperature increases or to decrease it as the soil dries out, etc. The rate modifiers for temperature, water content etc. are usually multiplied together (Hunt 1977; Van Veen & Paul 1981; Jenkinson *et al.* 1987; Van Der Linden *et al.* 1987; Parton *et al.* 1988), although this is by no means the only way of adjusting such models for environmental constraints (Frissel & Van Veen 1978; Woodmansee 1978). The models are usually adjusted so that decomposition is faster when soils are tilled (Parton *et al.* 1988) or, alternatively, is slowed when the soil is covered with vegetation (Jenkinson *et al.* 1987). Other things being equal, heavy clay soils contain more organic matter than light-textured sandy soils and any mechanistic model must take this into account. This can be done by using a rate modifier to decrease the rate constant as clay content increases (Parton *et al.* 1987) or by assuming that any decomposition product (including the microbial biomass) that is not stabilized by clay is decomposed very quickly (Van Veen & Paul 1981) or by decreasing the proportion of microbial substrate converted to CO_2 , relative to that remaining in the soil, as clay content increases (Jenkinson *et al.* 1987).

3. THE ROTHAMSTED MODEL FOR THE TURNOVER OF ORGANIC MATTER IN SOIL

The Rothamsted turnover model described in this paper is a descendant of earlier versions (Jenkinson & Rayner 1977; Hart 1984; Jenkinson *et al.* 1987). In it

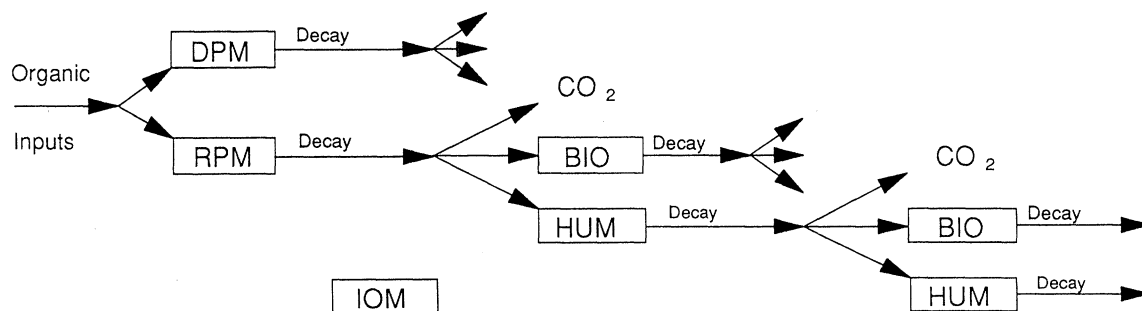


Figure 1. Flow of carbon through the Rothamsted turnover model. (DPM, decomposable plant material; RPM, resistant plant material; BIO, microbial biomass; HUM, humus; IOM, inert organic matter.)

(figure 1) we attempt to simulate the behaviour of soil organic matter by dividing it into compartments for which there is evidence that is independent of the data to be fitted. Each of these compartments is then assumed to behave as though it contains a single species undergoing biological decomposition by a first-order process. The priming action is assumed to be zero and the proportion of an input of organic matter that is decomposed after a given time is taken to be independent of the amount added.

The first two of the five compartments needed (called decomposable plant material (DPM) and resistant plant material (RPM)) represent plant carbon added monthly (in proportions P_{DPM} and P_{RPM}) from crop residues. Incoming organic carbon passes through these compartments once only and all incoming carbon is assumed to belong to one or the other. DPM and RPM both decompose to the same products: CO₂ (lost from the system), microbial biomass (BIO), and humified organic matter (HUM). When substrate is attacked, it is assumed that the ratio of BIO to HUM formed is the same for all soils. When HUM decomposes, CO₂, more microbial biomass (BIO), and fresh HUM are formed, again in the same proportion. The soil is also assumed to contain a small organic compartment that is inert to biological attack (IOM).

