Soil Biol. Biochem. Vol. 25, No. 12, pp. 1755–1762, 1993
Printed in Great Britain.

0038-0717/93 $6.00 + 0.00

MODELLING OF SOIL CARBON FORMS AFTER ORGANIC AMENDMENT UNDER CONTROLLED CONDITIONS

Z. SALLIH[1] and M. PANSU[2]*

[1]CEFE-CNRS, BP 5051, F-34033 Montpellier Cedex and [2]ORSTOM, BP 5045, F-34032 Montpellier Cedex, France

(Accepted 17 June 1993)

Summary—Two different soils were amended with ^{14}C-labelled plant material and incubated under controlled laboratory conditions for 2 yr. The dynamics of labelled and total (labelled + unlabelled) C remaining in the soil, in the microbial biomass and in the plant residue, were monitored throughout the experiment.

In order to fit these results simultaneously, a model was defined including five compartments with functioning concepts according to earlier proposals and with a relatively simplified mathematical presentation among those used to describe the soil C cycle. The simultaneous fitting of microbial, plant and total labelled C appears satisfactory in the two soils, with a plausible simulation of the humification process.

This model, focusing on the labelled C (added form), has allowed to fit the evolution of soil total C (labelled + unlabelled). The two fittings reveal the presence of a stable form of carbon with a half-life longer than that stabilized since the addition of plant material, but shorter than the 'chemically stabilized organic matter' named by Jenkinson and Rayner (*Soil Science* **123**, 298–303, 1977).

Mineralization and humification kinetics were different in the two types of soils. These differences are expressed by model parameters and discussed with the presentation of results. In this way, hypothesis were derived in agreement with the soil mineral status and the soil carbon forms. Nevertheless, complementary investigations are necessary to verify these hypotheses and perhaps take into account newly endogenous variables in kinetic equations.

INTRODUCTION

Different models of the soil carbon cycle have been developed using data from natural conditions (Jenkinson and Rayner, 1977; Anderson and Coleman, 1985; Parton *et al.*, 1988; Molina *et al.*, 1983; Houot *et al.*, 1989). They take into consideration more and more main factors that influence the dynamics of organic matter, such as nitrogen contents (Molina *et al.*, 1983; Hadas *et al.*, 1987), climatic conditions (Parton *et al.*, 1987), soil temperature (Parton, 1984), and soil texture, particularly the clay content (Sorensen, 1981; Parton *et al.*, 1987).

Except for some particular approaches on mineralization and humification (Parnas, 1974; Brunner and Focht, 1984; Ionenko *et al.*, 1986), most of the proposed models classify the soil organic matter into compartments according to a decreasing rate which follows first order kinetics (Pansu, 1989).

Parton *et al.* (1987) proposed a model using concepts similar to those of Paul and Van Veen (1978). Following Jenkinson and Rayner (1977), it consists of five compartments that seem to correspond with analogous substance groups. Plant residue is divided into two compartments: 'metabolic' or 'decomposable plant material' and 'structural' or 'resistant plant material'. The soil C is divided into three compartments: 'active soil' or 'biomass', 'slow soil' or 'physically stabilized organic matter' and 'passive soil' or 'chemically stabilized organic matter'. The flow diagram of the Parton *et al.* model appears to be more complex and needs a larger number of parameters than that of Jenkinson and Rayner.

The NCSOIL model (Molina *et al.*, 1983) is equally more complex since the decomposition products POOL1 and POOL2 are both divided into two compartments, as plant residue.

Pansu and Sidi (1987) proposed two models, containing two and three compartments respectively, to describe the mineralization and humification kinetics in amended soil. These models were situated between those of Henin *et al.* (1959) and of Jenkinson and Rayner (1977), with the same type of working concepts (Pansu, 1988). These preceding studies have led us to maintain the same logic in this present proposition.

Our aim was to develop the most simple and suitable model to describe data that were obtained from a laboratory experiment (Z. Sallih, unpubl. Ph. D. thesis Université Montpellier, 1990). Some of these data have been published in two papers concerning carbon metabolism in relation to the presence of roots (Sallih and Bottner, 1988) and to microbial activity (Bottner *et al.*, 1988). The present study takes

*Author for correspondence.

into account the results of C evolution in two soils incubated without plants. In addition, labelled C found both in the light plus coarse organic particles was measured and assimilated into non-humified plant residue. Thus, to fit our model, we used more detailed results in comparison to studies carried out by Jenkinson and Ladd (1981), who considered the microbial biomass, and by Van Veen *et al.* (1985) who considered both microbial biomass and total labelled carbon simultaneously.

