THE USE OF TRACERS TO DETERMINE THE

DYNAMIC NATURE OF ORGANIC MATTER

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Early experiments with ^{13}C, ^{14}C and ^{15}N established the high
rate of internal cycling of soil organic matter and reintroduced the
concept of an active and passive phase in soil humus turnover. Later
studies confirmed non-tracer investigations indicating that the per-
cent decomposition of added materials is relatively independent of the
rates of addition but dependent on its form and composition. The
initial decomposition rate, plus the stabilization of microbial
products in soil, must be taken into account when interpreting degra-
dation of ^{14}C enriched straw, roots, microbial tissue and specific
components or in carbon dating naturally occurring ^{14}C. Where initial
decomposition data could be described by first order kinetics we
calculated decay rate constants with and without the consideration of
biosynthesis. Decay rates for laboratory systems were twice those
for tropical field soils and eight times those calculated for tem-
perate climates. The data were used in a model incorporating the
concepts of microbial biosynthesis and recalcitrant and decomposable
soil organic fractions which can both be physically protected. This
realistically described the behaviour of soil-C in a Canadian grass-
land before and after cultivation.

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THE USE OF TRACERS TO DETERMINE THE DYNAMIC NATURE OF ORGANIC MATTER

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HISTORY OF TRACER RESEARCH

The advent during the 1940's of tracer research in organic matter studies came at a time when the principles affecting plant decomposition and the effects of cultural practices on total organic matter contents had been reasonably well investigated (Greaves and Carter 1920; Phillips et al. 1935; Guha Sircar, De and Bhowmick 1940). Uncertainties centered around the effects of plant decomposition (Waksman and Gerretsen 1931; Russell 1937) and C/N ratios (Engel 1931; Salter 1931; Rubins and Bear 1942) on degradation rates and stabilization values. The possibility of soil population turnover, with the subsequent release of N on decomposition, had been postulated (Richards and Norman 1931). However, normal methods of residue-C and N addition followed by mineralization studies could not separate the various aspects of the nutrient cycles (Pinck, Allison and Sherman 1950). Norman (1946) in reviewing the then current status of soil microbiology said "The availability of the stable nitrogen isotope N^{15} and the carbon isotope C^{13} will make it possible to verify quantitatively the various nitrogen transformations in relation to the carbon cycle and should aid greatly in establishing the forms of nitrogen present in soil".

The Pioneers

The initial investigation utilizing tracers for soil organic matter studies (Norman and Werkman 1943) labelled soybeans by growing them on ^{15}N-nitrate. The addition of this material to the soil and growth of a new crop showed that 26% of the organic ^{15}N applied in the tagged soybeans was recovered by the subsequent crop. Subsequent work (Broadbent and Norman 1946; Broadbent and Bartholomew 1948; Broadbent 1947) established the principles for utilization of ^{13}C-^{15}N tracers. It was concluded that decomposition of an available substrate was dependent on the amount added and increased the release of native soil C and N, i.e. priming. Studies with ^{14}C also noted the increased mineralization of soil C (Bingeman, Varner and Martin 1953; Kirkham and Bartholomew 1954). Similar increased turnover of soil organic materials were indicated with ^{15}N (Bartholomew and Hiltbold 1952; Hiltbold, Bartholomew and Werkman 1951). The reiteration of the priming process which Löhnis (1926) had postulated after experiments with green manure involved much of the earlier work on isotopic studies in soil organic matter.

Jansson (1955) carried out decomposition studies with straw incubated with ammonium nitrate in which one set of samples contained

labelled ammonium and other labelled nitrate. It was then possible to trace the N from the three original sources, added ammonia, added nitrate and straw N at different stages in the decomposition process. It was concluded that equilibration was caused by a cyclic mineralization-immobilization turnover in which the organic straw N and ammonia N participated whereas the nitrate N was practically excluded.

Development of Concepts Concerning the Dynamic Nature of Soil Organic Matter

Broadbent and Stojanovic (1952) and Stojanovic and Broadent (1956) in attempting to obtain more specific information about the rate of mineralization and immobilization applied the equations of Kirkham and Bartholomew (1954, 1955) to their data. This study appears to be the first in which a mathematical analysis was conducted together with ^{15}N. Other studies on organic N mineralization (Wallace and Smith 1954) showed subsequent loss of the mineralized N by denitrification and increased utilization of non-tagged N in the presence of ^{15}N (Walker, Adams and Orchiston 1956): the tagged N being removed by microorganisms and replaced by non-tagged N.

Jansson (1958) defined the preferential utilization of ammonia by microorganisms and the great extent of mineralization-immobilization. He showed that the priming reaction, which caused such a controversy during the early years of tracer work, was influenced by the general cycling of the nutrients. Previous authors had suggested the possibility of different fractions of soil organic matter turning over at different rates. Jansson's cross-wise tagging and mathematical treatment utilizing Kirkham and Bartholomew's 1954 and 1955 equations, established the presence of an active and passive phase. He found 10-15% of the N to be active. The concept of a passive and active organic phase and of ammonia being more closely related to microbial synthesis than nitrate is shown in Fig. 1.
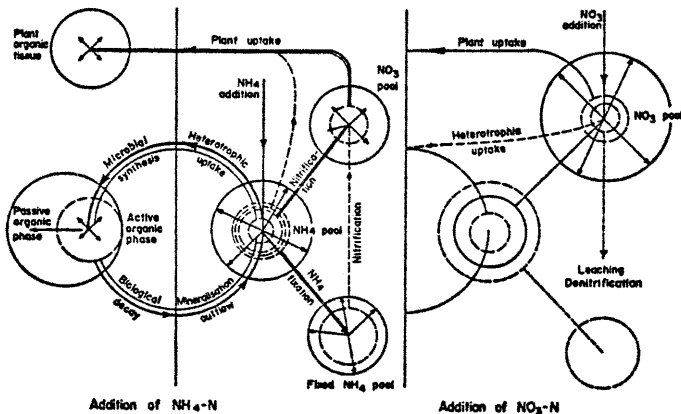

Fig. I. Relations between the internal nitrogen cycle and addition of inorganic nitrogen to the soil. Nitrifying soil, net mineralisation conditions. (Jansson 1958)

Development of Tracer Techniques

During the 1960's, experimental techniques for labelling and measurement of isotopes in soil organic matter studies were detailed (IAEA 1966, 1968). Most labelling is conducted by $^{14}CO_2$ assimilation via the leaves in a closed system. Growth to maturity is required so that uniform labelling occurs (Chekalov and Illyuviyeva 1962; Sauerbeck and Führ 1966; Smith, Allison and Mullins 1963; Scully et al. 1956). More recently, specific components of plants have been labelled by injection of ^{14}C-precursors (Crawford et al. 1977; Martin and Haider 1977).

Counting of enriched materials is now routinely done with scintillation equipment. The availability of techniques for conversion of large amounts of naturally occurring C into benzene for counting in a scintillation counter has made it possible for a number of laboratories to undertake carbon dating. However, gas counters for C_2H_2 and CO_2 also are still employed. Present methods for plant labelling and counting of soil organic matter as well as carbon dating have recently been described (IAEA 1976).

INTERPRETATION OF TRACER DATA ON ORGANIC MATTER DYNAMICS

The driving force for much of the organic matter turnover in soil is the microbial search for the energy tied up in reduced C compounds. An understanding of this process requires a knowledge of: 1) the chemistry of the soil organic matter constituents, 2) levels of input of plant and animal residues, 3) rate of decomposition of these residues, 4) the extent of stabilization of microbiologically produced decomposition products, and 5) the availability of mathematical concepts and modelling techniques to help interpret the data.

The following discussion will consider each of the fractions, i.e. plant residues, root exudates, microbial biomass, specific plant and microbial components, and resistant organic components under separate headings. A complete discussion involving N and C is impossible in one review. Comprehensive reviews (Hauck and Bremner 1976) and bibliographies (Hauck and Bystrom 1970) have been developed for ^{15}N investigations in soils. This paper concentrates on the use of C isotopes, either ^{14}C enriched materials, ^{13}C as a natural tracer in the atmosphere or as an enrichment, and ^{14}C occurring in the atmosphere both from cosmic radiation and from the more recent bomb tests.

Plant Residue Decomposition

Initial work with ^{13}C (Broadbent 1947; Broadbent and Bartholomew 1948) concluded that small quantities of plant residues decomposed more rapidly than large quantities. Pinck and Allison (1951) summarizing non-isotopic work on this subject, however, concluded that the percent decomposed was nearly always independent of the quantity added if the C addition did not exceed 1.5% of the soil dry weight and if decomposition was allowed to continue for at least 3 to 6 months. The non-tracer data were later confirmed with tracers (Stotzky and Mortensen 1958; Jenkinson 1965, 1977; Oberländer and Roth 1968). After extended incubation periods, the proportion of added plant material retained in various soils under different climatic conditions using different plant materials and rates of addition is very similar (Führ

and Sauerbeck 1968; Jenkinson 1964; Sauerbeck and Gonzalez 1977). This is often due to a similarity in production and stabilization of soil organic matter rather than to equal rates of decomposition (Paul and McLaren 1975). The curves in Fig. 2 show a wide divergence in original decomposition rates. The slowest process is represented by the Saskatchewan grassland which is affected by drought in summer and by extended periods of frost. Sauerbeck and Gonzalez (1977) found similar rates for a number of German soils and those in Costa Rica. The data for Rothamsted are similar to those for Germany, but different for Nigeria. Jenkinson and Ayanaba (1977) found that the Rothamsted and Nigerian data could be super.imposed if the Nigerian time scale was divided by a factor of four.
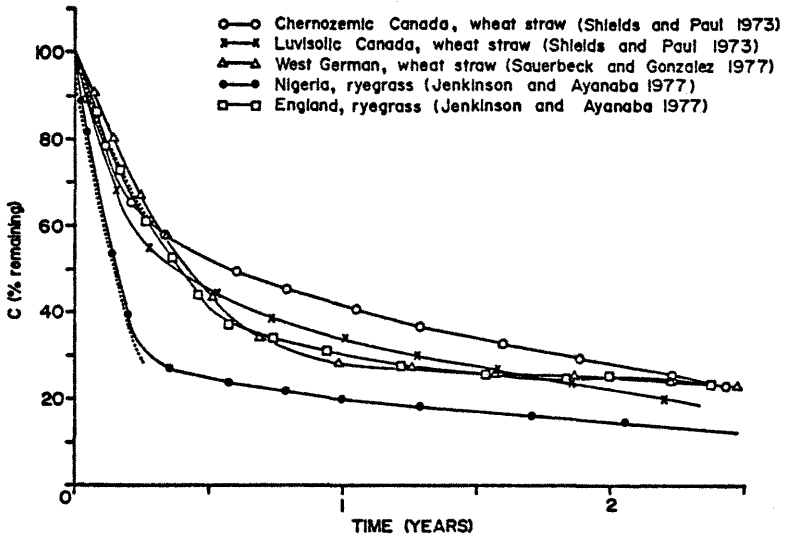