If a compartment in a particular soil layer contains y kg ha⁻¹† of carbon, this declines to $y e^{-kt}$ at the end of a specified time (one month), when t is time and k the rate constant for this compartment. A transition matrix in the model converts the quantity of organic matter in the compartment at the beginning of the month to that at the end, so that the model does not proceed continuously but in a stepwise fashion. Organic matter is likewise assumed to enter the soil monthly, stepwise. Soil temperature (taken for convenience to be the same as the mean monthly air temperature) and soil moisture content influence decomposition by altering the rate constants, so that decay during the month is given by $(1 - e^{-abekt})$, where a is the temperature rate modifying factor, b the moisture rate modifying factor, and c the plant retainment factor. Rate modifiers a and b (figure 2) are similar in concept but differ numerically from those used by Van Veen & Paul (1981). Decomposition is assumed to proceed at the maximum rate until there is a water tension of -100 kPa in the topsoil (roughly corresponding to a 20 mm moisture deficit in the top 23 cm of soil at Rothamsted). Water deficit is calculated from the balance between mean monthly evapotranspiration and mean monthly rainfall, assuming that the soil emerges from winter at field capacity, with a zero soil moisture deficit. The model

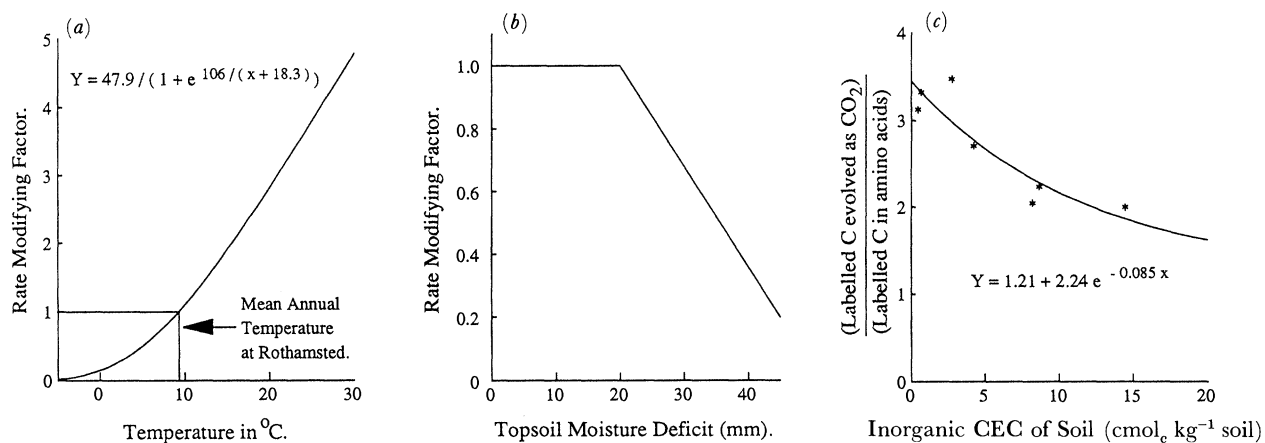


Figure 2. The effects of (a) temperature, (b) moisture, and (c) soil texture on rate-modifying factors used in the Rothamsted model. The influence of inorganic cation exchange capacity (CEC) on the proportion of substrate carbon evolved as CO₂ to that retained in soil (as biomass and microbial metabolites) is shown in (c), constructed from experiments (Sorensen 1975) on the decomposition of ¹⁴C-labelled cellulose in different soils over a 10-day period.

† 1 hectare = 10⁴ m².

