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CO_2 efflux by rapid decomposition of low molecular organic substances in soils

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Abstract. Decomposition rates of the [2-^{14}C]-glucose and [2-^{14}C]-glycine in four different soils of the long-term field trial of Moscow were investigated in a 3-months laboratory experiment in which $^{14}CO_2$ respiration was measured. A model with three decomposition components and two distribution parameters was developed and validated with the data of the experiment. The decay rate constants of free [2-^{14}C]-glucose (4–32 day^{-1}) were slower than those of [2-^{14}C]-glycine (16–44 day^{-1}). The calculated use efficiency for microbial biosynthesis of the second carbon atom was 47% for glucose and 31% for glycine. The potential half-life of labelled carbon in the microbial soil biomass ranged from 0.6 to 4.4 days, depending on the soil type and the initial amount of added substrate. The calculated total utilization of carbon by the soil biomass from glycine was about 2–5 times lower than that of glucose.

The modelled ^{14}C incorporation into the microbial soil biomass reached its maximum on the first day of the incubation experiment and did not exceed 22% of the ^{14}C input. Both of the investigated substances decomposed most rapidly in the soil samples from sites that have not being fertilised with organic or mineral fertilisers during an 81-years period.

Key words: Glucose – Glucose – Decomposition kinetics – Modelling – Microbial soil biomass – CO_2 – ^{14}C

Introduction

General Background

Studying the transformation of individual low molecular organic substances in soils is connected with the problem of their complete extraction from soil and determination of the original substances and the metabolites or mineralisation products in the extracts. At the same time, measuring the end product of mineralisation – CO_2 – is not a methodical problem [29]. Therefore the dynamics of CO_2 release is often used for kinetic studies of the decomposition of different compounds in soil, for example, plant residues [9, 24], saccharides [2, 11, 24, 31], amino acids [16, 17] and proteins [30], pesticides, products of incomplete combustion of fuels like polyaromatic compounds and many others. The kinetics of CO_2 efflux from soil is directly connected with the specific processes of substance decomposition, for example, quantity and decay rates of intermediate metabolites [9], binding of substance on clay minerals and humus, participation of chemical and biological processes [11] in original substance transformation, toxicity of a certain substance and its metabolites. The knowledge of the metabolic pathway of a substance in the soil allows for some conclusions to be drawn about its processes through the kinetics of CO_2 efflux.

A considerable number of publications about transformation of substances in soil have been devoted to plant residues [3, 18, 27, 32]. Plant residues play the main role in substrate delivery for soil microorganisms and turnover of humus substances and also for supplying of plants with mineral nutrients. At the intermediate stage plant residues were metabolised by soil microorganisms to lower molecular substances. Therefore the investigation of transformation of low molecular plant residues is particularly important. At the same time, it is very difficult to do this methodically, because of both the short-term nature of individual processes and the considerable participation of physico-chemical reactions in these processes.

The aim of this work is the development and verification of a simple model that will allow the estimation of decomposition rates of substances entered into the soil and their derivatives indicated by the kinetics of the CO_2 efflux.

Introduction of the Model

As proposed in the present model the following complete processes may occur with substances added to soil:

1. Biological and non -biological decomposition (mineralisation)
2. Transformation to organic metabolites
3. Sorption on humus and clay minerals
4. Moving through the soil with draining water
5. Uptake by plants

The role of each of these processes depends on the environmental conditions (moisture and temperature), the investigated substance and the soil type, so that the contribution coefficients of each of these processes may vary from 0 to 1 and the sum of the coefficients of all the processes is equal to 1. In laboratory experiments conducted for the investigation of decomposition of organic substances in bare soil we can accept that: pathways 4 and 5, mentioned above, are absent, and the rates of sorption on or chemical incorporation into soil components (pathway 3) are higher compared with the biological decomposition rates. In this case the scheme of substance transformation in soils is as shown in Fig. 1. So, the suggested model of

CO_2 efflux by mineralisation of low molecular substances in soils includes one physical (1 in Fig. 1) and three biological steps (2, 3 and 4 in Fig. 1). In this scheme the CO_2 efflux from three different soil compartments is shown: (1) the original substance in free state; (2) the original substance in adsorbed state on humus and clay minerals; (3) the microbial biomass formed out of the substance investigated