Fig. 2. Residual carbon left after field incubation of wheat straw and grass residues in different environments. The dotted lines (·······) represent output of the model, (Fig. 9) describing decomposition of complex substrates

Attempts to relate decomposition to plant composition have led to recalculation of some of the extensive non-tracer data. The data of Waksman and Tenney (1928) have been fitted (Herman, McGill and Dormaar 1977) to equations including carbon and nitrogen content and lignin and carbohydrate composition:

$$\frac{1}{CO_2 \text{ evolved}} = \frac{1}{CH_2O \text{ loss}} = \text{lignin-C loss} = \frac{[\frac{C}{N} \text{ straw} \cdot \% \text{ lignin}]}{\sqrt{\% \text{ carbohydrates}}}$$

Hunt (1977) found that the best equation describing Pinck et al.'s (1950) data on decomposition of a wide range of plant residues to be $S_O = 0.070 + 1.11 \sqrt[3]{(N/C)}$, where S_O is the initial proportion of easily decomposable constituents and N/C the N to C ratio, with $r^2 = 0.98$. Both equations include the C/N ratio but the relationship of Herman et al. (1977) takes more plant residue characteristics into account.

Lespinat et al. (1976) who summarized plant decomposition studies on various crops found that different soil types with varying concentrations of clay and organic matter resulted in carbon mineralization rates ranging from 30 to 81% for uniformly labelled plant materials added at rates ranging from 77 to 784 mg $C \cdot 100$ g^{-1} soil. In their experiments, leaves, whole plants and water soluble extracts mixed with Oxisols, Mollisols and Endosols gave no differences in mineralized C after two weeks. Differences, however, were significant during the first two weeks particularly for water soluble extracts and stem and leaves.

Pal and Broadbent (1975) found that turnover times of uniformly labelled immature rice straw ranged between 0.8 and 3.4 years depending on loading rate and soil type. Addition of plant material resulted in a net loss of C. Thus, actual priming in addition to increased turnover of organic constituents had occurred in their experiments. Immature materials often used in laboratory studies yield different decay values and stabilization rates than do mature residues.

Decomposition of Roots and Root Exudates

Roots constitute a major C reservoir in natural ecosystems and play a major role in continuously cropped systems where most above ground material is removed. Some work has indicated similar rates of decomposition for above and beneath ground materials (Jenkinson 1971, 1977); others have indicated slower rates for roots (Nyhan 1975). Root exudates are an additional source of C for microbial growth and soil organic matter production. Martin (1977a, b) showed that 5 to 15% of the photosynthically fixed C was excreted to soil by roots. In an experiment with wheat, 56% of the fixed C remained above ground, 28% was found in the roots, 6.6% in the soil and rhizosphere respiration accounted for 9.2%.

Wheat labelled at the heading stage in Saskatchewan had 52% of the labelled C in the shoots, 25% in the shoot bases and the roots, and beneath ground respiration accounted for 23% (Warembourg and Paul 1973). Labelling at the dough stage resulted in 69% of the photosynthate being present above ground, 14% in the roots and shoot bases, and 17% was lost by respiration. These data therefore are similar to that of Martin's (1977a, b) except that in the latter case, negligible C was found excreted to the soil matrix. Lespinat et al. (1975a, b) found a close relationship ($r = 0.94$) between the quantity of ^{14}C assimilated by the plants and that excreted by the roots with old maize plants excreting more C than young plants. They found an average of 0.7% of the total photosynthate excreted.

Sauerbeck and Johnen (1977) found that ^{14}C measurements resulted in 20% higher recovery of root material than mechanical determinations.

During their experiment, 20% of the total soil respiration was attri-
buted to root respiration and 80% came from decomposition. The total
respiration was three times as great as the root ^{14}C remaining at the
end of the experiment.

Natural grassland labelled under field conditions retained 52%
of the assimilated C above ground and 36% in the shoot bases and roots,
with 12% being respired during and immediately subsequent to the la-
belling period (Warembourg and Paul 1977). A half-life of 107 days
for the C in the root-soil system indicated that more than half the
residual root C was decomposed in one growing period. The work of
Dahlman (1968) indicated a turnover time of 3 to 4 years for roots to
grow, die and decompose. The turnover of living roots in a grassland
system, therefore, varies with the percentage of fine root hairs and
structural roots on the perennial plants.

Degradation of Specific Components

Aromatic compounds such as complexed phenolic and carboxylic
acids comprise 50% of the total soil C. Complexes of amino acids
account for 20%, whereas carbohydrates comprise 10 to 20%. The re-
maining 10 to 20% is found as a mixture including long chain fatty
acids, alkanes, lower fatty acids, cell wall components such as techoic
acids, nucleic acids, etc. Organic matter composition is remarkably
similar from soil to soil over a broad range of soils (Schnitzer 1977).
There have been a large number of studies which determine the label-
ling and turnover of classical soil fractions such as fulvic acids,
humic acids and humin (Jenkinson 1971; Swift and Posner 1977; Bailly,
Nkundikije-Desseaux and Agbeko 1977). Physical separation of labelled
materials associated with soil minerals also has been found useful in
organic matter dynamics studies (Paul and McGill 1977). However, most
meaningful turnover data probably come from techniques based on
measurement of specific chemical substances. Generally, fulvic acids
contain a greater proportion of phenolic aromatics whereas humic acids
contain more carboxylic acids (Flaig, Beutelspacher and Rietz 1975).
Fulvic acids also tend to be lower in molecular weight and contain the
soil carbohydrates soluble in sodium hydroxide. The humin contains
the carbohydrates insoluble in sodium hydroxide (Gückert 1972; Salfeld
and Söchtig 1977).

Simonart and Mayaudon (1961, 1962) fractionated the chemical
components of plant and microbial materials and studied the degrada-
tion of these materials. They showed that the ^{14}C of most components
rapidly entered the fulvic, humic and humin fractions and that pro-
teins could be stabilized by adsorption to soil humic acids (Mayaudon
and Simonart 1958, 1959, 1963; Mayaudon 1968). Plant pigments such as
chlorophyll and B-carotene were converted primarily to non-hydrolyzable
humins and hydrolyzable humic acids, whereas labelled cellulose, lig-
nin, vanillin, syringaldehyde and parahydroxybenzaldehyde were conver-
ted into hydrolyzable and non-hydrolyzable fractions of humic acids.

Carbohydrates.

Carbohydrates are particularly useful for following the turn-
over of individual plant or microbial constituents and for measuring
the stabilization of newly produced products (Cortez 1977). Individual

sugars are rapidly transformed. Mayaudon (1971) using radiorespiro-
metry over short time intervals found that the decomposition of glu-
cose followed first order kinetics. The initial mineralization rate
was temperature dependent rising from 1.6 µg $C \cdot min^{-1} \cdot 100 \ g^{-1}$ soil at
$4°C$ to 10.8 µg $C \cdot min^{-1} \cdot 100 \ g^{-1}$ soil at $37°C$. Also, the mineralization
rate varied from 3.1 at pH 5 to 6.7 µg $C \cdot min^{-1} \cdot 100 \ g^{-1}$ soil at pH 7.
Microorganisms contain different constituent monosaccharides than do
plant residues. Mannose is widespread in fungi, fucose and rhamnose
are frequently observed (Webley and Jones 1971; Wagner and Tang 1976).
In bacteria, the primary sugars are glucose, fructose, mannose, galac-
tose, rhamnose and fucose. Xylose and arabinose are not major com-
ponents. When hemicellulose containing residues are degraded, the
decrease in xylose and arabinose and the production of mannose is a
measure of microbial polysaccharide production and stabilization
(Table 1). Glucose was a constituent of the hemicellulose, but was
produced during microbial growth. Its initial degradation and stabil-
ization, therefore, involved a great deal of internal cycling.

Table 1. Alteration in sugar composition during incubation
of ^{14}C hemicellulose (Cheshire et al. 1974)

| Sugar | Original | | % of original | | | |
| | Amount (mg g^{-1}) | Specific activity (µCi g^{-1}) | Time (days) | | | |
			14	56	112	443
Rhamnose	0.8	3.1	--	44	68	60
Fucose	0.3	23.8	--	6	--	--
Arabinose	1.3	24.4	22	5.7	6.8	4.9
Xylose	2.6	128.6	19	5.1	4.4	2.3
Mannose	1.5	0.6	710	400	680	450
Galactose	1.6	8.6	54	30	11	17
Glucose	4.8	6.5	176	145	109	94
Reducing sugar as glucose	17.5					

Determination of ^{14}C activity of humic acid fractions brought
about by synthesis of aromatic structures from added ^{14}C carbohydrates
indicated that only 8-16% of the ^{14}C was found in aromatic constitu-
ents. This indicated that 92-84% of the residual ^{14}C from carbohy-
drates incorporated into humic acids was of a non-aromatic nature
(Martin et al. 1974).