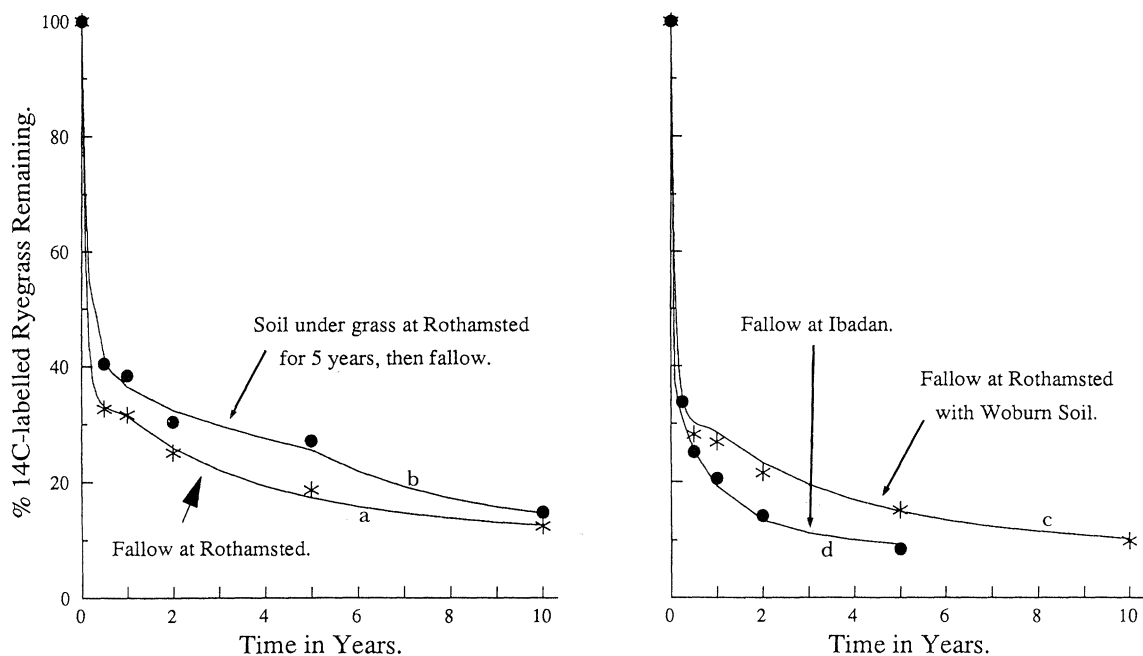


Figure 3. Decomposition of ^{14}C -labelled ryegrass under field conditions. Solid lines in this and in figure 4 show the model output as fitted to the data points. Curve a is fitted to decay in bare Rothamsted soil (23.4% clay), incubated at Rothamsted; curve b to decay in grassed Rothamsted soil incubated at Rothamsted, the soil being under grass for the first 5 years (retainment factor set at 0.6) and bare for the next 5 (retainment factor set at 1.0). Curve c is for decay in Woburn soil (10.7% clay), incubated at Rothamsted; curve d for decay in Egbeda soil (10.0% clay), incubated at Ibadan, Nigeria, where the mean annual temperature is 26°C .

calculates a and b on a monthly basis, from data on mean monthly air temperature, rainfall, and open pan evaporation, all taken from the long-term meteorological records for each site. The plant retainment rate modifying factor c is set at 0.6 (Jenkinson 1977) when plants are actively growing; when plants are not actively growing (e.g. in the period between harvest and emergence of the next crop, or where the soil is bare fallowed) this factor is set at 1.

The model is adjusted for soil texture in a different way. The rate constants for the several compartments are assumed to be unaltered by texture but the partition between CO_2 evolved and (BIO + HUM) formed during decomposition is assumed to depend on the cation exchange capacity of the soil inorganic colloids. The relation between inorganic cation exchange capacity and the ratio (substrate going to CO_2):(substrate carbon remaining in the soil as BIO plus HUM) was obtained from Sorensen's (1975) experiments (figure 2) on the decomposition of ^{14}C -labelled cellulose in soils of different textures. In applying the model to different soils, the ratio CO_2 :(BIO + HUM) was set at 3.5 for Rothamsted soil; the value read from figure 2 for Rothamsted soil (inorganic cation exchange capacity $10.8 \text{ cmol}_c \text{ kg}^{-1}$ soil) was 2.10, giving a scaling factor of 1.67. The ratios obtained for other soils from figure 2 were scaled by the same factor. If the inorganic cation exchange capacity of the soil is not known, the clay content can be substituted, multiplying percentage clay content by 0.46 to give inorganic cation exchange capacity. This should be regarded as a matter of expediency: cation exchange capacity is preferable as it gives more weight

to, for example, a montmorillonitic than to a kaolinitic clay. The rate constant for the BIO compartment was set at 0.66 a^{-1} , from recent measurements of the turnover time of the soil microbial biomass under Rothamsted conditions (Jenkinson & Parry 1989).

