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ORGANIC CARBON DYNAMICS IN GRASSLAND SOILS. 1. BACKGROUND INFORMATION AND COMPUTER SIMULATION

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The decomposition rates of ^{14}C-labelled plant residues in different parts of the world were characterized and mathematically simulated. The easily decomposable materials, cellulose and hemicellulose, were described as being decomposed directly by the soil biomass; the lignin fraction of aboveground residues and the resistant portion of the roots entered a decomposable native soil organic matter. Here it could be decomposed by the soil biomass or react with other soil constituents in the formation of more recalcitrant soil organic matter. The transformation rates were considered to be independent of biomass size (first-order). Data from ^{14}C plant residue incorporation studies which yielded net decomposition rates of added materials and from carbon dating of the recalcitrant soil organic matter were transformed to gross decomposition rate constants for three soil depths. The model adequately described soil organic matter transformations under native grassland and the effect of cultivation on organic matter levels. Correction for microbial growth and moisture and temperature variations showed that the rate of wheat straw decomposition, based on a full year in the field in southern Saskatchewan, was 0.05 that under optimal laboratory conditions. The relative decay rates for plant residues during the summer months of the North American Great Plains was 0.1 times that of the laboratory. Comparison with data from other parts of the world showed an annual relative rate of 0.12 for straw decomposition in England, whereas gross decomposition rates in Nigeria were 0.5 those of laboratory rates. Both the decomposable and recalcitrant organic matter were found to be affected by the extent of physical protection within the soil. The extent of protection was simulated and compared to data from experimental studies on the persistence of ^{14}C-labelled amino acids in soil. The extent of protection influenced the steady-state levels of soil carbon upon cultivation more than did the original decomposition rates of the plant residues.

Nous avons caractérisé et modélisé les taux de décomposition des résidus végétaux (marqués au ^{14}C) dans différentes parties du monde. Les matières facilement décomposables, comme la cellulose et l'hémicellulose, étaient décrites comme étant directement décomposées par la biomasse du sol, cependant que la lignine des résidus des parties aériennes des plantes et la portion résistante des racines s'incorporaient à la matière

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organique décomposable du sol originel. Là elle pouvait soit être décomposée par la biomasse du sol, soit réagir avec d'autres constituants du sol pour former des matières organiques plus résistantes (moins décomposables). Les taux de transformation étaient considérés comme indépendants de l'importance de la biomasse (équation du 1er ordre). Les données produites par les travaux sur l'incorporation de résidus végétaux marquis (^{14}C) ayant fourni des taux de décomposition nets des matières végétales ajoutées, ainsi que les données obtenues par la datation du carbone de la matière organique résistante ont été transformées en constantes de décomposition pour trois couches successives de sol (0-15, 15-40 et 40-80 cm). Le modèle s'est révélé satisfaisant pour décrire les transformations de la matière organique (MO) du sol sous prairie originelle ainsi que l'effet des pratiques culturales sur les taux de MO. La correction des données en fonction de la croissance microbienne et des variations hydriques et thermiques du sol a permis de constater que le rythme de décomposition de la paille de blé, d'après des observations conduites au champ pendant une année complète en Saskatchewan, était de 0.05 fois celui obtenu en conditions expérimentales optimales. Les taux relatifs de décomposition des résidus végétaux durant les mois d'été dans les Grandes plaines de l'Amérique du Nord étaient, pour leur part, de 0.1 fois ceux obtenus en laboratoire. Les comparaisons effectuées avec les données provenant d'autres régions du monde révélaient des taux annuels relatifs de décomposition pour la paille de seigle de 0.12 (Angleterre) et de 0.5 (Nigéria) par rapport aux taux obtenus en laboratoire. Le degré de protection physique apporté par la nature du sol influe à la fois sur le sort de la matière organique décomposable et de la MO résistante. Pour mesurer l'import ce de cette protection, les données ont été modélisées et comparées aux résultats des recherches réalisées sur la persistance des acides aminés marqués (^{14}C) dans le sol. Le degré de protection a exercé une influence plus marquée sur le niveau d'équilibre de C du sol sous culture que le taux de décomposition originel des résidus végétaux.

Organic matter has long been recognized as a reservoir of plant nutrients and a major factor in stabilization of soil structures (Allison 1965). On a global basis, it acts as a source-sink for carbon in the cycling of CO_2; recent calculations of world climatic CO_2 levels, with their long-term implication in climatic alterations, have made extensive use of soil organic matter data (Bolin 1977).

Tracers such as ^{13}C, ^{14}C and ^{15}N have made measurements of the flow of these nutrient elements through soils and ecosystems feasible. The determinations of gross decomposition rates for compounds such as sugars (Cheshire et al. 1974), acetate (Sørensen and Paul 1971), and amino acids (McGill et al. 1974) have shown their rapid degradation in soils. Even naturally occurring phenolic materials are degraded relatively rapidly (Martin and Haider 1977). Microbial populations generally utilize nutrients at a high efficiency and the tracer found in organic forms after the first few days incubation often represents the persistence of biomass and microbial metabolites rather than the original substrate added (Mayaudon and Simonart 1958, 1959; Martin et al. 1974).

Complex substrates such as plant residues have been shown to undergo decomposition rates relatively independently of the amount added (Jenkinson 1971, 1977). The content of proteins, cellulose, hemicellulose, and lignin within the residue, however, influences both the initial decomposition rate and the later stabilization of microbial products and soil humic compounds (Herman et al. 1977; Hunt 1977).