MATERIALS AND METHODS

Soils

The two soils used had developed under humid Mediterranean climatic conditions in southern France. Both were taken from the A1 horizon (0–15 cm) and classed according to CPCS (1976):

—soil 1: a fersiallitic calcic soil recently fallowed
—soil 2: a typical brown soil under grassland (*Brachypobium ramosum*).

The major characteristics of each soil are shown in Table 1. Main differences between the two soils were organic matter content, pH value and clay content. Illites are prevailing in soil 1, the most clayey one.

Experimental procedure

The experimental procedure was described by Sallih and Bottner (1988). Briefly, dried soil samples (5 mm) were split into portions of 800 g, mixed with 7 g mature uniformly ^{14}C-labelled wheat straw and then put in pots. The straw contained 1% N and 43% C with a specific activity of 2.59 MBq g^{-1} C; which corresponds to 3745 μg plant material $^{14}C\ g^{-1}$ soil. The procedure to obtain the labelled straw was described by Bottner (1982).

Pots were kept for >2 yr under controlled conditions in a growth chamber (daylight, 16 h at 25 ± 4°C; night 8 h at 15 ± 3°C). During this period, soil moisture was maintained at 75% WHC. Seven samplings were carried out at days 16, 29, 85, 121, 247, 422 and 690. At each sampling, the whole content of one pot was used for the analysis; 6–10 sub-samplings were carried out according to the type of analysis.

Analytical methods

Total carbon (organic plus inorganic) and labelled carbon (^{14}C) were measured using dry and wet combustion (Bottner and Warembourg, 1976).

Carbon of the microbial biomass (C-BM) was determined following the fumigation–incubation technique (Jenkinson and Powlson, 1976), using a K_c factor of 0.41.

The remaining plant material was separated from the soil using the procedure of Ladd *et al.* (1977) modified as below. Soil samples were shaken with 0.2 mol ($NaHCO_3$) L^{-1} (pH 8.3), centrifuged (12,000 rev min^{-1}) and filtered. The floating material was collected. The filtrate was concentrated and considered as the hydrosoluble fraction. The sediment was suspended again and fractionated into two parts by water sieving through a 50 μm mesh sieve. Within the fraction >50 μm, the sequestrated plant material was separated densimetrically by $ZnSO_4$ solution (density 1.4) and then added to the previous fraction. The total and labelled C of this fraction was determined by dry combustion. This procedure is detailed by Cortez (1989).

In our study, this fraction (light and coarse matter) is assumed to be the residual plant carbon.

Mathematical model

Figure 1 shows our present model compared with two other models (Pansu and Sidi, 1987; Jenkinson and Rayner, 1977). According to three principal types of organic matter, differences between these models are:

(1) Plant material: the present model separates this matter into two compartments; labile (V_L) and stable (V_R) which may correspond to the compartments 'decomposable plant materials (DPM)' and 'resistant plant materials (RPM)' of Jenkinson and Rayner. This approach is in agreement with that of Paul and Van Veen (1978), Molina *et al.* (1983) and Parton *et al.* (1987), but contrary to our earlier one which grouped these two organic fractions in one compartment with a variable kinetic order.
(2) Labile organic matter: the present model makes a distinction between microbial biomass (B) and other labile compounds (A). This is not the case in the model of Jenkinson and Rayner which takes into account only the microbial compartment (BIO), and in our earlier model which considered the sum of these two compartments (L).
(3) Stable organic matter: our data do not allow to take into account the 'chemically stabilized organic matter' (COM), obtained by Jenkinson and Rayner from dating measurements. But in short and medium term study

Table 1. Main characteristics of soils used

Soils	Particle size distribution (%) 2–0.2 mm	200–50 μm	50–20 μm	20–2 μm	<2 μm	Organic C (%)	N (%)	$CaCO_3$ (%)	pH(H_2O)
1	7	18	24	21	29	1.2	0.12	2.2	7.9
2	45	12	11	18	11	2.7	0.2	<0.1	6.5