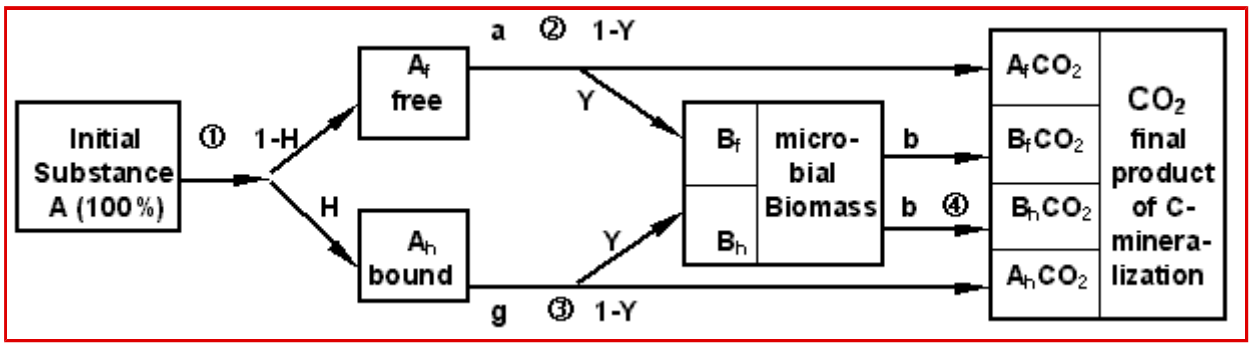

Fig. 1 Model scheme of decomposition of low molecular organic substances in soil. *A* Initial substance (100%); *Af* free substance (water soluble); *Ah* substance, adsorbed on humus and clays after addition of A to soil; *B* microbial biomass; *Bf* microbial biomass formed from free substance (zymogenous microflora); *Bh* biomass formed from substance bound on humus (autochthonous microflora); *H* adsorption ratio; *Y* use efficiency; *a* rate constant of microorganism utilisation of free substance; *b* rate constant of dying off and decomposition of microorganisms; *g* rate constant of microorganism utilisation of bound substance; CO_2 carbon dioxide formed from: $AfCO_2$ CO_2 emitted by microorganisms using free substance – Af-form; $AhCO_2$ CO_2 emitted by microorganisms using bound substance – Ah-form; $BfCO_2$ CO_2 emitted by dying off and decomposition of microorganisms – Bf-form; $BhCO_2$ CO_2 emitted by dying off and decomposition of microorganisms – Bh-form

The CO_2 release has been chosen as an indicator of transformation processes of organic substances in soils because it can be measured conveniently with simple instrumentation and with low disturbance of natural soil processes [10, 30]. The kinetics of CO_2 efflux clearly reflects the decomposition processes.

The physical interaction of the added substances with humus and clay minerals (stage 1) is a more rapid reaction than the biological steps (stages 2–4). So the equilibrium adsorption of a mixture of amino acids with clay minerals was reached after 5 min [12]. The half-life periods for low molecular organic composites of plant residues range from hours to days [5, 15, 23, 28]. Therefore the separation between free and adsorbed forms of the original organic substance takes place before its uptake by soil microorganisms starts. It is known that the decomposition of low molecular substancess in soil corresponds to monomolecular reaction [13, 33]. So the rate of physical sorption or chemical binding is considerably higher than the rate of biological steps. In addition, the overall decomposition corresponds to first order kinetics. Therefore the suggested model can be described by the following system of differential equations (see also Fig. 1):

$$\frac{dAf}{dt} = -a \cdot Af(t) \quad (1)$$

$$\frac{dAh}{dt} = -g \cdot Ah(t) \quad (2)$$

$$\frac{dB}{dt} = Y \cdot a \cdot Af(t) - Y \cdot g \cdot Ah(t) - b \cdot B(t) \quad (3)$$

$$\frac{dAfCO_2}{dt} = (1-Y) \cdot a \cdot Af(t) \quad (4)$$

$$\frac{dAhCO_2}{dt} = (1-Y) \cdot g \cdot Ah(t) \quad (5)$$

$$\frac{dAhCO_2}{dt} = b \cdot B(t) \quad (6)$$

where t is the time (in hours or days). Note that each of these three biological processes in the model actually consists of successive biochemical reactions, and the rate constants of these processes (a, b and g) characterise only the rate of each individual chain of reaction.