Soil organic matter equilibrium levels have been shown to be more dependent on the amount and degradation rate of resistant humic materials present than on decomposition rates of added residues. Atmospheric ^{14}C levels utilized in conjunction with carbon dating techniques have proven useful in measuring these calcitrant materials (Stout et al. 1980; Scharpenseel 1977; Martel and La Salle 1977).

Interpretation of tracer data on C and N turnover from the early days of tracers required the use of mathematics (Bingeman et al. 1953; Jansson 1958). First-order kinetics were generally applied in calculating plant residue decomposition rates and soil organic matter levels (Kirkham and Bartholomew 1955; Russell 1964, 1975; Greenland and Nye 1959). Jenkinson and Rayner (1977) utilized data from carbon dating of resistant fractions and the measurement of bomb-produced atmospheric ^{14}C in soil organic matter to measure plant residue incorporation rates. Decay rates for ^{14}C-labelled plant residues incubated in the field and estimates of the biomass of soil organisms were also incorporated into the mathematical analysis which described the turnover and the equilibrium levels of soils at the Rothamsted Experimental Station in England.

Paul and Van Veen (1978) reviewed the literature on carbon dynamics and developed a model that corrected raw decomposition data for microbial growth and microbial product stabilization. The concepts of microbial growth and soil organic matter turnover are developed further in this paper. The available information on soil organic matter formation, turnover and stabilization is also mathematically described and tested by the use of data from field sites.

Data Analysis

Modelling of the dynamics of ecosystems requires meaningful mathematical expressions for the biological, chemical and physical processes involved (Frissel and Van Veen 1978). Soil organic matter decomposition has been experimentally shown to follow first-order rate kinetics. This means that the decomposition rate is linearly proporational to the organic matter content, but that the rate constant is independent of the content (Eq. 1). The use of first-order kinetics for the decomposition of soil organic matter implies that the biological potential of soil will not be rate-limiting at any time (Van Veen et al. 1980). This is attributable to the large soil biomass and its fast growth rate in conjunction with the addition of low levels of substrate relative to the population size.

The rate of decomposition of a substrate as described by first-order kinetics is:

$$V = -\frac{dC}{dt} = kC \qquad (1)$$

where

V = decomposition rate (amount · time^{-1})
C = substrate (amount)
t = time
k = rate of constant with dimension time^{-1}

Only a portion of the decomposition is accounted for when determining the decomposition rate by measuring CO_2 output or the amount of C left in the soil. Microorganisms use C compounds for biosynthesis forming new cellular or extracellular material and as an energy supply. In the latter process, C compounds are converted into CO_2 and to a lesser extent low molecular weight compounds. Biosynthesis can be taken into account when calculating the actual decomposition rate from CO_2 output data:

$$CO_T = CO_2\,[1 + Y/(100 - Y)] \qquad (2)$$

where

C = actual amount decomposed
CO_2 = CO_2 produced
Y = efficiency of the use of carbon for biosynthesis is expressed as percentage of the total C uptake.

Even when the original compound can be determined chemically, measuring the true decomposition may be hampered by microbial production of that particular compound, as in the case of sugars (Cheshire et al. 1974). The decomposition rate constant (k), corrected for biosynthesis, differs significantly from the uncorrected ones (Table 1). Growth efficiencies of 50–60% are generally considered to be realistic for the decomposition of carbonaceous compounds in soil (Payne 1970; Verstraete 1977; Ladd and Paul 1973). However, where only tabular data over extended periods are available, it is not possible to calculate k at 60% efficiency because of corrections for sequential microbial growth can not be made. The data show that one may

Table 1. First-order rate decay constants (with and without correction for microbial biosynthesis) during decomposition of organic matter added to the soil under laboratory conditions

Material	Time (day)	k (day^{-1}) Uncorrected	Corrected efficiency (%) 20	60	References for uncorrected data
Straw-rye (<53 113m)	14	0.02	0.03	0.11	Cheshire et al. (1974)
Straw-rye (<1000 μm)	14	0.02	0.02	0.04	Cheshire et al. (1974)
Straw-wheat (avg of 3 soils)	28	0.02	0.03	—	Sauerbeck and Fuhr (1968)
Straw-wheat (avg of 12 soils)	45	0.006	0.008	—	Sauerbeck and Fuhr (1968)
Straw-wheat	180	0.005	0.08	—	Shields and Paul (1973)
Straw-wheat	365	0.002	0.003	—	Sauerbeck and Gonzales (1977)
Hemicellulose	10	0.08	0.11	—	Simonart and Mayaudon (1958)
Hemicellulose	14	0.03	0.04	0.11	Cheshire et al. (1974)
Hemicellulose	365	0.003	0.006	—	Mindermann (1968)
Glucose	1	—	—	4.0	Voroney (1979)
Glucose	1.5	—	—	2.22	Ladd and Paul (1973)
Glucose	8	0.11	0.16	—	Wagner (1968)
Glucose	10	0.11	0.19	—	Simonart and Mayaudon (1958)

make a serious mistake when assessing decomposition rates of fresh amendments without accounting for microbial biosythesis.

We developed a simple computer simulation model (Fig. 1) to obtain a better understanding of the quantitative aspects of decomposition of a complex substrate such as crop residues and subsequent microbial production. The complex substrate was considered to consist of three fractions which were progressively more resistant to decomposition. These were: (1) carbohydrates and proteins, (2) cellulose and hemicellulose, and (3) lignin. The decay rate constant of the biomass is a function of all processes that require substrate other than for growth. The statements in the literature concerning maintenance energy of the soil population (Babiuk and Paul 1970; Verstraete 1977; Barber and Lynch 1977) have raised a number of significant questions concerning the turnover and stability of the soil population. However, for modelling purposes we have chosen to incorporate the maintenance requirements in the decay rate constants. This allows for cryptic growth and predation; it also bypasses the need to establish separate maintenance coefficients for the various active and resting portions of the very large soil biomass relative to the available energy supply.