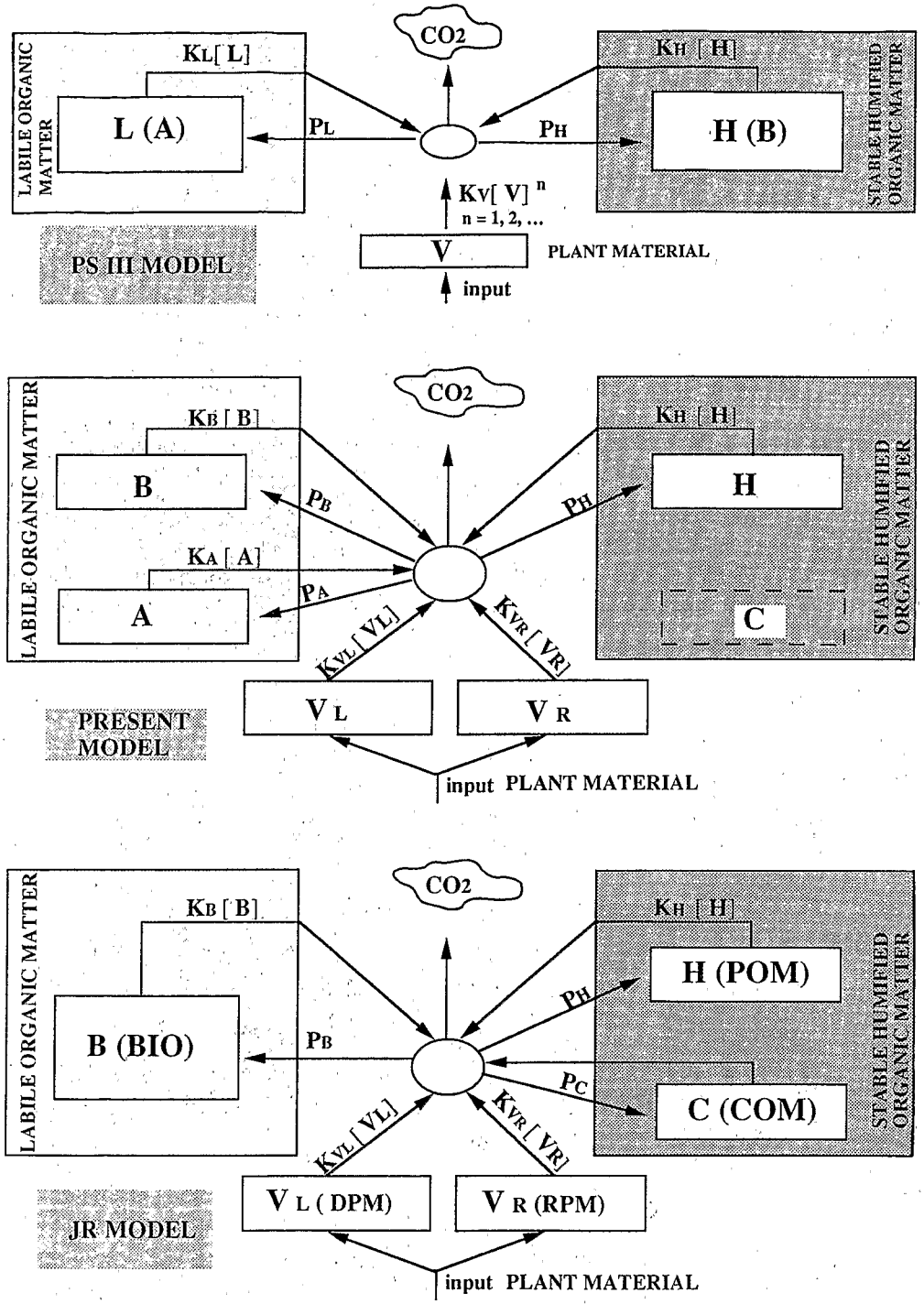

Fig. 1. Flow diagram for the present model compared to the propositions of Pansu and Sidi (1987; PSIII model) and Jenkinson and Rayner (1977; JR model). m = Organic input; V, V_L, V_R = plant material (PSIII), Labile plant material, Resistant plant material (JR and present model); B = microbial biomass (JR and present model); H = stable humified organic matter (present model, last called B in PSIII, last called 'Physically stabilized Organic Matter POM' in JR); C = chemically stabilized organic matter (COM in JR); A = labile soil organic matter, except microbial biomass and plant fragments (present model); L = labile soil organic matter, except plant fragments (PSIII model, last called A); P_L, P_A, P_B, P_H, P_C = input proportion in L, A, B, H, C compartments; Kv, Kv_L, Kv_R, K_A, K_B, K_H, K_C = kinetic coefficients of decays in the compartments V, V_L, V_R, A, B, H, C; n = kinetic order of decay in V compartment (PSIII).

of soil biochemical functioning, we can, as Molina *et al.* (1983) did, not take into account the 'passive organic phase'. In our model, the humified compartment (H) is analogous to that of our preceding model and similar to the 'physically stabilized organic matter' (POM) named by Jenkinson and Rayner.

Carbon dynamics vs time 't' is fitted according to a system of five first order differential equations. For any compartment 'm' among i compartments, this evolution is directed by:

$$\frac{dC_m}{dt} = -k_m C_m + P_m \sum_{i=1}^{5} k_i C_i \qquad (1)$$

$$m, i \in [V_L, V_R, A, B, H]$$

where:

C_m, C_i = carbon contents of compartments
k_m, k_i = rate constants of compartments (t^{-1})
P_m = proportion of carbon input into m compartment.