Aromatics.

The turnover rate of aromatics is a major factor in determining

soil organic matter dynamics. To study the degradation of aromatics natural ligno-celluloses containing ^{14}C in either lignin or cellulose components were prepared by feeding plants with ^{14}C phenylalanine or ^{14}C glucose (Crawford, Crawford and Pometto 1977). Lag periods were very pronounced for lignin oxidation. Rates of CO_2 evolution for the ^{14}C cellulose component increased rapidly after short lag periods. The degradation rate for the lignin was one-fourth that of the associated cellulose indicating that even closely associated materials decompose at different rates.

The degradation of coniferyl alcohols, ferulic acid and caffeic acid, which have similar structures to lignin subunits, have been studied by Martin and Haider (1977). The [14]COOH group of many aromatics is removed by decarboxylation with little or no incorporation into soil organic constituents (Fig. 3). This figure also shows the relative degradation and stabilization rates for glucose, simple amino compounds and the ring ^{14}C of aromatics. Incorporation of the caffeic acid into humic-like polymers stabilized all carbons but the [14]COOH still showed preferential decarboxylation (Haider and Martin 1975).
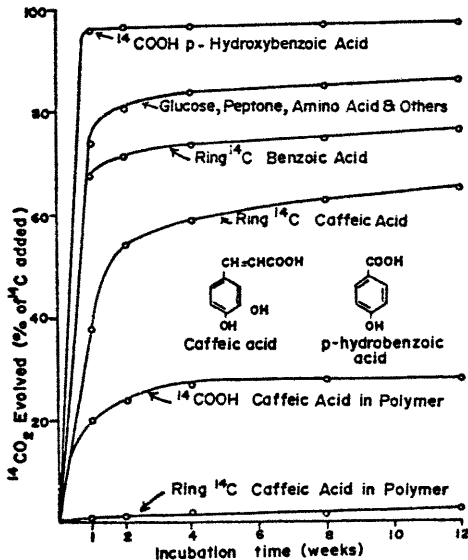

Fig.3. Decomposition of specifically ^{14}C-labeled benzoic and caffeic acids, caffeic acid linked into phenolic polymers, and several simple organic compounds in Greenfield sandy loam (Haider and Martin 1975)

Martin and Haider (1977) showed that the bulk of the partially degraded coniferyl alcohol C incorporated into lignin was recovered in the humic acid fraction. Humic acid obtained by sodium hydroxide

extraction and precipitation with acid, therefore, contained both humic acid derived ^{14}C and partly decomposed lignins. Hydrolysis with 6 N HCl removed 38% of the ring ^{14}C and 45 to 47% of the side chain and OCH[3] groups of the free alcohols that had been incubated in soil. This suggests that the majority of the side chain lignin fragments were present in microbial products such as proteins and polysacchar-ides, while more of the ring C was present in the non-hydrolyzable aromatic components. Andreux et al. (1977) also found that specific labelled catechol polymers formed structures similar to residues of humic acid after acid hydrolysis. The first five days of incubation in soil saw active decarboxylation of the ring derived OCH[3] and pre-ferential degradation of the glycine incorporated in the less stable, polymerized fraction. The second stage was characterized by very slow mineralization of stable polymers resulting from physico-chemical stabilization.

Amino compounds.

Amino acids comprise about 20% of the soil C and 35 to 40% of the soil N but contribute a larger percentage of the potentially min-eralizable N (Stewart, Porter and Johnson 1963a, b; Bremner 1965). A large number of labelled amino acids are formed during microbial growth on materials such as carbohydrates (Sørensen 1967, 1969) and ace-tate (Paul 1976). An example of the production, stabilization and subsequent degradation of amino acids and amino sugars is shown in Fig. 4. Both amino acids and amino sugars were rapidly produced by
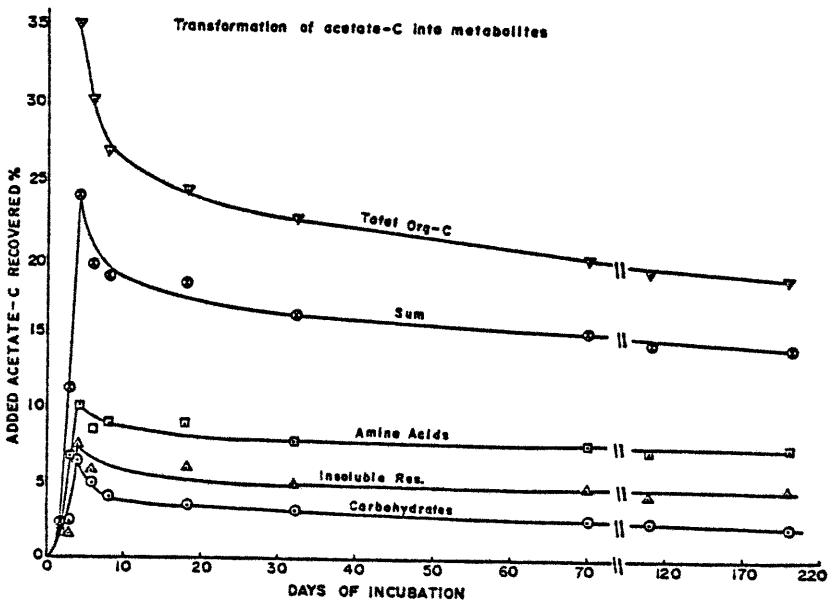

Fig. 4. Recovery of labelled carbon from soil during decomposition of ^{14}C-labelled acetate. (Sørensen and Paul 1971)

day 4 at the peak of microbial activity after the addition of ^{14}C ace-
tate and ^{15}N ammonium sulphate. At this time, amino acids accounted
for 59 µg·g^{-1} labelled N out of a total of 187 µg organic labelled N·
g^{-1} soil, whereas amino sugars accounted for 20 µg N·g^{-1} soil. At day
71, amino acids accounted for 44 and amino sugars for 9 µg N·g^{-1} soil
out of a total of 155 µg N·g^{-1} soil remaining. The decay of these two
constituents had contributed 54% of the net nitrogen mineralized be-
tween days 4 and 71. The unidentified hydrolyzable fraction had in-
creased in percentage to 50% of the total [15]N. Its turnover, however,
accounted for only 25% of the mineralized [15]N. The half-life of amino
sugars ^{14}C was 224 days during the latter stages of incubation (90 to
268 days). The ammonia released on hydrolysis had a half-life of 940
days and the amino acids a half-life of 2700 days under these labora-
tory conditions (McGill, Paul and Sørensen 1974).

Data similar to the above laboratory findings have also been
obtained under field conditions (Legg et al. 1971). Under these con-
ditions it was hypothesized that half of indigenous N in soil was bio-
logically unavailable because of inaccessibility to microorganisms of
organic N compounds or complexes incorporated within aggregates. Acid
hydrolysis released this N. Thus, the use of N released on acid hy-
drolysis results in an over-estimation of turnover rates. Nitrogen
turnover rates after acid hydrolysis are best calculated on the basis
of the turnover of C and calculations based on C/N ratios of the
fractions before acid hydrolysis.

It is generally agreed that peptides are less sensitive to de-
composition than amino acids (Haider and Martin 1975). Although link-
age of the amino acids into the synthetic polymers greatly reduces the
availability to soil organisms, the amino portions of the soil organic
matter molecules are more susceptible to decomposition than the [14]C
labelled phenolic portions. In addition, data on the decomposition of
[14]C labelled algal protein indicate that mixing with the freeze dried
humic acids reduced decomposition by over 50% (Verma, Martin and
Haider 1975). These data substantiated Simonart and Mayaudon's (1961)
conclusions that proteins were stabilized by adsorption to humic
substance.

USE OF ATMOSPHERIC CARBON ISOTOPES

The two naturally occurring minor isotopes of carbon, ^{13}C which
comprises 1.1%, and ^{14}C which account for 1 molecule in 10^{12} of the
atmospheric-C offer a number of opportunities for measuring C dynamics
when space or time limitations restrict the use of enriched materials.
Humus in soils developed from plant residues which utilize the Calvin
photosynthetic system has shown consistent ^{13}C/^{12}C ratios, with a
slightly higher ^{13}C content in the humic acids than in the vegeta-
tion from which they were produced (Campbell et al. 1967) and
with the humin showing the greatest discrimination ($\delta = -3.9\%_o$) rela-
tive to wheat (Martel and Paul 1974). Similar uniformity of various
humic fractions with regard to the ^{13}C content indicates that no grad-
ual transformation of organic compounds from one class to another
occurs, i.e. fulvic acids are not converted to humic acids (Nissenbaum
and Schallinger 1974). Scharpenseel (1977) utilized the relative [13]C
content of soil organic matter to discount the participation of litho-

genic inorganic carbonates in soil organic matter formation and to argue against the possibility of biologically inert C being present within the soil as suggested by Gerasimov (1974).

The ^{13}C content of soil can be used to identify the sources of organic C in soils or sediments. Vascular plants separate into two groups relative to their ^{13}C isotope composition. Those with the C_3 (Calvin) pathway of photosynthesis have ^{13}C contents δ = -22 to -33 relative to reference "Belemnite carbonate". Plants which follow the C_4 (Hatch-Slack) mechanism contain carbon with δ = -10 to -20 (Bender 1971). Haines (1976a, b), therefore, could differentiate between terrestrial C which came primarily from C_3 plants and decomposition products of Spartina which is a C_4 plant growing in estuaries. Similar comparisons on specific sites where an intermixing of known sources of C_3 and C_4 plant vegetation occurs may lead to other identifications of the specific C source in soil organic matter.