Rates follow first-order rate kinetics. The model output (Fig. 2) shows a great difference between the true decomposition and the decomposition as measured from CO_2 evolution. This is attributed primarily to microbial production. Differences in decomposition rates of the separate compounds of a complex substrate (Jenkinson and Rayner 1977) such as straw are therefore not the only cause of the decrease in decomposition rates with time as shown in Table 1.

Effect of Environmental Factors

Data for decomposition rates of added organic matter in different climatic conditions are shown in Table 2. The corrected k values in this table were determined by simulating the decomposition of the plant residues using the model of Fig. 1 and fitting the output to experimental data (Paul and Van Veen 1978). The effects of different climatic conditions are primarily due to differences in temperature and moisture. The difference between the decomposition rates for wheat straw in Saskatchewan calculated for the summer and that for the entire year is caused

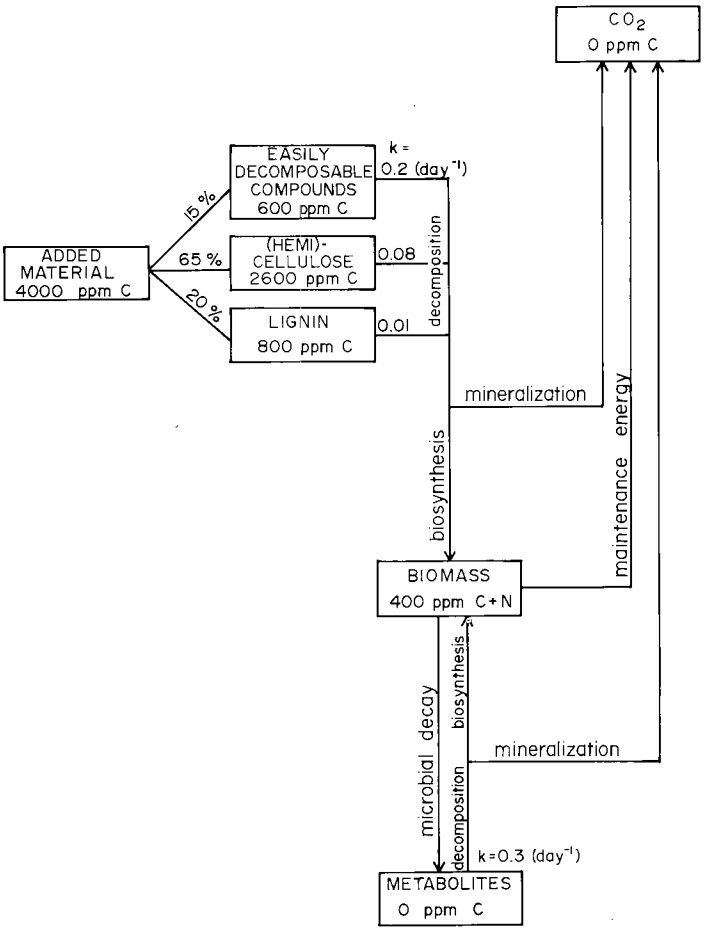

Fig. 1. Model describing decomposition of a complex substrate (numbers in boxes represent initial levels).

by the severe winter, which virtually stops biological activity. A factor of 4 in the decomposition rates for Nigeria and England fits the data for Jenkinson and Ayanaba (1977) who found that the decomposition of ^{14}C-labelled ryegrass proceeded four times as rapidly in Nigeria as in England. Incubation at room temperature and field capacity in the laboratory yields decomposition rates twice as great as those found in the field in Nigeria.

A great deal of information is available on the independent effect of climatic factors, but very little is known about the quantitative aspects of the combined effect (Woodmansee 1978). Expressing the effect of environmental factors by using reduction factors ranging from a value of 1, at optimum conditions, down to zero, depending on the particular environmental condition, is now common in soil organic matter simulation models (Beek and Frissel 1973; Van Veen 1977; Hunt 1977; Cole et al. 1978). The combined effect is expressed by multiplying the reduction factors with each other, or by considering the smallest value expressing the greatest limitation (Frissel and Van Veen 1978: Woodmansee 1978). Figure 3 shows the reduction factors for temperature and moisture.

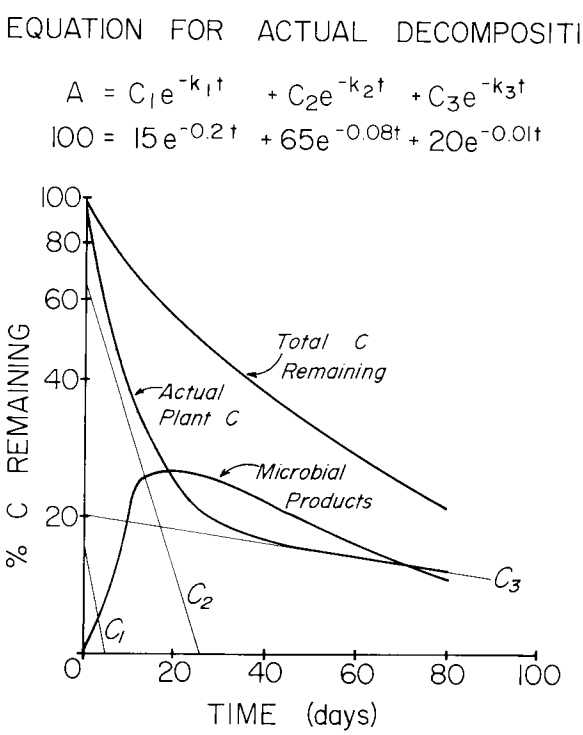

Fig. 2. Decomposition of straw-C in the laboratory, plotted as a series of first-order reactions after correction for microbial production. The ACTUAL PLANT-C remaining is comprised of proteins and solubles (C_1), cellulose and hemicellulose (C_2), and lignin (C_3).