The equation of mineralization of carbon (C_T) is assumed to be:

$$\frac{dC_T}{dt} = -\sum_i k_i C_i (1 - \sum_i P_i) = -M \sum_i k_i C_i \qquad (2)$$

We defined M as the mineralization coefficient of the amended soil. From this, $I = \Sigma_i P_i = 1 - M$ is the renewed proportion of soil C.

Calculations were made using Turbo–Pascal Toolbox numerical methods (Borland).

RESULTS AND DISCUSSION

Study of different measurements

In preceding publications, we described:

—the decrease of added carbon according to the sum of two negatively exponential functions (Sallih and Bottner, 1988).
—the dynamic of microbial biomass and the respiratory quotient (Bottner *et al.*, 1988).

The best fitting for the non-transformed organic matter (separated by water sieving and densimetry) was obtained using the sum of two negative exponential terms. Parameters of these equations were supplied entering values for V_{L0}, V_{R0}, K_{VL} and K_{VR} (Fig. 2, Table 2). This type of fitting is different from that used by Pansu and Sidi (1987) where the light matter decreased according to an exponential or an hyperbolic function. However, preceding data are different and possibly not so accurate because they were obtained by densimetry only and from an unlabelled plant material.

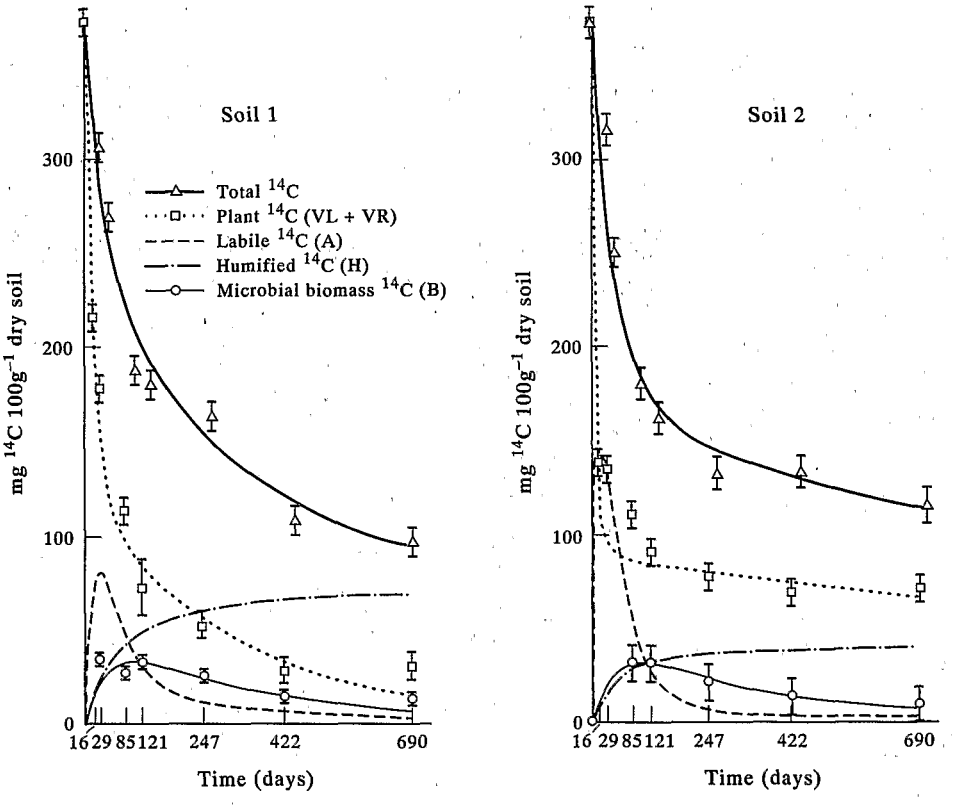

Fig. 2. Simultaneous model fitting of labelled carbon (added form) in the whole soil and in each compartment (confidence intervals of experimental data at 95%).

Table 2. Parameters of the model for labelled and total carbon of two soils

Compt.	Soil 1 I.V.	Soil 1 K_i	Soil 1 P_i	Soil 2 I.V.	Soil 2 K_i	Soil 2 P_i
			Labelled carbon			
V_L	246	0.05	0.0	283	0.1	0.0
V_R	125	0.0031	0.0	91	0.00043	0.0
A	0	0.05	0.58	0	0.1	0.79
B	0	0.006	0.08	0	0.004	0.033
H	0	0.0004	0.08	0	0.0001	0.025
			Total carbon			
V_L	246	0.05	0.0	283	0.1	0.0
V_R	125	0.0031	0.0	91	0.00043	0.0
A	9	0.05	0.58	220	0.1	0.79
B	60	0.006	0.12	120	0.004	0.033
H	1153	0.00005	0.08	2390	0.00002	0.025

I.V. = initial value of each compartment in mg C 100 g^{-1} dry soil.
K_i = kinetics constant in day^{-1}.
P_i = turnover proportion.
V_L = labile plant material.
V_R = resistant plant material.
A = labile soil organic matter (except microbial biomass and plant fragments).
B = microbial biomass.
H = humified organic matter.