Carbon Dating

Since the development of carbon dating in 1949 it has been used to investigate buried profiles in soil pedology and organic matter dynamics. Scharpenseel and Schiffmann (1977) reviewed soil carbon dating on the basis of 2,000 to 3,000 dates available for terrestrial and hydromorphic soils. They attribute the first soil carbon dates to Broecker, Kulp and Tucek (1956) and De Vries (1958) who investigated the contaminating effects of soil constituents on fossil soils used for archeological investigations. Soil pedological investigations have included C movement and residence in podzols (Guillet 1972; Tamm and Holmen 1967; Gerasimov and Chichagova 1971; Rapaire and Turenne 1977).

The use of flotation to remove plant constituents combined with acid hydrolysis and peptization in NaOH results in meaningful separations for carbon dating. Table 2 shows that the mean residence time (MRT) of a brown Chernozemic soil was 350 years before treatment (Martel and Paul 1974). The fraction containing the greatest amount of ^{14}C (δ = +243‰) was the material floated on $ZnBr_2$ with a density of 2.0 g·cm^{-3}. The C/N ratio of 17:1 and microscopic observation indicated that this consisted of partially decomposed plant materials. The δ ^{14}C for plant vegetation at this time was δ = +700 ‰ (Fig. 5) indicating that the material floated by $ZnBr_2$ contained a fair amount of C originating before nuclear bomb testing.

The δ ^{14}C of the 0.5 N and 6 N HCl hydrolyzates were +7 and +61‰, respectively. They accounted for 57% of the total C and left a residue with a δ ^{14}C = -197 ‰, equivalent to 1765 mean residence time (MRT). When the soil was amended with ^{14}C acetate and incubated for 30 days, 70% of the ^{14}C added was hydrolyzable compared to 61% of the ^{14}C in the radiocarbon dated field sample.

The humic acids of Chernozems tend to show the greatest MRT (Gerasmov and Chichagova 1971; Scharpenseel 1977; Paul et al. 1964). Fulvic acids contain polysaccharides and a variety of low molecular weight microbial products with a fast turnover time. They are therefore often the youngest fraction. Table 3 shows that the fulvic acids

Table 2. Mean residence times and $\delta^{14}C$ of the fractions of Brown Chernozemic soil and
distribution of organic C and ^{14}C as it occurs in nature and 350 days after the
addition of labelled ^{14}C-acetate (Martel and Paul 1974)

| Fraction	Radiocarbon dated soil Ap 0-10 cm*					Incubated soil Ah 0-15 cm[†]		
	MRT	$\delta^{14}C$	^{14}C	Soil-C	$^{14}C/soil-C$	^{14}C	Soil-C	$^{14}C/soil-C$
	yr B.P.±1σ	‰ ±σ	% of total			% of total		
Total soil	350±65	-43±9	100	100	1.0	100	100	1.0
Light material	Modern	+243±18	8.0	6.0	0.30	5.0	5.0	1.0
ZnBr$_2$ residue	505±105	-61±16	97	94	0.98	95	95	1.0
0.5N hydrolyzate	Modern	+7±15	37	35	1.1	49	35	1.4
0.5N residue	855±70	-101±15	55	59	0.93	46	60	0.78
6N hydrolyzate	Modern	+61±22	24	22	1.2	21	20	1.1
6N residue	1,765±65	-197±16	31	37	0.84	25	40	0.63
NaOH extract	1,910±105	-212±16	22	27	0.82	16	23	0.70
Water extract	1,790±120	-200±15	2.6	3.1	0.84	3.4	7.0	0.48
Humin	1,330±100	-153±17	6.4	6.9	0.93	5.6	10.0	0.56

*Carbon content 1.9%   [†]Carbon content 2.1%
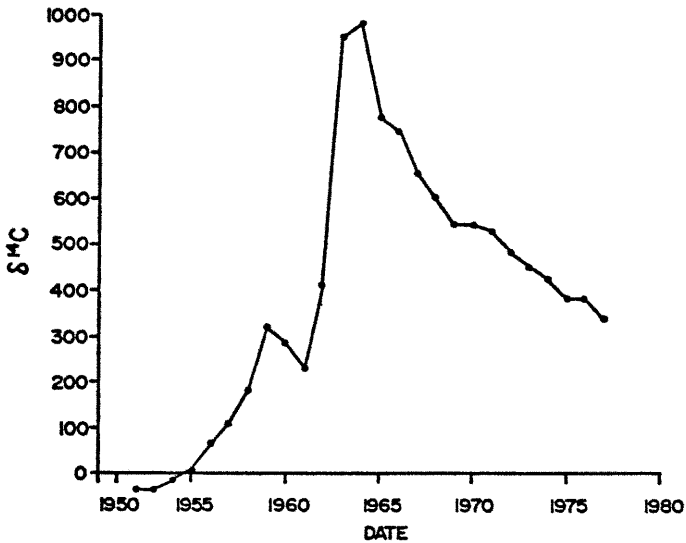
Fig. 5. Change in ^{14}C content of the wheat grown in the Northern
Hemisphere (McCallum and Wittenberg 1962, 1965; Rutherford, Wittenberg
and Wilmeth 1978)

Table 3. Mean residuence time (MRT) of soil organic matter
from the Ap horizon of a Gleysolic soil (Martel and
La Salle 1977)

Soil and fractions	% of total soil C	MRT (yr B.P.$\pm1\sigma$)	$\delta^{14}C$ (‰ $\pm1\sigma$)
Total soil	100	Modern	+173$\pm$14
Fulvic acids	24	Modern	+874$\pm$64
Humic acids	17	1,220$\pm$150	-140$\pm$19
Humin	59	180$\pm$100	-23$\pm$12
Hydrolyzed carbon	41	Modern	+670$\pm$38
Unhydrolyzed carbon	59	1,530$\pm$110	-173$\pm$14

of Eastern Canadian Gleysolic soils with a $\delta^{14}C$ = +874 ‰ were nearly equal to new plant material ($\delta^{14}C$ = +900 ‰, Fig. 5). The humic acids had a δ of -140 ‰ equivalent to 1220 years MRT accounting for 17% of the C. The unhydrolyzed C accounting for 59% of the total C had a MRT equal to 1530 years (-173‰). The hydrolyzed C, representing 41% of the total soil C, was composed primarily of new material but had less ^{14}C than the fulvic acids.

Deeper soils (Scharpenseel 1977), some podzols (Scharpenseel 1972a, b) as well as new soils dated on a chronological sequence (Goh et al. 1976) show lower ^{14}C in the humin. The higher MRT of humin, therefore, shows less mixing with recent materials. Although, fulvic acids are usually the youngest fraction, Goh et al. (1976) found that they were the oldest fractions in a soil where the movement of fulvic acid occurred. Thus, the relative MRT of the various fractions is dependent on soil pedological properties (Goh, Stout and Rafter 1977).

The general increase in mean residence time with depth for a large number of soils was summarized by Scharpenseel and Schiffmann (1977). The example for Chernozemic soils is shown in Fig. 6. The regression equations between depth and MRT (Table 4) shows that surface soils before the influence of bomb carbon had MRT's varying from modern to approximately 1,000 years. Samples 1 to 2 meters deep increased in MRT from 5,000 to 10,000 years B.P. Contamination with bomb produced ^{14}C is not the only factor influencing the increase of MRT with depth (Herrera and Tamers 1973). Samples obtained in 1881 from Broadbalk show a similar trend. The increase with depth must be due to differences in C input and decomposition and shows much slower turnover rates for the organic matter. Most of the soils had a slope approximating 46 yr MRT per cm depth. Soils with significantly different slopes included the Plaggen and Podzol soil which were formed under quite specific climatic conditions. The cultivated Gleysol of
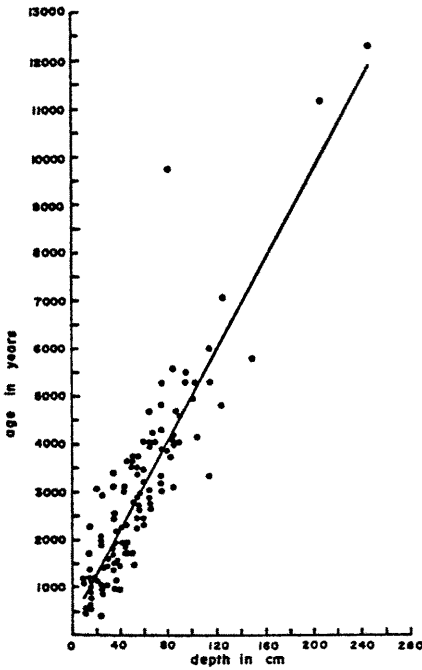
Fig.6. Correlation between age and depth of organic matter in 122 samples from Udolls (chernozems) from the FRG, USSR, CSSR, Hungary, Bulgana. Regression: y = 46.95 x + 351.74 Correlations = 0.888 (Scharpenseel 1972)

Table 4. Regression values showing MRT versus depth of a range of soils with Y = MRT (years) and X = depth

Soils	General description	Regression	(r)*	No. of samples	References
Podzols	Germany	Y = 7.47X + 1265	(.33)	32	Scharpenseel 1972a
Udalfs	Parabrown cinnamon soils	Y = 46.51X - 4.87	(.74)	86	Scharpenseel 1972a
Udolls	Chernozems	Y = 46.95X + 351	(.89)	122	Scharpenseel 1972a
Plaggen	Sod soils Germany and Ireland	Y = 2.25X + 837	(.21)	34	Scharpenseel 1972a
Vertisols	Western Europe Australia	Y = 40.14X -421	(.77)	271	Scharpenseel 1972a
Broadbalk 1881	England	Y = 48.9X + 695.8	(.92)	3	Jenkinson 1969
Deciduous forest soils	Venezuela	Y = 54X - 18.21	(.96)	-	Herrera and Tamers 1973
Eluviated Gleysol	Western Canada	Y = 67.5X + 177.4	(.94)	3	Martel and Paul 1974

*
r = correlation coefficient

Canada had a buried Ah horizon at depth.