The fourth stage (4) consists of a sum of two simultaneously proceeding processes: $BCO_2 = BfCO_2 + BhCO_2$ (CO_2 evolved after die out and decomposition of microorganisms, formed from free and adsorbed substances accordingly). The rates of $BfCO_2$ and $BhCO_2$ efflux are independent; therefore each component of this equation system has a simple algebraic solution [14]. Adding up these equations followed by a transformation of CO_2 efflux from each of four blocks leads to an equation of total CO_2 efflux from soil:

$$CO_2(t) = A \cdot \left[1 - ea + H \cdot (ea - eg) - \frac{Y \cdot a}{b - a} \cdot (ea - eb) + Y \cdot H \cdot \left[\frac{a}{b - a} \cdot (ea - eb) - \frac{g}{b - g} \cdot (eg - eb)\right]\right] \quad (7$$

where $ea = e^{-at}$, $eb = e^{-bt}$ and $eg = e^{-gt}$.

Besides general CO_2 efflux, an algebraic solution exists for every block of the scheme. It is also possible to calculate the substance uptake and use by the microbial soil biomass:

$$B(t) = A \cdot Y \cdot \left[\frac{a}{b - a} \cdot (1 - H) \cdot (ea - eb) + \frac{H \cdot g}{b - g} \cdot (eg - eb)\right] \quad (8)$$

The proposed model can be used as a component of the models of behaviour, especially of labile forms of soil organic matter. The model can also be used to study the decomposition kinetics of many toxic substances, for example, pesticides and their metabolites in soil.

Materials and Methods

For model verification we carried out an experiment under laboratory conditions to estimate the $^{14}CO_2$ efflux by decomposition of [2-^{14}C]-glycine and [2-^{14}C]-glucose in a Podzoluvisol treated by different management and fertilisation grades. The substances chosen for the experiment were labelled at only one atom of the molecule, because each of the C atoms of both molecules has its own biochemical decomposition and can easy be described by examination of chains of reaction with one atom.

Samples of a loamy dystric Podzoluvisol (FAO) soil were taken from the upper 10 cm of the Ap horizon in the long-term field experiment of Pryanishnikov [22]. The first soil sample was taken from an eternal fallow plot, the second from an eternal rye plot and the third from a crop rotation with N, P, K fertilisers plus lime and manure. The fourth soil sample was taken from the upper 10 cm of an Ah horizon at the forest experimental station of Moscow Agricultural Academy, from the plot with *Pinus sylvestris* (L) close to the first experimental field. The soil samples were taken in autumn 1993, were air dried, grounded, mixed and sieved (1 mm mesh sieve). The chemical characteristics of the soil samples were published elsewhere [1, 22] and are presented here in Table 1.

Table 1 Characteristics of investigated soil samples. Samples 1, 2 and 3 were taken from long-term field experiments of Pryanishnikov – 81 years old [1]. Sample 4 was taken from the forest experimental station of Moscow Agricultural Academy

Sample	Use	Depth of soil	Plants	Fertilisers	C org.	pH (KCl)	Hydrolytic acidity	Clay content (≤0.01 mm)
		(cm)			(%)		(meq 100 g^{-1}	(%)

							soil)	
1	Agriculture	0–20	Eternal fallow	No	0.63	3.76	6.40	22.07
2	Agriculture	0–20	Eternal winter rye	No	1.10	3.96	5.57	25.80
3	Agriculture	0–20	Crop rotation[a]	N, P, K, lime, manure[c]	1.20	4.90	4.48	25.51
4	Forest	0–15	*Pinus sylvestris*[b]	No	2.03	3.85	10.50	19.30

[a] Six-field crop rotation: fallow, winter rye, potato, winter barley, clover, flax.

[b] *Pinus sylvestris* L, about 80 years old.

[c] N:P:K, 50:30:50 kg ha^{-1} yea^{-1}; lime $CaMg(CO_3)_2$, Ca:Mg, 2:1, 4.6 t ha^{-1} 6 $years^{-1}$; manure 10 kg ha^{-1} $year^{-1}$.

The sites where the first three soil samples came from, the long-term field trial of Pryanishnikov, have been in use for agricultural for 81 years. The first samples represent the soil with very low fertility, because they did not receive any organic and mineral fertilisers and any plant residues for 81 years. The second category of samples represents the soil with low fertility and low pH value because they did not receive any mineral fertilisers and any lime for the whole trial period. The third category of samples represents the soil under long agriculture use typical for the region. The fourth category represents the soil under the natural south taiga vegetation.