Model fitting

The parameters of Table 2 and Fig. 2 show the simultaneous fitting of total-labelled C, plant-labelled C ($V_L + V_R$) and microbial-labelled C (B). The dotted lines represent the simulation of labile (A) and stable (H) humified labelled C. These two compartments were not measured but must be taken into account to equilibrate the balance of 'total-labelled C' minus 'plant-C plus microbial C'.

Moreover, the measurement of labelled C in the hydrosoluble fraction (unpubl. data) is closely correlated with the simulation of labile carbon (A) ($r = 0.89$*** for soil 1 and $r = 0.73$* for soil 2), with a maximum towards day 15–30. This is clearly earlier than the maximum for microbial development. Nevertheless, the water-soluble fraction represents only about 10% of the simulated labile C, so it would be necessary to search for other labile products principally amongst the polysaccharides in the range between cellulose and simple sugars.

In the two soils, the labile compartment (A) decreased at the same rate as the plant labile compounds. This shows a very rapid incorporation of these compounds into the soil in such a way that it becomes impossible to distinguish them by granulometry or by densimetry. Both types of labile compounds are used to feed the microorganisms which reach their maximum growth after *ca* 3 months of incubation. Most of the labile compounds are consumed after 6 months, so microbial biomass decreases gradually.

Humified compounds increased progressively during the experiment to approach, at the end of the incubation, the level of the remaining added C. Nevertheless, as the degradation of the labile compounds, the major part of the humification process seemed to stabilize after 6 months of incubation.

The fitting of the model is as good as that of individual simulation of total-labelled C (Sallih and Bottner, 1988), and microbial biomass (Bottner *et al.*, 1988). A slight discrepancy of the microbial compartment fitting is noticed at the end of the experiment in soil 1. However, new experiments are necessary to define the cause of this deficit: experimental errors or a defect of model linearity would need a correction of the mathematical formulation.

Concerning the plant C, since renewal proportion P_i is zero for V_L and V_R compartments, the fitting is the same as that obtained by the sum of two exponential terms. The greater lack of fitting was noted at the end of experiment in soil 1 (as for microbial biomass), and at day 84 in soil 2. In each soil, the slope of plant C curve became close to that of total-labelled C when the labile fraction is already consumed. Then, the role of resistant plant C (V_R) becomes preponderant in the evolution of the system.

Soil type and evolution kinetics

Important differences in the mineralization process were found between the two types of soil. Mineralization is more intense in soil 1 than in soil 2; M (mineralization coefficient, equation 2) is 0.26 and 0.15 for the two soils respectively.

However, at the beginning of the experiment this order was reversed. At this time, more intensified mineralization occurred in soil 2. Conversion of rate constant of V_L and A compartments in half-life, according to Jenkinson and Rayner (1977), gives a value of 2 weeks for soil 1 but only 1 week for soil 2. This could be explained by the recent history of each soil. Soil 2 has been developed under grassland. Root input induces more labile organic matter and a microflora adapted to metabolize these substances or other labile products like the cellulose and polysaccharides of added plant material. Another explanation could be in relation to the stabilization of labile plant matter due to clay content (Van Veen and Paul, 1981) which is highest in soil 1.

When labile material was completely decayed after 2–3 months, the decrease in mineralization rate was particularly clear in soil 2. Half-life of the V_R compartment would be about 7 months in soil 1 but >4 yr in soil 2. So, at the end of the experiment, about 18% of the added plant material was not degraded in soil 2, whereas only 4% in soil 1.

The simulation by the model of the humification process (H compartment) is notably higher in soil 1 than in soil 2. This is consistent with former hypotheses about the role of clays in humification (Martin and Haider, 1986). The isohumic coefficient, calculated according to the original definition of Henin and Dupuis (1945) from 'H' compartment simulation, is equal to 0.18 for soil 1 and 0.11 for soil 2. We note here the importance of the compartmented simulation in the calculation of this coefficient, because calculations considering added carbon decrease only, may have led to an inverse conclusion

concerning humification. Effectively, at the end of the experiment, the ratio of remaining ^{14}C to initially added ^{14}C is equal to 0.25 in soil 1 and 0.31 in soil 2; the isohumic coefficient seems to be more important in sandy soil than in clay soil.