Thermonuclear bombs have created high levels of ^{14}C, nearly doubling its atmosphere content. Figure 5 shows that the lowering of ^{14}C because of industrial pollution with fossil fuels up to 1952 was rapidly overcome and reached a peak in 1964. This flush of ^{14}C is now dropping rapidly. It presents both a challenge and opportunity to the soil scientist as this ^{14}C has now entered the active phase of organic matter where it provides a sensitive universally available tracer. Goh et al. (1976) used atmospheric bomb ^{14}C to investigate the turnover of fractions in newly developing soils. Jenkinson and Rayner (1977) had data for ^{14}C plant residue decomposition over a 14-year period at Rothamsted. They also had available carbondates of the soil in 1881 and at present. The flush of bomb ^{14}C in the atmosphere was therefore used to calculate incorporation of residue C into the soil.

A large number of other laboratories have information on plant growth and C input but do not have the detailed C tracer data available at Rothamsted. These laboratories also should have soil samples in storage that represent well characterized sites, sampled before the advent of the hydrogen bomb in 1952. By resampling the same soils and carbon dating both the pre-bomb and the modern soils in conjunction with acid hydrolysis, it should be possible to calculate the turnover rate of the active fraction of these soils. Such data would be of great use in estimating the contribution of organic matter to soil fertility. It also is essential in understanding the effect that man is having on the global C cycle (Bolin 1977).

SOIL BIOMASS

The soil biomass has a unique position among the soil organic C fractions because it is both a sink and a transformation station for C. Biomass C does not represent a major portion of the total soil organic C, however, it is a significant part of the active phase. Jenkinson (1966) found that the biomass C was only 2.5% of the total C, but up to 12% of the ^{14}C from labelled ryegrass roots was found in the biomass after one year. In the past, the role of biomass as a sink was not readily recognized because biomass was determined primarily by plate count techniques. Plate counts account for only 1-15% of the bacteria identified by direct microscopy (Jensen 1968; Babiuk and Paul 1970). At one time it was thought the direct count over-estimated the biomass, as this technique cannot differentiate between dead and living cells (Parkinson, Gray and Williams 1971). However, chemical techniques such as the measurement of CO_2 evolution after killing the biomass with chloroform followed by reinoculation and incubation (Jenkinson 1976; Jenkinson and Powlson 1976; Powlson and Jenkinson 1976; Jenkinson, Powlson and Wedderburn 1976) or the conversion of ATP values to biomass by the factor of 250 to 1 (Holm-Hansen 1973; Ausmus 1973) give still higher values.

Jenkinson (1966) found that after $CHCl_3$ sterilization of a soil previously incubated with ^{14}C materials, the CO_2 evolved during 10 days incubation was heavily labelled. Results with experiments in which the soil was amended with ^{14}C labelled microorganisms gave strong evidence that this heavily labelled $^{14}CO_2$ came from the biomass.

The larger estimation of biomass by measuring CO_2 evolution after fumigation with $CHCl_3$ than by the direct count of bacteria and fungi was attributed to some solubilization of extracellular material as well as killing of organisms during treatment (Shields, Paul and Lowe 1974). Anderson and Domsch (1977), however, could not find any significant increase in mineralization of prekilled fungal materials after further $CHCl_3$ treatment. The data of Shields et al. (1974) included counts for only bacteria and fungi. Organisms such as those with diameter larger than 3 μm make up a significant portion of the total biomass (Jenkinson et al. 1976) although their true nature in the soil is not known. As shown in Table 5, correcting the direct count for these organisms significantly diminishes the difference in biomass as measured by the two techniques. The chloroform treatment involves a correction factor for percent of biomass C evolved as CO_2 after chloroform treatment. The k value of 0.5 represents the data of Jenkinson and Powlson, whereas Anderson and Domsch suggest that an average of only 41% of the C is evolved as CO_2 after chloroform treatment with the consequent k of 0.41. ATP measurements are highly affected by the presence of clay which is known to decrease the available P concentration. In addition to the high sensitivity of ATP content to P availability, the inconsistency of the data of Table 5 and the known variation of ATP in a microbial cell during different growth stages makes this technique of biomass measurement difficult to interpret.

Table 5. Comparison between biomasses calculated by direct count, $CHCl_3$ flushes and ATP measurement after 122 hrs of incubation (Nannipieri, personal communication)

		ug/g soil						
		Bacterial-C from direct count after 122 h	Fungal biomass-C from direct count after 122 h	Total biomass-C by direct count after 122 h	Corrected to include large spheres $x \frac{100}{64}$	Biomass calculated from $CHCl_3$ flush		Biomass from ATP after 122 h
						k = 0.5	k = 0.41	
Parent material	Low P	21.7	102.0	123.7	198	297	362	400
	High P	18.3	88.7	107.0	167	163	199	512
Parent material + clay	Low P	27.2	93.2	120.4	189	225	274	175
	High P	26.5	92.2	118.7	185	171	208	237

The transforming action of the biomass can be considered to consist of three interrelated processes: uptake into the cell, intracellular transformation, and excretion including decay of microbial cells. When using C as a substrate, microbes take up a fraction for biosynthesis and a fraction for energy supply. Carbon used for energy under aerobic conditions is converted to CO_2 and under anaerobiosis to CO_2 plus low molecular weight organic molecules. The percentage of the total C used for biosynthesis is found to be as low as 2.5% under anaerobic conditions (Tusneem and Patrick 1971) and as high as 65% under aerobic conditions (Payne 1970; Ladd and Paul 1973; Van Veen 1977). This means that studies on the rate of CO_2 evolution in which

uptake of C for biosynthesis is not considered cannot be used for assessment of the actual decomposition rates, but are restricted to the determination of the mineralization of C or the activity of microbes.

Biomass Decomposition

Based on their biological function and chemical composition, it is reasonable to suppose that cell walls are more resistant to biological decomposition than are cytoplasmatic components (Wagner and Mutakar 1968). After cell decay, the cell wall fraction contributes more to stable soil organic matter fraction than the cytoplasm. Hurst and Wagner (1969) showed that this is not always true since the cell wall of the fungus Aspergillus niger degraded faster and to a greater extent during 160 days of incubation than did the cytoplasm of this fungus. The reverse held for another fungus called S/4. They concluded that the hyphal walls of dark colored fungal species are highly resistant to soil decomposition, and are an important contributant to soil organic matter formation. Verma and Martin (1976) did not find significant differences in the mineralization rate of whole cells, cell walls and cytoplasm of five algae. After 22 weeks, 61 to 81% of the added C was evolved as CO_2. Decomposition of cell walls was reduced by 40% and of cytoplasm 70% after complexing cell wall and cytoplasm fractions with synthetic humic acid-type polymers, indicating the strong effect of protection by adsorption on the organic matter turnover.

Wagner and Mutakar (1968) indicate that fungi contribute more to soil organic matter formation than do bacteria. This agrees with data of Mayaudon and Simonart (1963), who found that the mineralization of Aspergillus niger was less than that of Azotobacter vinelandii.

Maintenance Energy of the Biomass

The rate at which C is mineralized from the biomass depends on respiration for growth and maintenance of the individual cells. In pure cultures, the C requirement for maintenance is high. Barber and Lynch (1977) adapted Pirt's (1965) value of 0.04 hr^{-1} in their model of microbial growth in the rhizosphere. However, if this value was used for the total soil population the turnover of the biomass would be 96% per day. This is highly improbable since the biomass C is often nearly as great as the total C input from plant residues during the growing season. Behera and Wagner (1974) published data from which it could be derived that the turnover in soil was 8.6% per day. A turnover of 4.8% per day can be calculated from the soil data of Shields et al. (1973). Verstraete (1977) found that pure culture data for maintenance cannot be applied to mixed cultures. The lack of knowledge concerning the relationship between maintenance of the individual cell and maintenance of a mixed population in a complex substrate makes it difficult to extrapolate pure culture data other than for discussion purposes. Hunt (1977) applied different rates of maintenance energy to an active and inactive portion of the population. In this way the inactive population could have very low maintenance rates, whereas the actively growing organisms might approach values found for pure cultures in the literature.

DATA ANALYSIS

Pal and Broadbent (1975) found that C loss data could not be described properly by first order rate kinetics and used the form of:

$$C = kt^m$$

where C = cumulative loss of C, k = constant, t = time, m = constant. However, it is generally accepted that decomposition of organic matter constituents can be described according to first order rate kinetics (Jenkinson and Rayner 1977; Russell 1964; Stanford and Smith 1972; Hunt 1977; Gilmour, Broadbent and Beck 1977; Sinha, Sinha and Sinha 1977).