The laboratory experiment was carried out by the following procedure: 20 g of soil for each replication was put in a 100-ml glass vessel, closed and incubated for 10 days at 25 °C and 60% field capacity for the beginning of the experiment. 0.2 mg each of labelled [2-^{14}C]-glycine (3.95 MBq of ^{14}C total activity) and [2-^{14}C]-glucose (2.61 MBq) were added as aqueous solutions to 20 g of pre-incubated soil. A small bowl (Ø = 12 mm) with 1 ml of 1 N NaOH was put on the soil in each vessel. The soil with labelled substances was incubated furthermore at 25 °C and 60% field capacity for 3 months.

During the 3 months of incubation the $^{14}CO_2$ was absorbed in 1 N NaOH, which was replaced periodically [19]. To measure the ^{14}C activity of the CO_2 trapped in the NaOH, 1 ml NaOH along with 2 ml distilled water were added to 6 ml gel scintillation cocktail Luma Gel (Lumac Co.). The ^{14}C activity measurement was performed at the end of chemoluminescence in a beta spectrometer "Rackbeta" (LKB Wallac, model 1219). The standardisation for ^{14}C absolute activity was carried out using an extended standard method [SQP(E)] with addition of NaOH solution as a quencher. The ^{14}C activity measurement error did not exceed 2%.

The experiment was carried out in duplicate. The differences in ^{14}C activity between parallels did not exceed 3.5% of measured ^{14}C activity.

Results and Discussion

Rapid degradation occurs after addition of labelled glucose and glycine to the soil. The experimental data resulting from $^{14}CO_2$ efflux from the soil are presented as points on cumulative curves (Fig. 2). Glycine decomposed faster than glucose in all soil samples studied. The $^{14}CO_2$ evolution rates of glycine on the first day are 2–4 times higher than those of glucose. On the first day of incubation more than 50% of the ^{14}C input activity of glycine was liberated, but only 25% of glucose input activity was evolved. After 1 week of incubation the $^{14}CO_2$ efflux rates were stabilised and did not exceed about 1% of the input activity per day afterwards.

Both of the investigated substances were decomposed most rapidly in the soil samples from eternal fallow plots and from eternal rye plots (see the decomposition parameters in Table 2).