After 2 yr of incubation, and in spite of a relatively stabilized curve of global labelled C, we are still far from the equilibrium in soil 2, whereas in soil 1, the residual added C becomes close to humified carbon. The initially greater C content of soil 2 is originated probably from the preponderance of plant C that is incompletely transformed.

Finally, both mineralization and humification process are more important in soil 1 (clay soil), and express an intense biological functioning, except at the beginning of the experiment. The model shows this phenomenon by the parameters that characterize the microbial biomass. Although global aspects of microbial dynamic curves appear similar in the two soils, half-life of microbial biomass is slightly shorter in soil 1 than in soil 2 (about 4 months instead of 6 months) and the renewal proportion in soil 1 is more than twice. This higher turnover of the microbial compartment may suggest an important availability of nitrogen in soil 1, but this hypotheses must be verified.

Moreover, if humification is less intense in soil 2 (sandy soil) than in soil 1 (clayey soil), it suggests that formed humus in soil 2 is more stable; with a half-life of 'H' compartment about 19 yr against only 5 yr in soil 1.

Total carbon simulation

Before the model can be tested in natural conditions, we must verify if it is possible to fit the dynamics of total soil C (labelled + unlabelled) without major modifications in parameters. This may allow to check the validity of the model: does pre-existing organic matter in the soil behave in the same way as added matter?

Parameters of Table 2 and Fig. 3 show the simultaneous fitting of total C, plant C and microbial C. As above, the simulation of humified total C of compartments labile (A) and stable (H) are represented by dotted lines. The model seems satisfactory because similar results were obtained after changing the initial values of A, B and H compartments.

The rate constants are the same as above, except that of stable compartment (H) whose half-life would pass from 5 to 38 yr in soil 1 and from 19 to 95 yr in soil 2. This difference could be explained by the fact that the very stable compartment (COM) of soil organic matter has not been taken into account in the calculation.

With these data, we tried to estimate the stability of this compartment; assuming that K_H, k_H^*, k_H^0 are the rate constants of humified total, labelled and native carbon respectively, the [H], [H*] and [H^0] are their corresponding contents, then the equation of the flow between these compartments is:

$$k_H[H] = k_H^0[H^0] + k_H^*[H^*] \qquad (3)$$

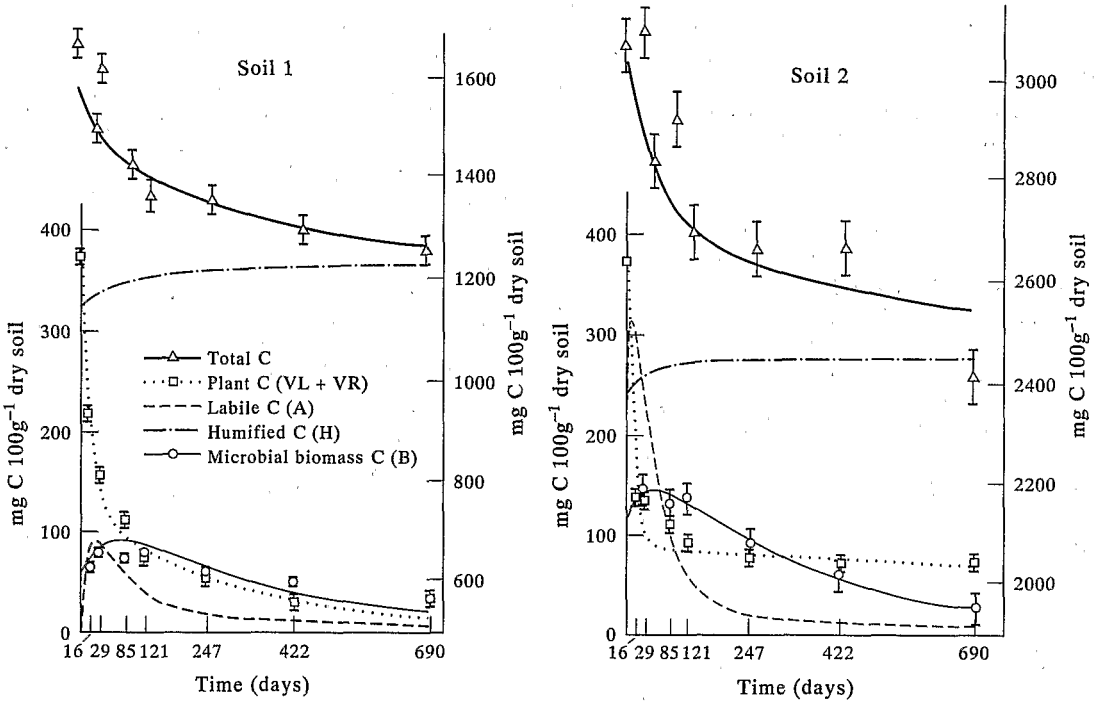

Fig. 3. Simultaneous model fitting of total carbon in the whole soil and in each compartment (plant, labile and microbial carbon on the left scale, total and humified carbon on the right scale; confidence intervals of experimental data at 95%).