According to first order rate kinetics, the decomposition rate, V_{dec}, is:

$$V_{dec} = - \frac{dA}{dt} = kA$$

where k is the decomposition rate constant $(time^{-1})$ and A is the concentration of the added organic matter. Integration of this equation gives:

$$A = A_o \cdot e^{-kt} \quad \text{or} \quad \ln \frac{A}{A_o} = - kt$$

where A_o = the concentration of A at t = 0. Values of k can be determined by plotting ln (A/Ao) vs t. In most studies, decomposition of a certain compound is determined by using ^{14}C and measuring $^{14}CO_2$ evolution or ^{14}C remaining in the soil. Neither method gives actual decomposition rates. When microorganisms utilize C, the C-compounds enter: CO_2, biosynthesis and to some extent low molecular weight metabolites. If X is the amount of CO_2-C evolved during decomposition of a certain compound and Y is the efficiency of the use of C for biosynthesis expressed as percentage of the total C uptake under aerobic conditions and non-cell metabolite production is negligible and disregarded, the actual amount decomposed is: $X (1 + Y/(100 - Y))$.

A problem arising when assessing the actual decomposition rate from experimental data is the microbial production and recycling of labelled material. It is sometimes possible to determine, by chemical procedures, the amount left in soil. However, microbial production may interfere in the determination of the real decomposition rate as in the case of sugars (Cheshire et al. 1974). So ^{14}C will still be left in soil or evolved as CO_2 when the original labelled compound is completely decomposed.

Tables 6 and 7 give a number of decomposition rate constant (k)-values calculated from literature data for two values of Y, 20 and 60%, at particular times in the incubation period. Where only tabular data over extended periods were available, it was not possible to calculate k at 60% efficiency because corrections for sequential microbial growth could not be made. The gross efficiency (efficiency assuming only growth) for soil organisms under aerobic conditions is generally considered to be between 40 and 60% (Payne 1970; Verstraete 1977). In

Table 6. First order rate constants corrected for microbial biosynthesis during plant residue and microbial tissue decomposition in soil

Product	Time (day)	k (day⁻¹)			References
		Uncorrected	Corrected efficiency (%)		
			20	60	
Plant Residues:					
Straw - rye (<53 μm)	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 (average for 3 soils)	28	0.02	0.03	--	Sauerbeck and Führ (1968)
Straw - wheat (average for 12 soils)	45	0.006	0.008	--	Sauerbeck and Führ (1977)
Straw - wheat	180	0.005	0.008	--	Shields and Paul (1973)
Straw - wheat	365	0.002	0.003	--	Sauerbeck and Gonzalez (1977); Oberländer and Roth (1974)
Grass - rye	5	0.07	0.09	0.24	Jenkinson (1977)
Grass - rye	10	0.04	0.06	0.23	Simonart and Mayaudon (1958)
Blue gramma herbage	30	0.006	0.008	0.02	Nyhan (1975)
Grass Stipa	180	0.004	0.005	--	Shields and Paul (1973)
Roots - maize (average of 3 soils)	5	0.05	0.06	0.15	Sauerbeck et al. (1972)
Roots - maize (average of 8 values)	24	0.02	0.03	--	Cited by Lespinat et al. (1976)
Rye tissue (54 day tissue)	10	0.02	0.02	0.06	Stotzky and Mortensen (1958)
Rye tissue (82 day tissue)	10	0.02	0.03	0.06	Stotzky and Mortensen (1958)
Microbial Tissue:					
Microcoleus sp. proteins	7	0.09	0.13	--	Verma et al. (1975)
Chlorella pyrenoidosa proteins	7	0.07	0.10	--	Verma et al. (1975)
Fungal (S/4) cell wall	10	0.02	0.03	0.07	Hurst and Wagner (1969)
Fungal (S/4) cytoplasm	10	0.04	0.05	0.17	Hurst and Wagner (1969)
A. niger cytoplasm	10	0.05	0.07	--	Hurst and Wagner (1969)
A. niger cell wall	10	0.06	0.09	--	Hurst and Wagner (1969)

addition to factors such as the type of substrate other processes such as maintenance and sequential growth will decrease apparent efficiency. Two sequential populations of organisms each growing at 60% efficiency would have an apparent efficiency of 36%. Therefore, when using graphical data the incubation period over which the k-values in Tables 6 and 7 were calculated, was taken as short as possible.

The data in Tables 6 and 7 show that there is a wide variety in k-values for different compounds. The differences between the uncorrected k-values and the corrected ones is a factor between 0 and 2 when assuming 20% efficiency but up to a factor of 5-7.5 for an efficiency of 60%. This indicates that one may make a serious mistake when assessing decomposition rates of fresh amendments without accounting for the microbial biosynthesis. Another striking point is the decrease of k-values as in the case of wheat straw with time from 0.03

Table 7. First order rate constants corrected for microbial biosynthesis during decomposition of specific compounds in soil

Product	Time (day)	k (day^{-1})			References
		Uncorrected	Corrected efficiency (%)		
			20	60	
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)
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	--	Hinderman (1968)
Cellulose	10	0.02	0.03	0.08	Simonart and Mayaudon (1958)
Cellulose	365	0.003	0.004	--	Hinderman (1968)
Lignin	365	0.001	0.002	--	Hinderman (1968)
Waxes	365	0.0006	0.0008	--	Hinderman (1968)
Phenols	365	0.0002	0.0003	--	Hinderman (1968)
Acetate	5	0.05	0.06	0.14	Sørensen and Paul (1971)
Plant solubles	10	0.06	0.09	--	Simonart and Mayaudon (1958)
Glycine	7	0.2	0.4	--	Verma et al. (1975)
Alanine	7	0.2	0.4	--	Verma et al. (1975)
Lysine	7	0.13	0.2	--	Verma et al. (1975)
Leucine	7	0.13	0.2	--	Verma et al. (1975)
Arginine	7	0.2	0.5	--	Verma et al. (1975)
Aspartic acid	7	0.2	0.4·	--	Verma et al. (1975)

day^{-1} at 14 days of incubation to 0.003 day^{-1} at 365 days. Jenkinson and Rayner (1977) and Gilmour et al. (1977) suggested that the decomposition rate of organic material such as straw decreased with time, because this material consists of several products such as decomposable soluble compounds, lipids, cellulose, lignin, etc., each having their own decomposition rate. K-values of single compounds, such as hemicellulose (Table 7), also decrease in time due to the earlier mentioned recycling processes.

A simple computer simulation model (Fig. 7) describing the decomposition of a single compound by the amount of CO_2 evolved shows how recycling affects the apparent decomposition rate as measured. Rates of C and biomass decay follow first order rate kinetics. The rate constants of the decomposition were set for those of cellulose under laboratory conditions at 0.08 day^{-1}. Estimated values for the rate constants of the decay of biomass and decomposition of microbial products were 0.05 and 0.04 day^{-1}, respectively. Carbon used for maintenance energy was assumed to be 40% of the amount of C used by biomass for maintaining the population, the rest was released as microbial products. Efficiency of the use of C was assumed to be 60%.

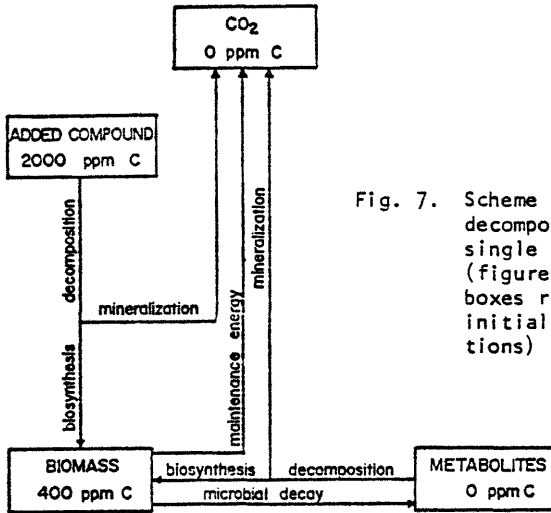The percentage of the added C left in soil, the microbial pro-

Fig. 7. Scheme of model for decomposition of a single compound (figures in the boxes refer to the initial concentrations)

duction and the decomposition calculated from the CO_2 output are presented in Fig. 8. Although the decomposition rate of biomass and the microbial products was assumed to be rather fast, accumulation of microbial products occurred. This results in a significant discrepancy between the actual decomposition and the decomposition as derived from the computed CO_2 evolution.
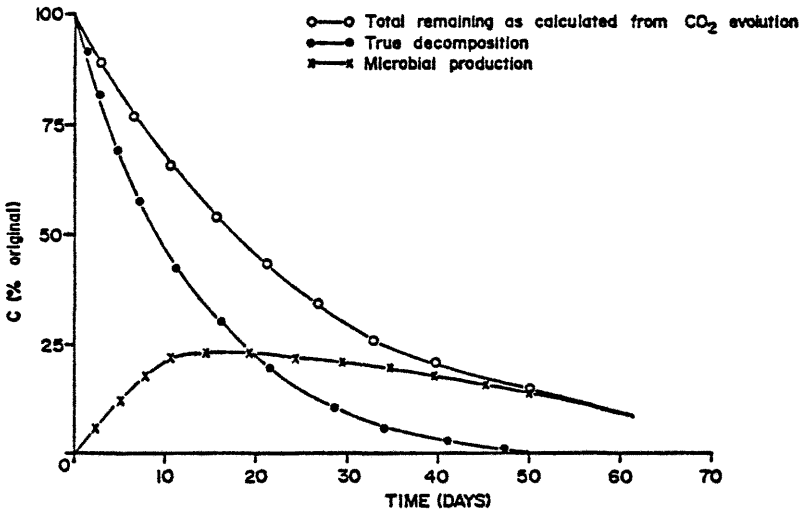

Fig. 8. Calculated decomposition of carbon added to the soil as a single compound, i.e. cellulose.