Table 2. Effect of the environment on the decomposition rate of plant residues added to the soil

Environmental condition	$T_{1/2}$ (days)		k (day^{-1})		Relative rate
	Uncorrected	Corrected (60%)	Uncorrected	Corrected (60%)	
Wheat straw, laboratory†	17	9	0.04	0.08	1
Rye straw, Nigeria‡	28	17	0.02	0.04	0.5
Rye straw, England‡	125	75	0.006	0.01	0.125
Wheat straw, Sask. summer§	125	75	0.006	0.008	0.10
Wheat straw, Sask. year§	230	160	0.002	0.003	0.05

†Paul and Van Veen (1978).
‡Jenkinson and Ayanaba (1977).
§Shields and Paul (1973).

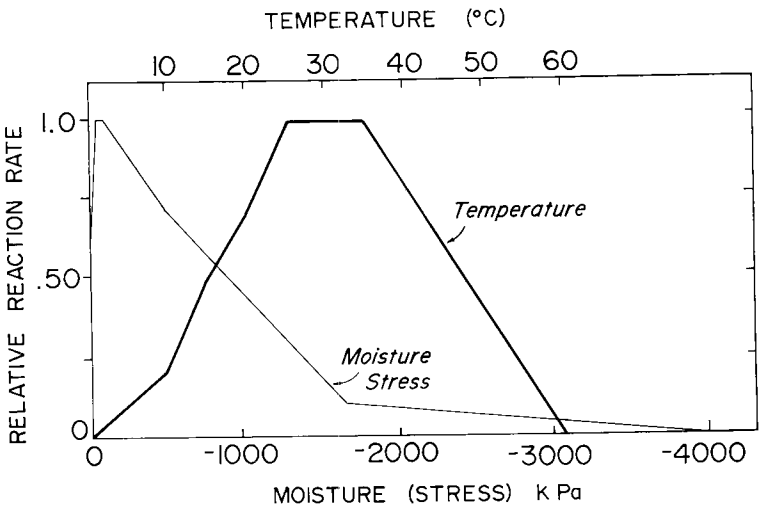

Fig. 3. Relative reaction rates for organic matter decomposition at various moisture stresses and temperatures (1 kPa = 0.01 bar).

Data for these graphs were derived from literature values (Van Veen 1977; Hunt 1977).

Organic Matter Protection by Soil Components

Large differences between the turnover rate of particular compounds in liquid, microbial cultures and in soil indicate that soil provides a measurable degree of protection against microbial decomposition. Amino acids added to liquid culture or soil had turnover rates of less than 1 day whereas soil amino acids produced during microbial growth in situ and incorporated into soil organic matter had turnover times as high as 2200 days (Sørensen and Paul 1971; Sørensen 1975).

Proteinaceous materials have been shown to be resistant to microbial attack through adsorption to inorganic colloids or organic matter (Simonart and Mayaudon 1961; Sørensen 1967; Pinck et al. 1954). Aringhieri and Sequi (1978) showed that the organic matter of aggregates stable to wet sieving was more tightly bound to the inorganic colloids and was less oxidizable by H_2O_2 than the organic matter of the more unstable aggregates. However, the biological meaning of sensitivity to oxidation by peroxides is unknown. Indirect evidence of the protective effect on organic matter by soil is obtained from data which show that disruption of soil results in an increase of the mineralization of both C and N (Hiura et al. 1976; Rovira and Graecen 1975; Craswell and Waring 1972; Waring and Bremner 1964).

To obtain indications of the magnitude of some of the main aspects of the protective process, i.e. the proportion of the organic compounds that is protected and how protection affects the decomposition rate, we analyzed the Sørensen and Paul (1971) data with the computer simulation model shown in Fig. 4. The decomposition rate constants of the non-protected amino acids and the acetate (initial concentration 2000 ppm C) were set at 0.3 day^{-1}; other parameters were the same as shown in Fig. 1. The best fit (Fig. 5) was obtained by assuming that 50–60% of the amino acids were protected, with the decomposition rate constant being 0.01–0.005 times the rate constant of the non-protected metabolites. Alteration of the decomposition rate constant for the amino acids had little effect during the simulation period being examined. This means that the level of stabilization and not the initial decomposition rate controlled