If we take for [H], [H*] and [H^0], the values at the end of the experiment (with simulation of non-addition for [H^0]), equation 3 gives a k_H^0 of 0.00003 d^{-1} for soil 1 and of 0.000019 d^{-1} for soil 2; this corresponds to a half-life of 63 and of 102 yr for the two soils respectively. These half-lives are considerably smaller than that of 1980 years found by Jenkinson and Rayner for their [COM] compartment. So it is illusory to try to estimate this compartment from this type of experimentation. But it seems that it exists a part of soil C with an intermediary half-life between [H] and [COM]. This could explain the often observed decrease of native C in comparison to added C, and confirms some preceding suggestions (Jenkinson and Ayanaba, 1977; Pansu and Sidi, 1987). However, we must be careful with the estimation of stable compounds from a short-term experiment.

Renewal proportions P_i are all the same as those used for ^{14}C, except that of the microbial biomass of the soil 1, which had been increased slightly. This would confirm our preceding remarks that suggest a little anomaly of the model in this soil which have an intense biological activity, but complementary investigations will be necessary to determine precisely this observation.

On the other hand, in soil 2 the fitting of the microbial biomass by our model seems still more precise than the fitting of this only compartment (Bottner *et al.*, 1988). A choice of high initial values of both microbial and labile (A) compartments was necessary for the realization of the adjustment. This is in agreement with one of the above hypotheses about the intense mineralization activity at the beginning of the experiment in this soil from grassland.

The fitting of soil total C is acceptable despite the relatively important variability of the measurements, especially in soil 2. This variability would confirm the above hypothesis about the presence in this soil of incompletely decomposed fragments of plant C.

In spite of these restrictions, the transposition of the model on the soil total C is satisfactory. This gives a validation to the model in our experiment. The number and the type of proposed compartments appear necessary and sufficient to explain globally the soil C cycle (added or native).

Perspectives

This model, tested by experimental data, is interesting by its relative simplicity as only one equation (equation 1) can describe the evolution of every compartment. It can also be adapted to obtain the more suitable description of the soil C cycle at a given situation. For example, the model with two or three compartments (Pansu and Sidi, 1987) could be described by a similar equation with $i = 2$ or $i = 3$ (if $n = 1$ for PS III, Fig. 1) and a new definition of the compartments. The model can be used in predicting studies of the organic pools dynamics for one soil type (where organic inputs could be estimated as well as k_i and P_i). The influence of climate could be expressed by changing the k_i constants of formula (1) by k_i^{eff} such as:

$$k_i^{eff} = k_i l_{(T)} m_{(M)} \quad (4)$$

with $l_{(T)}$, $m_{(M)}$ = correcting factors for temperature and moisture which could be those provided by Van Veen and Paul (1981) or Parton *et al.* (1987). Moreover, experimental data should be of interest for a precise fitness of the model.

In addition, data provided from various experiments, comparable with ours, would be of great significance in considering the edaphic factors (nitrogen, clays, cultivation and biomass ...) which may influence the model parameters in order to make progress towards its generalization.

REFERENCES

Anderson D. W. and Coleman D. C. (1985) The dynamics of organic matter in grassland soils. *Journal of Soil and Water Conservation*, **40**, 211–216.

Bottner P. (1982) Biodégradation du matériel végétal en milieu herbacé. *Acta OEcologica/OEcologa Generalis* **3**, 155–182.

Bottner P. and Warembourg F. (1976) Method for simultaneous measurement of total and radioactive carbon in soils, soil extracts and plant material. *Plant and Soil* **45**, 273–277.

Bottner P., Sallih Z. and Billes G. (1988) Root activity and carbon metabolism in soils. *Biology and Fertility of Soils* **7**, 71–78.

Brunner W. and Focht D. (1984) Deterministic three-half-order kinetic model for microbial degradation of added carbon substrates in soil. *Applied and Environmental Microbiology* **47**, 167–172.

Cortez J. (1989) Effect of drying and rewetting on mineralization and distribution of bacterial constituents in soil fractions. *Biology and Fertility of Soils* **7**, 142–151.

CPCS (1967) Classification des sols. Ecole Nationale Supérieure d'Agronomie (E.N.S.A), 87 pp., Grignon.

Hadas A., Molina J. A. E., Feigenbaum S. and Clapp C. E. (1987) Simulation of Nitrogen-15 immobilization by the model NCSOIL. *Soil Science Society of America Journal* **51**, 102–106.