The model, programmed in FORTRAN 77, was first fitted by iterative adjustment of the parameters to data from experiments (figure 3) in which the decomposition of labelled plant material in different soils was followed for 10 years in the open under Rothamsted conditions. The values finally selected for the input proportions were $P_{\text{DPM}} = 0.79$, $P_{\text{RPM}} = 0.21$. The rate constants (in a^{-1}), were $k_{\text{DPM}} = 10.0$, $k_{\text{RPM}} = 0.3$ and $k_{\text{HUM}} = 0.02$. These rate constants are divided by 12 to give the monthly rate constants and apply at 9.3°C (mean annual air temperature at Rothamsted; see figure 2) and at a soil moisture deficit of less than 20 mm of water. The value selected for the ratio (C going to BIO):(C going to HUM) was 0.85.

This version of the Rothamsted turnover model differs from the previous model (Jenkinson *et al.* 1987) in two ways. The earlier split of the soil microbial biomass into 'zymogenous' and 'autochthonous' populations is abandoned as there are no data to test this separation. The other difference is that the rate constant for the new (single) biomass compartment is set from external measurements, not, as earlier, treated as another parameter to be fitted.

(a) Model performance

Predictions from the model for two of the long-term classical experiments are shown in figure 4 (Broadbalk

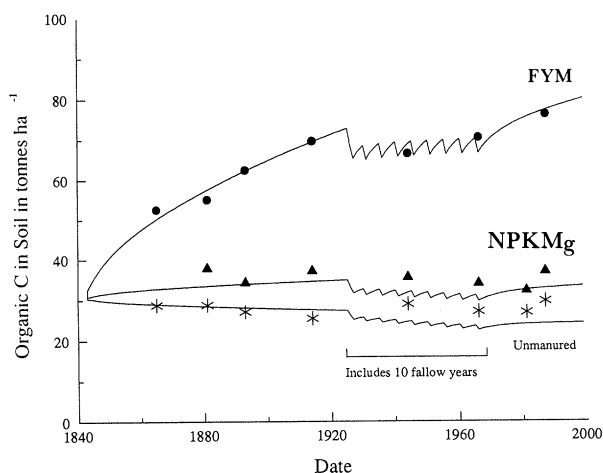


Figure 4. Organic carbon in the top 23 cm of a Rothamsted soil (23.4% clay) under continuous wheat (Broadbalk). The FYM plot (22) receives 35 t FYM ha⁻¹ annually, and the NPKMg plot 144 kg N, 35 kg P, 90 kg K and 12 kg Mg ha⁻¹, all annually apart from fallow years. The FYM, applied in early autumn, was assumed to retain 75% of the carbon in the original plant material from which it was formed and to contain DPM, RPM and HUM (but no biomass) in the proportion 0.65, 0.30 and 0.05, respectively. In fallow years, decomposition was assumed to proceed as usual with no fresh FYM or plant debris entering the soil. The IOM compartment contained 3.0 t C ha⁻¹. The carbon inputs used, all in t C ha⁻¹ a⁻¹ were: unmanured plot 1.2 (fitted); NPKMg plot 1.9 (fitted); FYM plot 1.9 (plant debris, fitted) + 3.0 FYM (set).

continuous wheat) and figure 5 (Broadbalk wilderness). Organic matter contents were assumed to have attained steady-state conditions when both field experiments started. In fitting the model to these data the only parameter allowed to vary was the annual input of carbon, with certain qualifications set out in the figure legends.