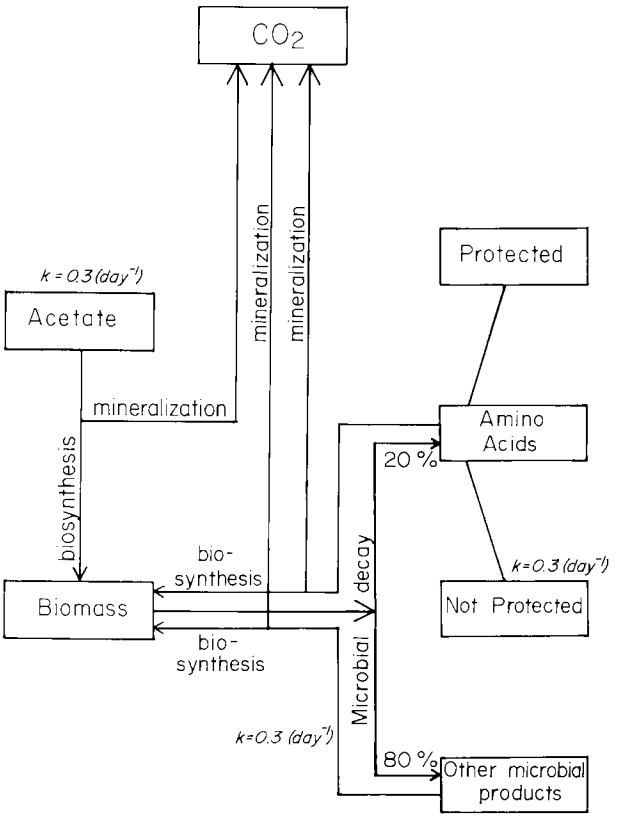

Fig. 4. Model used to quantify the effect of physical protection on microbial product stabilization in soil.

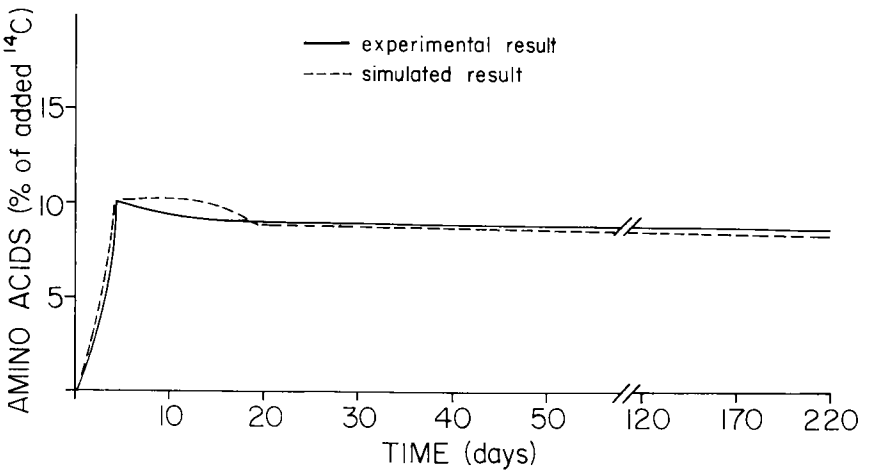

Fig. 5. Experimentally determined (Sørensen and Paul 1971) and simulated stabilisation of amino acids in Bradwell soil after addition of acetate-^{14}C.

the amount of amino acid present. However, the present knowledge of the quantitative aspects of this stabilization process is poor. In earlier work, Paul and Van Veen (1978) assumed that approximately 50% of the soil organic matter in Canadian soils was protected. This is in agreement with Anderson (1979) and Legg et al. (1971). However, the extent of protection will vary with the degree of aggregations and the clay content (Sørensen 1975).

Long-Term Organic Carbon Model

The previously mentioned concepts and data were integrated to model soil organic matter turnover in virgin and cultivated grasslands over extended periods of time (Fig. 6). The soil profile was divided into three layers, 0–15 cm, 15–40, cm and 40–80 cm; the decay constants were considered to be identical for all three layers (Table 3). Differences in biological activity were due to differences in organic matter input, temperature and moisture conditions. Exchanges between the layers were not included. All materials except the lignin fractions of aboveground plant residues and roots were considered to be taken up by the biomass and transformed into CO_2, biomass or metabolic products. The lignin fraction was considered to enter the decomposable native soil organic matter fraction. There it could be decomposed or it could supply aromatics for polycondensation, thus forming recalcitrant native soil organic matter. The decomposable native soil organic matter fraction also included microbial products such as amino sugars and amino acids.

According to data of Coupland et al. (1975), the native grassland at the Sceptre site in the Brown Soil Zone in Saskatchewan, which was used in this paper for the verification of the model, produced 2000 kg litter-

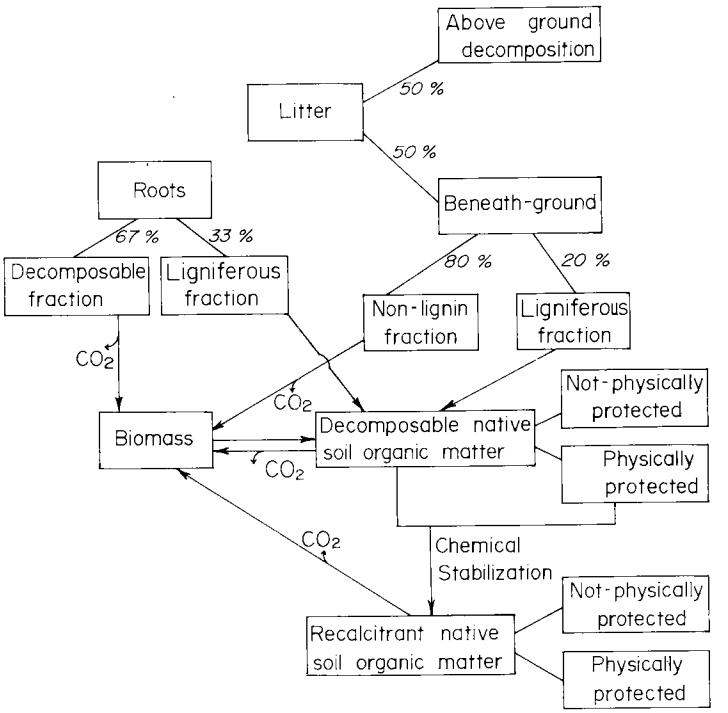

Fig. 6. Scheme of the long-term carbon turnover model.