Henin S. and Dupuis M. (1945) Essai de bilan de la matière organique du sol. *Annales Agronomiques* **15**, 17–29.

Henin S., Monnier G. and Turc L. (1959) Un aspect de la dynamique des matières organiques du sol. *Comptes Rendus de l'Académie des Sciences-France* **248**, 138–141.

Houot S., Molina J. A. E., Chaussod R. and Clapp C. E. (1989) Simulation by NCSOIL of net mineralization in soils from the Deherain and 36 Parcelles fields at Grignon. *Soil Science Society of America Journal* **53**, 451–455.

Ionenko V. I., Batsula A. A. and Golovachev Ye. A. (1986) Kinetics of humification. *Soviet Soil Science* **18**, 33–42.

Jenkinson D. S. and Ayanaba A. (1977) Decomposition of carbon-14 labelled plant material under tropical conditions. *Soil Science Society of America Journal* **41**, 912–915.

Jenkinson D. S. and Ladd J. N. (1981) Microbial biomass in soil; measurement and turnover. In *Soil Biochemistry* (E. A. Paul and J. N. Ladd, Eds), Vol. 5, pp. 415–471. Dekker, New York.

Jenkinson D. S. and Powlson D. S. (1976) The effect of biocidal treatments on metabolism in soil: V. a method for measuring soil biomass. *Soil Biology & Biochemistry* **8**, 209–213.

Jenkinson D. S. and Rayner J. H. (1977) The turnover of soil organic matter in some of the Rothamsted classical experiments. *Soil Science* **123**, 298–303.

Ladd J. N., Parsons J. W. and Amato M. (1977) Studies of nitrogen immobilisation and mineralization in calcareous soils. I. Distribution of immobilised nitrogen amongst soil fractions of different particle size and density. *Soil Biology & Biochemistry* **9,** 309–318.

Martin J. P. and Haider K. (1986) Influence of mineral colloids on turnover rates of soil organic carbon. *Soil Science Society of America* **17,** 283–303.

Molina J. A. E., Clapp C. E., Shaffer M. J., Chichester F. W. and Larson W. E. (1983) NCSOIL, a model of nitrogen and carbon transformation in soil: description, calibration and behaviour. *Soil Science Society of America Journal* **47,** 85–91.

Pansu M. (1988) Proposition de modèles descriptifs de la dynamique des matières organiques des sols. (C. R. Journée de pédologie ORSTOM Sep. 1988), Cahiers ORSTOM Série Pedologie XXIV (4).

Pansu M. (1989) Cinétique chimique et modèles compartimentaux: application à l'étude de l'évolution du stock organique des sols. In *SEMINFOR 2: La Modélisation Aspects Pratiques et Méthodologie, 2° Séminaire Informatique ORSTOM, Sep.* 1988. ORSTOM, Paris.

Pansu M. and Sidi H. (1987) Cinétique d'humification et de minéralisation de mélanges sols-résidus végétaux. *Science du Sol* **25,** 247–265.

Parnas H. (1974) Model for decomposition of organic material by microorganisms. *Soil Biology & Biochemistry* **7,** 161–169.

Parton W. J. (1984) Predicting soil temperature in a short-grass steppe. *Soil Science* **138,** 93–101.

Parton W. J., Stewart J. W. B. and Cole C. V. (1988) Dynamic of C, N, P and S in grassland soils: a model. *Biogeochemistry* **5,** 109–131.

Parton W. J., Schimel D. S., Cole C. V. and Ojima D. S. (1987) Analysis of factors controlling soil organic matter levels in great plains grasslands. *Soil Science Society of America Journal* **51,** 1173–1179.

Paul E. A. and Van Veen J. A. (1978) The use of tracers to determine the dynamic nature of organic matter. *Transactions of the 11th International Congress of Soil Science Edmonton, Alta* **3,** 61–102.

Sallih Z. and Bottner P. (1988) Effect of wheat (*Triticum aestivum*) roots on mineralization rates of soil organic matter. *Biology and Fertility of Soils* **7,** 67–70.

Sorensen L. H. (1981) Carbon–nitrogen relationships during the humification of cellulose in soils containing different amounts of clay. *Soil Biology & Biochemistry* **13,** 313–321.

Van Veen J. A. and Paul E. A. (1981) Organic carbon dynamics in grassland soils. I. Background information and computer simulation. *Canadian Journal of Soil Science* **61,** 185–201.

Van Veen J. A., Ladd J. N. and Amato (1985) Turnover of carbon and nitrogen through the microbial biomass in a sandy loam and clay soil incubated with [^{14}C(U)]glucose and [^{15}N]$(NH_4)_2SO_4$ under different moisture regimes. *Soil Biology & Biochemistry* **17,** 747–756.