Farmyard manure (FYM) roughly trebled soil organic carbon in 140 years and this could be closely matched by the model predictions (figure 4). Inorganic fertilizer alone caused a smaller increase in organic matter content, presumably by increasing the return of stubble, roots and other plant debris to the soil. Again the difference between the inorganically fertilized plot and the unfertilized could be modelled by using plausible (Jenkinson & Rayner 1977) values for the annual inputs of organic carbon. The model (figure 5) can also be made to give an acceptable fit to the accumulation of organic matter in the old arable Broadbalk soil as it reverts to wilderness, if the annual input is taken to be 3.5 t ha⁻¹ a⁻¹ of carbon.

One of the problems in modelling the turnover of organic carbon in soil is the great age of soil organic matter as measured by radiocarbon dating (see, for example, Scharpenseel & Schiffmann (1977)). Thus topsoil (0–23 cm), sampled in 1881 from the unmanured plot of the Broadbalk continuous wheat experiment, contained 27.5 t ha⁻¹ of organic carbon (figure 4), with a measured radiocarbon age (calculated back to 1881) of 1330 years. If the model is run without an inert organic matter (IOM) compartment, then an input of 1.61 t ha⁻¹ a⁻¹ of carbon would give an

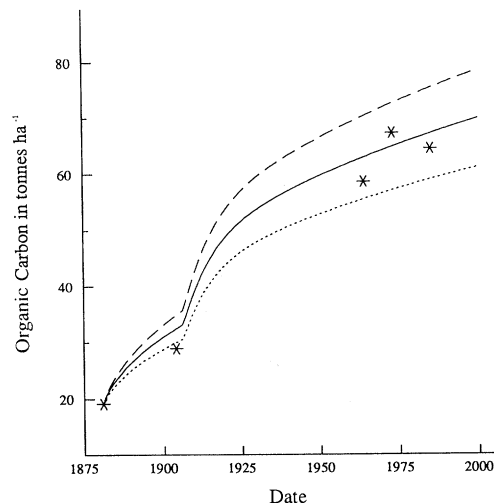


Figure 5. Accumulation of organic carbon in a Rothamsted soil (Broadbalk Wilderness) that was arable prior to 1883 and then allowed to revert to deciduous woodland (Jenkinson 1971). The sampling depth in 1987 was 23 cm; the earlier results are adjusted for the decrease in soil bulk density during reversion; IOM compartment as above. The modelled outputs shown are for plant carbon inputs of 3.0, 3.5 and 4.0 tonnes C ha⁻¹ a⁻¹. The DPM:RPM ratio is set at 79:21 for the first 25 years when the developing wilderness was dominated by herbaceous vegetation, thereafter at 20:80, as the trees began to take over. (---, 4.0 tonnes C ha⁻¹ a⁻¹; —, 3.5 tonnes C ha⁻¹ a⁻¹; ·····, 3.0 tonnes C ha⁻¹ a⁻¹.)

equilibrium carbon content of 27.5 t, exactly as observed, but the predicted average age would be only 104 years. Clearly soils must contain a proportion of organic matter that is extremely resistant to biological attack.

The introduction of an IOM compartment is a somewhat arbitrary way of dealing with this problem. By postulating that Broadbalk topsoil contains 3.0 t ha⁻¹ IOM-carbon and that the annual input of fresh plant carbon is 1.43 t ha⁻¹ a⁻¹, the model predicts that the soil will contain 27.5 t ha⁻¹ of carbon at equilibrium, again as observed, but now with an average age of 1400 years. An earlier version of the model (Jenkinson & Rayner 1977) solved this problem in a more elegant way, by postulating that a very small

Table 2. Measured and modelled values for soil microbial biomass

experiment	plot	soil microbial biomass (kg biomass C ha ⁻¹ in 0–23 cm layer)	
		measured	modelled
Broadbalk continuous wheat	unmanured (03)	486 ^a	476
	NPKMg (08)	776 ^a	738
	FYM (22)	1260 ^a	1890
Broadbalk wilderness	wooded section	1330 ^b	1620

^a Jinshui Wu, personal communication.