Table 3. Organic matter levels and the decomposition rate constant for optimal conditions under grassland (Sceptre soil)

Depth (cm)	Organic matter level (kg C · ha^{-1}) 0–15	15–40	40–80	Decomposition rate constants (day^{-1})
Litter	800	200	—	8×10^{-2}
Root	5 300	2 100	2 900	8×10^{-2}
Biomass	700	400	150	3×10^{-2}
Decomposable organic matter, not protected	2 100	1 200	1 100	8×10^{-2}
Decomposable organic matter, protected	23 400	10 800	9 900	8×10^{-4}
Recalcitrant organic matter, not protected	7 500	5 000	4 500	8×10^{-6}
Recalcitrant organic matter, protected	7 500	5 000	4 500	8×10^{-8}

C · ha^{-1} · yr^{-1}, of which 50% entered the soil. Root-C input at this site was 1300 kg C · ha^{-1} · yr^{-1}, being 40% of the total photosynthate produced (Warembourg and Paul 1977). Under cultivated conditions, wheat plant residue-C and root-C input rates were 897 and 529 kg C · ha^{-1} · yr^{-1}, respectively (Campbell et al. 1977). Both the plant litter and the root-C were assumed to consist of an easily decomposable fraction, i.e. 63% of the root-C and 80% of the litter-C, and a recalcitrant ligniferous fraction.

Native soil organic matter was divided into three major fractions: the biomass, the decomposable organic matter comprising microbial products and the lignin fractions of litter and roots, and a recalcitrant fraction. The latter two fractions are affected by the physical and chemical protection previously discussed. The percentage of both fractions that is protected is indicated by a protection coefficient, FOPV. Protection leads to a decrease in the decomposition rate constant of the decomposable soil organic C fractions.

The transformation rates were considered to be independent of the size of biomass (first-order) because of its large size relative to the amount of available substrate. A model such as this, which includes microbial growth and metabolite production, requires gross in- and output process data; in most cases, only net results are available. This is especially true for the decomposition rates of the native soil organic C fractions considered. Radiocarbon dating measurements and ^{14}C plant residue incorporation studies of the fraction obtained after acid hydrolysis of the Sceptre soil indicate that the young organic matter fraction, i.e. the decomposable one, comprised 60% of the total soil organic matter content.

The rate constant for the recalcitrant organic C fraction was derived from data on the equivalent age (formerly referred to as mean residence time (MRT) (Martel and Paul 1974). The equivalent age from carbon dating of either the total soil or a particular fraction does not give turnover rates. However, equivalent age and turnover time are similar for old recalcitrant materials. Jenkinson and Rayner (1977) calculated a turnover time of 2857 years for the Rothamsted recalcitrant organic matter which has a MRT (equivalent age) of 2565 years. The decomposition rate constant, k, can be calculated from the turnover time, T, according to:

$$k = \frac{1}{T} \qquad (3)$$

The equivalent age differs significantly from the turnover time for young materials with a fast turnover time. Jenkinson and Rayner (1977) calculated a turnover time of 2.4 yr for the biomass; the calculated radiocarbon age was 25 yr because of the utilization by the microorganisms of some C from the recal-

citrant fraction that was thousands of years old.

The model included the option of calculating average temperatures (°C) and moisture tensions (kPa) per layer at any time, depending on the integration step. Average moisture tensions under both cropped and fallow conditions for the three layers considered in the model are shown in Fig. 7a-c. Temperatures of the subsurface layers were assumed to be proportional to that of the surface horizon (Fig. 7a), 0.8 and 0.6 of the surface soil temperature for the second and third horizons, respectively. The data on soil moisture tensions and temperature were derived from the data for the Matador site obtained during the IBP project (MacDonald et al. 1973; Ripley 1972). The temperature and moisture effects were taken into account using reduction factors derived from Fig. 3. The combined effect was accounted for by multiplication of the two reduction factors with the rates for optimal conditions.

The S/360 CSMP 3 (System 360 Continuous System Modelling Program, 3rd version) was used as a computer language. The rectangular method of integration uses intervals of 0.1 (yr).

Model Performance and Discussion

An important test of the validity of the model is the simulation of the organic C content of the native grassland soil. It is known to be constant or increasing very slowly. Figure 8 shows that the organic C level of the three layers were calculated to be nearly constant in time, with only a slight increase in the uppermost layer. In preliminary modelling studies, we divided the soil into layers of 0–10, 10–40, and 40–80 cm. Under these conditions, the C of the second layer dropped significantly below the experimentally determined values. The use of a 0- to 15-cm upper layer which coincided with a depth of the Ah horizons lead to the equilibrium predictions shown.