A second model (Fig. 9) describes the decay of a natural product such as straw which consists of four components each having their own decomposition rate: soluble compounds, and proteins both with a $k = 0.2$ day^{-1}, hemicellulose $k = 0.08$ day^{-1}, and lignin $k = 0.02$ day^{-1} (Table 7). Decay constants for biomass and microbial products as well as the data on efficiency and maintenance were equal to those of the previously mentioned model. The output (Fig. 10) shows the same pattern as for a single compound except that in the latter stage the real decomposition curve levels out when only the recalcitrant fraction of lignin is left. The actual decomposition rate will differ significantly from the measured one, using CO_2 evolution data, even when differences in decomposition rate constants are taken into account.
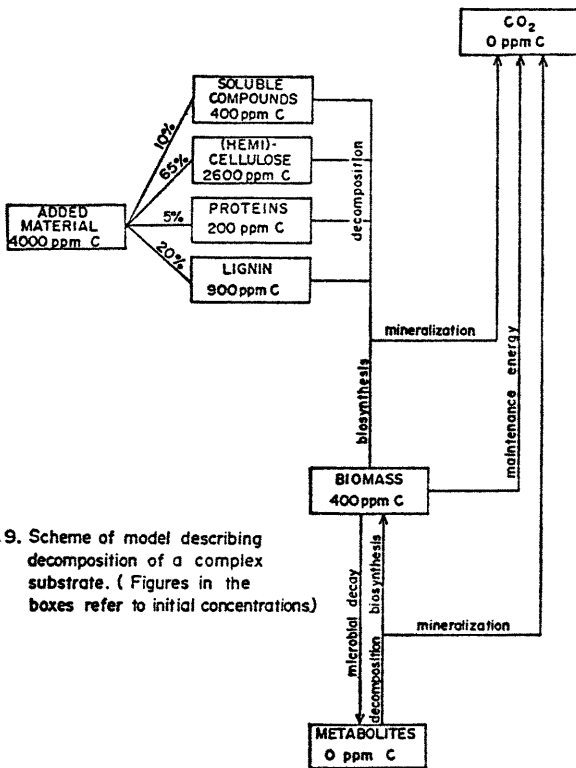

Fig. 9. Scheme of model describing decomposition of a complex substrate. (Figures in the boxes refer to initial concentrations.)

To estimate the real decomposition rate constant from field data, we fitted our calculations to data in Fig. 2. The fit between the model and the curve for decomposition of ryegrass under tropical conditions was optimal when decreasing the laboratory values of k for the four compounds considered by a factor of about 2. An eightfold decrease resulted in a good fit with the curves which represent decomposition for temperate climates. This means that the model shows a
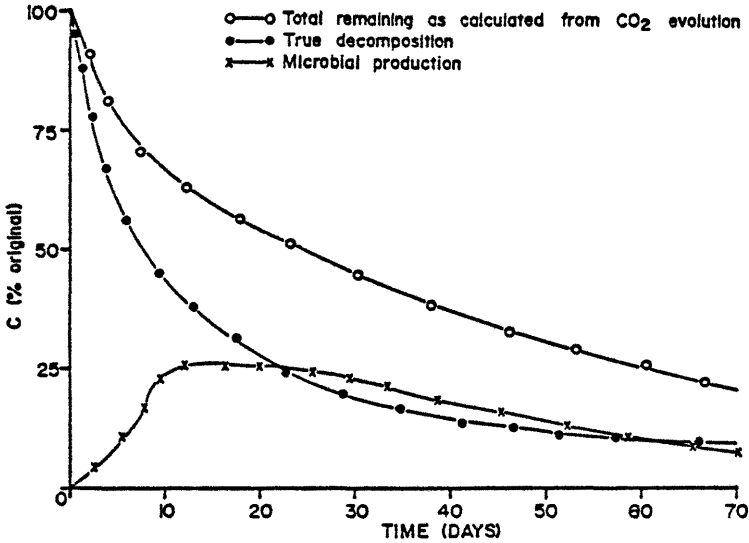
Fig. 10. Calculated decomposition of carbon added to laboratory soil as a complex substrate

difference of a factor of four between the decomposition rate in the tropics and in temperate climates. Jenkinson and Ayanaba (1977) found that decomposition of ^{14}C residue proceeded four times as rapidly in Nigeria as in temperate England.

The half-life for the observed decomposition rate in Saskatchewan as determined from CO_2 output is 125 days. This agrees with data of Shields and Paul (1973) whose data also are presented in Fig. 2. The calculated real half-life time is 75 days. The k-values as derived from the curve in Fig. 11 over the first 15-30 days is 0.01 per day.

Mathematical Description of C Dynamics in Grassland

Among the many mathematical descriptions presented during the last fifteen years very few deal with soil organic C dynamics. Russell (1964) used the following expression of the rate of change of organic matter:

$$\frac{dN}{dt} = -k_1(t) \, N + k_2(t)$$

where $k_1(t)$ and $k_2(t)$ are the time-dependent decomposition and addition coefficients, respectively. The changes in these coefficients are represented by Fourier series which results in:
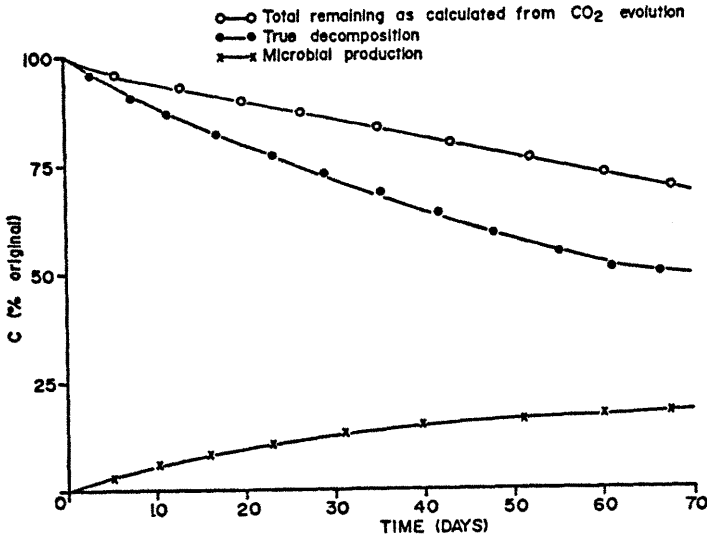
Fig. II. Calculated decomposition of a complex substrate added to field soils representative of temperate climates

$$\frac{dN}{dt} = -\left(\tfrac{1}{2}\alpha_0 + \alpha_1 \cos t + \beta_1 \sin t + \alpha_2 \cos t + \ldots\right)\cdot N +$$
$$\left(\tfrac{1}{2}\gamma_0 + \gamma_1 \cos t + \delta_1 \sin t + \gamma_2 \cos t + \ldots\right)$$

Although this description results in difficult numerical solutions, it is said to be a more comprehensive representation of soil organic matter changes than the generally used equation:

$$\frac{dN}{dt} = -k_1 N + k_2$$

where k_1 and k_2 are constant in time. This equation used by Jenny (1941) to describe changes in organic N is still in common use for describing input and decomposition processes of soil organic matter (Campbell 1978).

Jenkinson and Rayner (1977) were probably the first to publish a simulation model describing soil organic matter turnover for a long period of time (up to 10,000 years). The data they used came from: a) the long term Rothamsted plots of 10-100 years; b) incubation experiments during 1-10 years using ^{14}C-labelled plant material, c) radiocarbon dating; d) the effect of thermonuclear radiocarbon on radiocarbon age (bomb effect); e) CHCl$_3$ data on biomass. Five soil fractions were considered: decomposable plant material (DPM) which was calculated to have a half-life of 0.165 years; resistant plant material

(RPM) with a half-life of 2.31 years; soil biomass (BIO), half-life of
1.69 years; physically stabilized organic matter (POM), half-life of
49.5 years, and chemically stabilized organic matter (COM), half-life
of 1980 years. The decomposition rate of each of these components was
assumed to be proportional to its actual content. It was assumed that
after decomposition any of the five components decay to the same pro-
ducts, CO_2, BIO, POM and COM in the same proportions. The fit between
the model and experimentally determined results suggested that the
model is a useful representation of the turnover of organic matter in
cropped soils.

To integrate some of our own data with the wealth of informa-
tion available in the literature as reviewed earlier in this paper,
and to test some of our concepts concerning organic matter dynamics,
we developed a computer simulation model of soil organic matter dyna-
mics. This model was used to describe the organic matter turnover in
the top 10 cm of a native grassland, and to mimic man's impact when
the virgin grassland was brought into cultivation. The model is
schematically presented in Fig. 12 with the input data being shown in
Table 8. In contrast with Jenkinson and Rayner's model, all material
but the lignin fraction is transformed by passing through the biomass.
While soil fauna are present and may act in increasing the turnover of
biomass in this model all C is assumed to be consumed by microorgan-
isms, where it is either transformed into CO_2 or subsequently released
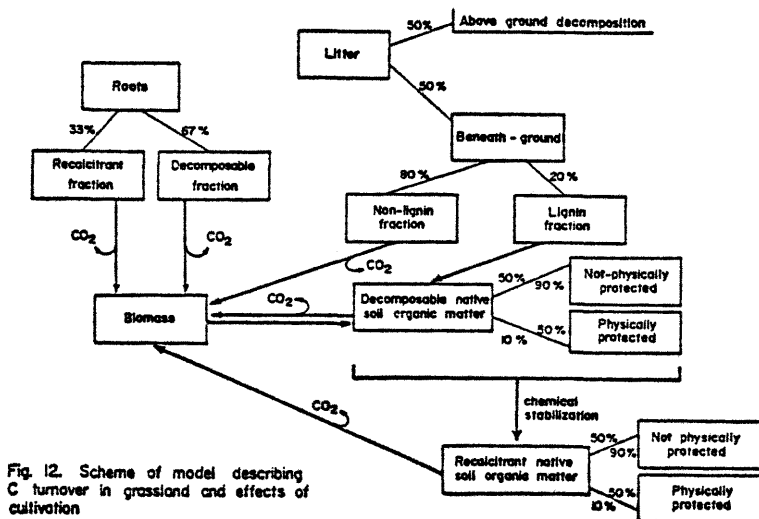by decay of microbial cells or by exudation of metabolites.