^b E. D. Vance, personal communication.

portion of the incoming plant material entered a highly resistant (but not inert) compartment, with a rate constant of 0.00035 a^{-1} . However, this version of the model predicted that the decline in carbon content of an old grassland soil brought under the plough was much slower than observed (Jenkinson *et al.* 1987) and was therefore abandoned in favour of the present *deus ex machina* solution.

Microbial biomass measurements provide an independent test of the validity of the model in figure 1. Table 2 shows calculated and measured values for the soil microbial biomass in the experiments listed in figures 4 and 5; apart from the farmyard manure plot, agreement is tolerable.

4. CONCLUSIONS

Models (e.g. figure 1) are useful for bringing scattered data together into a coherent and comprehensible whole. One of the aims of scientific modelling is to see how closely our ideas, expressed as a model, correspond with reality. Multicompartmental models like the Rothamsted turnover model are less useful here because the model outputs are brought into correspondence with reality by adjusting the model parameters to give the desired fit, not from independent assessments of these parameters. Models fitted in this empirical way are however useful for predictive purposes, provided they have been tested over a wide range of conditions and are not used outside their timespan.

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Discussion

S. P. S. ANDREW (*The Wynd, Stainton, Middlesborough, U.K.*). The long-term experiments suggest that the predominant route to the injection of very long life (half-life greater than 20 years) organic nitrogen into the soil is either root residues or ploughed-in surface crop or FYM. Does not this imply that the supply of inorganic nitrogen fertilizer to the soil continuously over a long period must result in increased nitrogen leaching as there is no substantial means of increasing the leach resistant long-life nitrogen store?

D. S. JENKINSON. The repeated use of inorganic fertilizer can lead to a small increase in the stock of 'stable' soil organic N. Thus the topsoil (0–23 cm) of the plot on the Broadbalk Continuous Wheat Experiment that receives 144 kg inorganic N ha⁻¹ a⁻¹ contained

3.3 t N ha⁻¹ in 1980, compared to 2.9 t ha⁻¹ in the plot not receiving inorganic N. During the period 1843–1980 almost 20 t fertilizer N ha⁻¹ had been supplied, of which only 2% was retained in the soil. This tiny increase is almost certainly caused by the increased input of organic C arising from the use of inorganic N fertilizer.

Once steady-state conditions have been attained, inputs of N must, of course, balance outputs. However, leaching is not the sole output: our current N turnover model indicates that at equilibrium only 41 kg N ha⁻¹ a⁻¹ will be leached from the Broadbalk plot receiving 144 kg N ha⁻¹ a⁻¹ (N. J. Bradbury, personal communication). The remainder is either removed in grain and straw, denitrified or lost as NH₃ during crop senescence. Current work at Rothamsted suggests that, although nitrate leaching does increase with increasing applications of fertilizer N, only a small proportion of the added N is leached until the ability of the (harvested) crop to remove N is exceeded.

S. P. S. ANDREW. Setting aside the supply to the soil of organic matter from the residues of dead and damaged roots (by far the main source) the cause and function of root exudate gels and their relation to the soil environment is worthy of speculation. Many soil-living microbial organisms produce extracellular gel-forming material when supplied with an abundant carbon source and all essential nutrients for growth, except one, for instance, no N, QRS. Could it be that this behaviour is an evolved response to an increase in water tension in the soil which would deny access to a 1 µm sized microbe of these nutrients even though there is an inadequate supply in soil solution held in the clay component unless these organisms can make contact with the clay through a gel capable of making conducting the nutrient solution. Might not root hairs behave in a similar manner under a similar provocation?

D. S. JENKINSON. Many soil organisms do indeed produce extracellular polymers during the decomposition of plant material, particularly if the plant material is of wide C:N ratio. These gums have been widely studied because of their role in stabilizing soil structure. It is possible that these gums (and likewise those produced by root hairs) can continue to bridge the space between an organism and its substrate as soils dry out and water bridges disappear. Soil organisms usually multiply close to their substrate, for example, sitting tightly in or on decomposing plant material. It is also possible that in these circumstances the production of an extracellular gum can protect a particular organism from its predators or competitors.