The effect of cultivation of the surface horizon on the organic C level in the separate layers is also shown in Fig. 8. Under grassland conditions, 50% of the organic matter was considered to be protected. Under cultivation, this value was reduced to 20% for the 0- to 15-cm layer and 40% for the lower layers. The model was very sensitive to the estimates used for physical protection (Fig. 9). Cultivation, at least initially, should not change the extent of adsorption by clays. Disruptions of aggregates should be one of the major factors that enhances mineralization of both C and N. Hiura et al. (1976) found a strong correlation ($r = 0.98$) between the increased mineralization of N after grinding and the clay/humus ratio. A soil with a clay humus ratio of 2 showed a 20% increase in N mineralization after grinding. A soil with eight times as much clay as humus showed a 100% increase in N mineralization after grinding. However, no field data quantifying the effect of disruption of soil by cultivation on mineralization were found. Cultivation further results in a single large input of C in the form of the large reservoir of grass and forb roots. The rapid decrease in organic matter at the beginning of cultivation is in large part due to the degradation of these roots.

Sensitivity analyses of this model indicated that moisture had a great impact on the model performance. However, moisture also affects crop yield and thus C input. Therefore, a true test of the moisture effect would involve a simultaneous calculation of the effects of moisture on crop growth with its consequent effects on above- and beneath-ground litter inputs and the possible alteration of organic matter availability in the presence of plant roots. This is supported by model output of the McGill et al. (1980) model, PHOENIX, which shows that moisture has a profound effect on soil microbes and plants and that moisture, therefore, is a very critical parameter in the description of C and N dynamics in soil.

The present model is a deterministic description of events and processes involved in soil organic matter stabilization. For ease of calculation, discontinuous processes such as crop residue input and rainfall were included either as a process occurring only once or as a

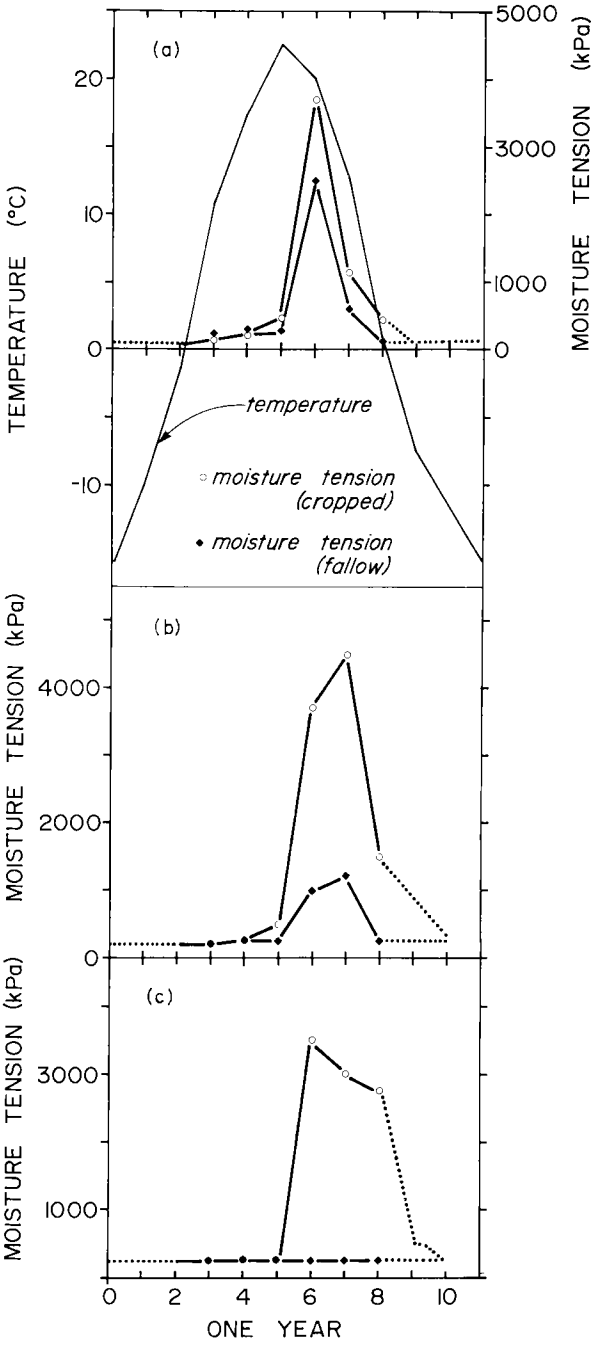

Fig. 7. (a) Soil temperature (——) and soil moisture tensions for cropped (o——o) and fallow (x——x) conditions of the 0- to 15-cm layer of a Sceptre soil. (b) Soil moisture tensions of the 15- to 40-cm layer under cropped and fallow conditions of a Sceptre soil. (c) Soil moisture tensions of the 40- to 80-cm layer under cropped and fallow conditions of a Sceptre soil (data derived from unpublished measurements during IBP project).

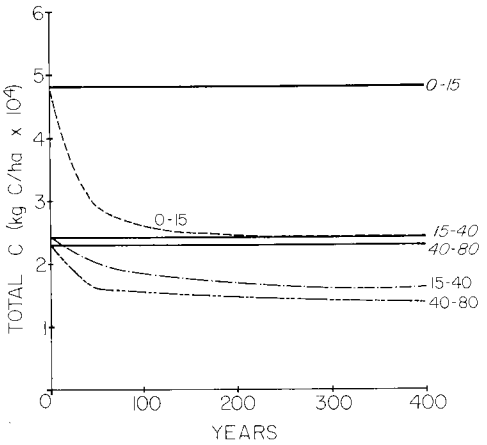

Fig. 8. Effect of cultivation on the total C content of a grassland soil (Sceptre). Factors utilized: continuous cropping, physical protection of virgin sites 50% of cultivated, 20% in the surface layer, 40% in subsurface.

continuous process. Early versions of the model described crop residue input as a discontinuous process occurring only during the growing season. However, on a long-term basis, similar results were obtained by the use of a simpler model which added the stated amount of plant residues as a continual process.