Fig. 12. Scheme of model describing
C turnover in grassland and effects of
cultivation

The lignin fraction of the incoming litter while not recalci-
trant in itself was assumed to supply the majority of aromatics for
soil humic materials. It enters the non-recalcitrant organic matter
fraction which is also made up of microbial materials such as the

Table 8. Input data simulation model

State variables	Initial value (ppm)	Annual input (ppm)	Decay rate* constants (day^{-1})
Litter (in soil)	780	780	0.01[†]
Roots - well decomposable	4290	666	0.02
Roots - recalcitrant	2210	334	0.002
Biomass	500	--	0.01
Decomposable native soil organic matter - not physically protected	0[†]	--	0.02
Decomposable native soil organic matter - physically protected	10000	--	$2 \cdot 10^{-4}$
Recalcitrant native soil organic matter - not physically protected	5500	--	$2 \cdot 10^{-6}$
Recalcitrant native soil organic matter - physically protected	5500	--	$2 \cdot 10^{-6}$

*Decay constants are expressed year^{-1} in the model

[†]Rate constant under virgin grassland conditions is 3.0 (year^{-1}) and for cultivated land 3.6 (year^{-1})

[†]This fraction decays very rapidly and is considered to be decayed completely at the end of a growing season when this model is assumed to start

amino acids and amino sugars stabilized in soil with a half-life of 5 to 20 years. In this fraction the lignin is either decomposed by the biomass or a portion can react directly with other constituents to form the recalcitrant organic matter fraction.

Organic C enters the soil via litter or roots. Approximately 50% of the above ground litter is decomposed before it hits the soil surface (Coupland et al. 1975). The remaining 50% enters the soil to be acted on by the biomass. The proportion of root C entering the soil was calculated as 42% of the total photosynthate (Warembourg and Paul 1973, 1977). This value includes root exudates. Earlier discussion on roots indicated that they were composed of two fractions: a resistant fraction persisting for fairly long periods, and a fraction consisting of root hairs and possibly exudates with a fairly quick turnover rate as shown in the description of the model.

Soil organic matter consists of a number of fractions, the biomass, non-recalcitrant metabolites of the biomass, and a recalcitrant fraction. Physical protection affects the decomposition of 50% of these materials (Legg et al. 1971). The physical protection coeffi-

cient (FOPV) therefore was set at 50% for the virgin conditions. Under cultivation, this physical protection was dropped to 10%. Physical protection results from adsorption of organic C and entrapment in aggregates where it is not susceptible to microorganisms or extra-cellular enzymes. In this example, physical protection of the recal-citrant material was considered not to result in a further decrease of the already very low decomposition rate constant for the recalcitrant portion of the humic materials (Campbell et al. 1967).

Transformation rates follow first order kinetics and are inde-pendent of biomass because the large biomass results in an excess con-centration of organisms present at any one time in a substrate deficient system.

Very little of the extensive literature on soil organic matter turnover is directly applicable to modelling. Data on decomposition of organic matter usually yield end results, i.e. ^{14}C remaining in the soil or CO_2 evolved from the system. Models including microbial growth and metabolite production require gross in and out process data. The ^{14}C loss data in Fig. 2 show the end results of a sequence of pro-cesses while the model should use individual rate constants for the processes.

The rate constants for the decomposition of the non-recalcitrant fractions of the litter and roots were obtained from Tables 6 and 7 and from calculations with the model describing plant residue turnover (Fig. 11). The rate constant for the recalcitrant organic matter was derived from data on MRT (Martel and Paul 1974). Direct data from carbon dating could not be utilized in our model. The mean residence time (MRT) (or equivalent age utilized by some other authors) is cal-culated directly from the ^{14}C content of the organic matter. This value is not the same as the turnover time used in mathematical analy-sis. In old, slowly decomposable materials such as the humic fraction of soil organic matter, MRT and turnover time are nearly equal under equilibrium conditions. Jenkinson and Rayner (1977) calculated an equivalent age (MRT) of 2565 years for recalcitrant organic matter and a turnover time of 2857 years. The reciprocal of the decomposition rate constant k is equal to turnover time in first order rate kinetics. They calculated the turnover time for organisms in their model to be 2.4 years. However, the calculated radiocarbon age was 25 years be-cause of the utilization by the microorganisms of some C from the recalcitrant fraction that was thousands of years old.

Environmental factors such as temperature and moisture were not taken into account separately in this model. Most of the data are de-rived from field results which represent average values under dif-ferent temperature and moisture regimes in the Canadian prairie region during the growing season. The frozen period was taken into account by a modelling program.

The S/360CSMP (Systems/360 Continuous System Modelling Program) (IBP Manual GH20-0240-3 and Y20-0111-0) was used as a computer langu-age. The rectangular method of integration used intervals of 0.1.

Total soil organic matter for the virgin grassland over a 200

year period and the effect of cultivation of the grassland is given in
Fig. 13. On the prairie soils, man's impact is thought to result pri-
marily from changing the fraction of the soil organic matter which is
physically protected. In this model this is caused by destruction of
soil structural components. This was taken into account by changing
the value of the physical   protection coefficient (FOPV) from 0.5 to
0.1, resulting in an increase of the decomposition rates of soil or-
ganic matter. It has been shown that disruption of soils increased
the mineralization of both soil organic C and N (Hiura, Hattori and
Furusaka 1976; Rovira and Greacen 1975; Craswell and Waring 1972;
Waring and Bremner 1964; Edwards and Bremner 1967). The total C input
remained the same before and after cultivation. Cultivation resulted
in a single large input of C in the form of the large store of grass
roots present under virgin conditions. The large decrease in organic
matter at the beginning of cultivation is at least in a large part due
to the degradation of the roots. Although the model levels out after
approximately 50 years, it does not reach steady state conditions
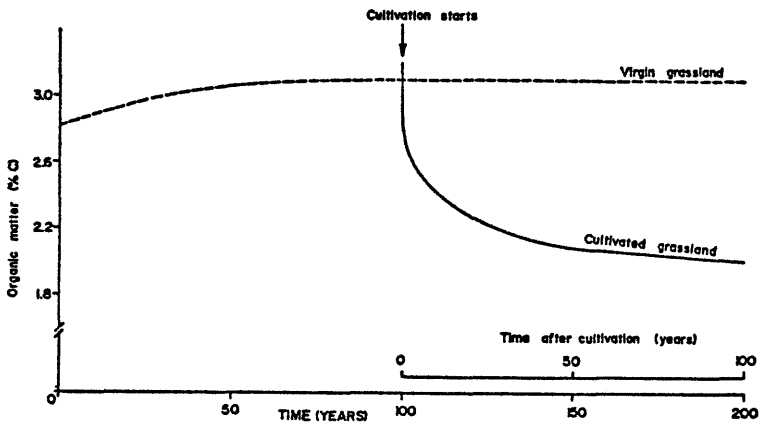during the period it is operable.

Fig. 13. Calculated organic matter vs time for virgin and cultivated grassland

        The model predicted a decrease in organic C after cultivation
to be 26% after 20 years cultivation. Martel and Paul (1974) found
19% loss in soil organic matter after 20 years cultivation of a Mata-
dor grassland; when the roots were taken into account the loss was 29%.
The output is also very similar to other data in Canadian grasslands
(Campbell, Paul and McGill 1976). Soils with a higher moisture con-
tent and where cropping practices include extensive fallow periods
show higher losses (Martel and Paul 1974; Paul 1976).

        We don't consider the predictive aspect to be the most impor-
tant aspect of this mathematical analysis. The analysis has allowed
us to test many of the concepts derived from the review of the liter-

ature on organic C decomposition. The major points considered or arising from the analyses are: (1) plant residues entering the soil are transformed by the biomass except for the lignin fraction. (2) The lignin fraction enters the non-recalcitrant organic C where physico-chemical reactions with microbial products can form resistant frac-tions. The non-recalcitrant fraction is decomposed by the biomass so that only a portion of the original lignin enters the recalcitrant fraction. Since microbial products also enter the recalcitrant frac-tion, this does not preclude microbiologically produced aromatics from forming a portion of humic materials. (3) The efficiency of the use of C by the biomass, biomass turnover, and maintenance are of major importance in calculating microbial production and organic matter dynamics. Studies utilizing soil indicated that data for gross growth efficiency appears to fit the pure culture microbiological data. How-ever, microbial turnover rates and maintenance energy concepts must be developed specifically for complex systems such as soil or sediments. (4) Physical 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 assumes physi-cal protection such as adsorption and entrapment within soil aggre-gates for both chemically resistant and well decomposable organic matter. (5) Growth and turnover rate data from residue decomposition or ^{14}C studies may have to be recalculated to produce values for math-ematical analysis. Microbial production results in slower apparent decomposition rates, and the final amount of material remaining in soil is much more dependent on turnover of products of decomposition, i.e. the recalcitrant fraction than on the decomposition rate of the plant residues added to soil. (6) The decrease in percentage of or-ganic soil C was accurately predicted by altering the amount consider-ed to be physically protected.

On this site there is very little difference in primary produc-tivity between the virgin and cultivated grasslands. The major dif-ference in plant structure is within the large reservoir of roots with-in the grassland. Other influences such as differences in moisture availability during non-cropped periods and differences in the time at which organic C is deposited within and on the soil surface could affect the model. These, however, will probably result in better fits to specific field data rather than in a complete change in the inputs into the mathematical system.

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