J. M. LYNCH (*AFRC Institute of Horticultural Research, Littlehampton, West Sussex, UK*). Work by Dr Whipps and I in the U.K., Professor Sauerbeck in Germany and Dr van Veen in Holland indicates that the carbon flowing from roots as rhizodeposition varies between about 20–40% of the dry matter production by the plant. These results have generally been obtained with 3-week old plants and have not been extrapolated to

field or global scales. Recently, Dr van Veen's group has shown that increased ambient CO₂ can increase rhizodeposition.

M. J. Goss (*The Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen, U.K.*). Earlier today, Dr Lynch referred to 40% of photosynthetically fixed carbon passing into the rhizosphere. Do results from Dr Jenkinson's model for fallow and permanent grass plots cast any light on the claim made by Dr Lynch?

D. S. JENKINSON. The input of organic C to the soil (0–23 cm) of the permanent grass plot in the High-field Ley-Arable experiment at Rothamsted is 4.0 t C ha⁻¹ a⁻¹, as calculated by our C turnover model. The offtake of herbage from this plot contained 3.7 t C ha⁻¹ a⁻¹ (mean of 1986, 87 and 88). Thus 52% of net primary production enters the soil each year. This input differs from rhizodeposition as defined by Lynch & Whipps, in that it includes any above-ground plant material that enters the soil but excludes CO₂ from root respiration, which Lynch & Whipps consider part of rhizodeposition. It is difficult to relate Lynch & Whipps 'rhizodeposition' to the turnover of organic matter in soil, because of the way they combine both organic C and CO₂-C. Organic (i.e. reduced) C provides the energy for almost all biological activity in soil, whereas CO₂-C supplies no energy.

P. B. TINKER (*NERC, Polaris House, North Star Avenue, Swindon, U.K.*). I should like to ask Dr Jenkinson about the predictions of changes in organic matter after a temperature rise, which showed a major decline. The work of Zinke *et al.* comparing large numbers of field soil profiles, do not seem to show an overwhelming effect of temperatures, moisture relations seem more important. Also, if the temperature change led to a change in vegetation type, the organic matter level could even increase. I wonder if Dr Jenkinson could expand on this very important issue?

D. S. JENKINSON. Soil from the unmanured plot on the Broadbalk continuous wheat experiment at Rothamsted contains 27.5 t C ha⁻¹ in the 0–23 cm layer. Our turnover model predicts that an input of 1.43 t organic C ha⁻¹ a⁻¹ is necessary to maintain this steady-state content at 9.3 °C, the mean annual temperature at Rothamsted. Bolin suggested that the increase in global temperature brought about by human activities would be between 1.5 and 5.5 °C. If the mean annual temperature at Rothamsted rose by 1.5 °C, an input of 1.43 t would maintain a steady-state content of 22.6 t C ha⁻¹; if by 5.5 °C, 16.0 t C ha⁻¹. Increasing concentrations of CO₂ in the atmosphere usually increase plant growth and, presumably, the annual return of reduced C to the soil. However, it is unlikely that this increase in annual return will be enough to maintain present soil organic matter levels. Such a decline in soil organic matter could well be important on the global scale, since there is roughly twice as much organic C in soil than CO₂-C in the atmosphere. Any such decrease in soil organic matter brought about by greenhouse heating could give rise to a positive feedback, further increasing atmospheric CO₂ and hence temperature.

Changing patterns of rainfall will indeed influence net primary production (NPP) and thus eventually soil organic matter levels, as you rightly imply. NPP will probably increase in some areas and decrease in others. We do not yet know how greenhouse heating will influence the quantity and geographical distribution of rainfall on a world-wide basis, indeed current climate models are considered to be much better at predicting changes in temperature than in rainfall. We need to know, firstly, what shifts there will be in the major vegetational zones of the earth and, secondly, how increases in CO₂ concentration influence the annual return of plant debris to the soil in each of these zones before we can be sure of the net effect of greenhouse warming on the amount of C held in terrestrial soils.