This model does not include a description of stochastic events. In a second paper (Voroney et al. 1980), we include losses of organic matter due to erosion, i.e. runoff. It is known that the largest losses occur due to a single very heavy rain storm or snowmelt. Erosion, therefore, would be described more realistically with a stochastic rather than a deterministic model. However, the stochastic description requires much more data than are presently available. Modern simulation languages such as the CSMP utilized in this study contain features such as a random number generator which allows for a description of stochastic events. The question of whether a deterministic or stochastic model should be used probably will not be decided by the available mathematical concepts but on the basis of the objectives of the model and the availability of data.

Incompleteness of the description, due primarily to a lack of data, limits the predictive power of the model; limitations include

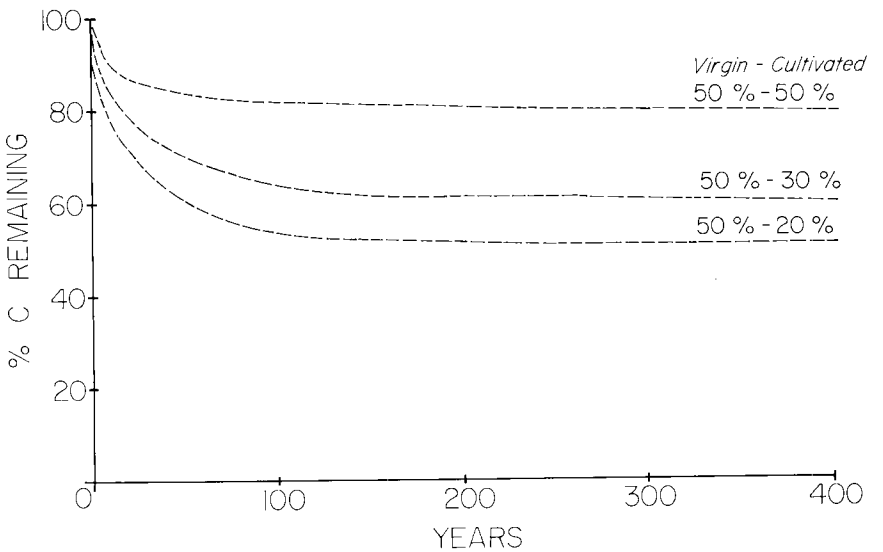

Fig. 9. Effect of changing the physical protection factor on the total C content of the 0- to 15-cm layer of a Sceptre soil under continuous cropping (50%–50% refers to protection in virgin and cultivated soils, respectively).

the interactions of crop growth and residue input with soil organic matter formation, effects of nutrients such as N, P and S, and transport of soluble organics through the soil profile. Changes in soil organic matter content will influence crop growth which in turn will affect plant residue production and the C input into soil. The present model, which considers a constant crop residue C input, would therefore overestimate the annual C input as the soil organic matter declines (Fig. 8) unless other management practices overcome this deleterious effect.

Although outputs from this and other similar models (e.g. McGill et al. 1980) will no doubt be utilized in predicting future management practices and fertilizer input requirements, we consider the predictive value to be secondary to the primary goal of obtaining a better understanding of the complex system under study. The model has allowed us to test many of the concepts derived from the review of the literature on organic C decomposition. The major points considered to arise from the analysis are:

(1) Plant and root residues, with the exception of lignifierous material, are transformed by the biomass.

(2) Growth and turnover rate data from ^{14}C residues decomposition studies have to be recalculated to produce values for mathematical analysis; unless corrected for microbial production, the results lead to low decomposition rates.

(3) The lignin fraction can enter the non-recalcitrant organic C where physical chemical reactions with microbial products can form resistant organic matter. Since this non-recalcitrant fraction is decomposed by the biomass, only a portion of the original lignin enters the recalcitrant fraction without microbial transformation.

(4) Microbial products also enter the recalcitrant fraction where microbiologically produced aromatics can also be involved in humate formation. Microbial production of compounds which directly enter the recalcitrant fraction without chemical stabilization might be realistic, but is not considered in this model.

(5) The efficiency of C use by the biomass and biomass turnover rates are of major importance in calculating microbial production and organic matter dynamics. Data for gross growth efficiency appear to fit the pure culture microbiological data. However, soil microbial turnover rates and maintenance energy data must be obtained if we wish to obtain a proper understanding of the fate of C and N and other microbially affected nutrients in soil.

(6) Protection and chemical recalcitrance do not result in different soil organic matter fractions as suggested by the model of Jenkinson and Rayner (1977). Our mathematical analysis assumces protection such as adsorption and entrapment within soil aggregates for both chemically resistant and easily decomposable organic matter.

(7) The equilibrium level of soil organic matter is more dependent on the turnover of products of decomposition, i.e. the recalcitrant fraction, than on the decomposition rate of the plant residues added to soil. This is in agreement with the statement made by Jenny in 1930 and quoted by Joffe (1955) that the long-term organic matter levels of soil are primarily dependent on the zonality principle; management practices of cultivated soils can alter soil organic matter levels as long as the practice is maintained. However, on termination of the practice, levels will reapproach their long-term equilibrium, depending on soil type and climate.

Table 4. Annual input rates of root and litter C under virgin and grassland conditions

	kg · ha^{-1}	
Cropping system	Litter-C	Root-C
Virgin	1000	1300
Crop-Fallow	1264-126	746-75
Crop-crop-fallow	1264-906-125	746-530-75
Continuous crop	897	529

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