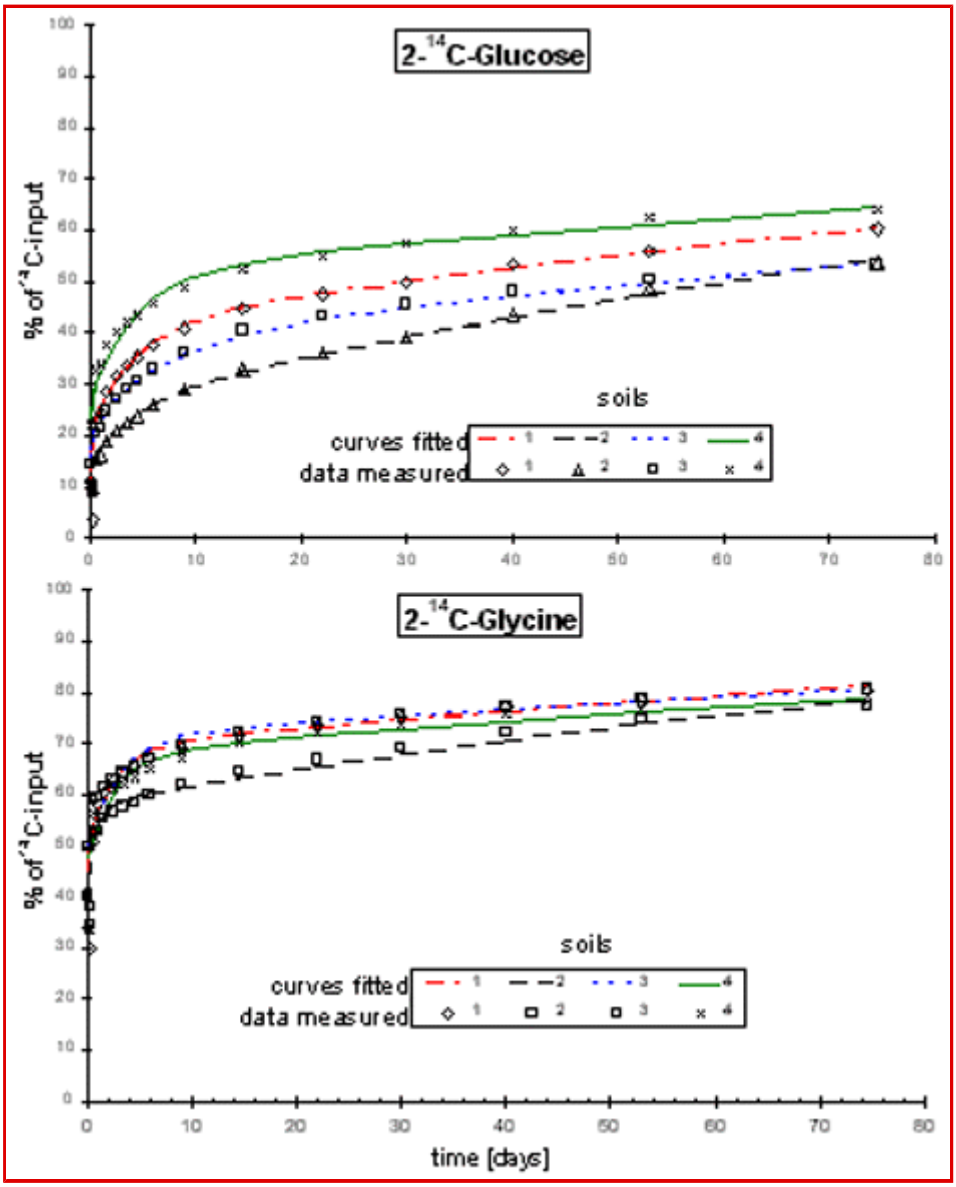

Fig. 2 Experimental cumulative $^{14}CO_2$ efflux from four different soils (1–4) during decomposition of [2-^{14}C]-glucose (above) and [2-^{14}C]-glycine (*below*), and their non-linear regression lines calculated according to the model. ^{14}C in percentage of input. (*1* eternal fallow soil; *2* eternal rye; *3* crop rotation; *4* forest soil)

Table 2 Model parameters based on decomposition of [2-^{14}C]-glucose and [2-^{14}C]-glycine in four different soils and calculated by given use efficiency (Y)

	[2-^{14}C]-glucose (Y=0.47)				[2-^{14}C]-glycine (Y=0.31)			
	a	b	g	H	a	B	g	H
Sample	(day^{-1})	(day^{-1})	(day^{-1})	(%)	(day^{-1})	(day^{-1})	(day^{-1})	(%)
1, Fallow	4.3	0.22	0.0053	0.58	14	0.43	0.0068	0.31
2, Rye	23	0.23	0.0065	0.73	44	1.1	0.0090	0.42
3, Rotation	8.0	0.15	0.0038	0.61	36	0.35	0.0054	0.29

4, Forest	9.9	0.23	0.0042	0.48	28	0.39	0.0057	0.32
Mean	11.3	0.21	0.0055	0.60	30	0.57	0.0067	0.33
Correlation coefficient (glucose–glycine)					0.83	0.41	0.98	0.73

a, Rate constant of microorganism utilisation of free substance;
b, rate constant of dying off and decomposition of microorganisms;
g, rate constant of microorganism utilisation of bound substance;
H, adsorption ratio.

From these results we calculated the model parameters.

At first, the ^{14}C content in soil was calculated by:

$$^{14}C_{soil} = \left[100\%_{of\ ^{14}C\ input\ activity}\right] - \left[^{14}CO_2\ _{(emitted\ activity)}\right] \quad (9)$$

This procedure is very useful because the ^{14}C content in soils allows the estimation of the model parameters using proportional weighting. The first CO_2 samples have higher absolute errors than later ones, and the proportional weighting takes these errors into consideration. The errors of values are proportional on using proportional weighting to the measured values. This corresponds with our experiment measurements.

Secondly, all five characteristic model parameters – constants of decay rates for original free glycine or glucose (a), microbial biomass (b) substances adsorbed to humus (g) as well as the values of Y and H – were calculated by using Eq. 7 by the non-linear regression method with least squares procedure (these calculated parameters are not presented here).

The value of the coefficient Y of glucose and glycine (the portion of carbon used for biosynthesis by microorganisms) is similar to the use efficiency of easily decomposed substances, which are utilised by many microorganisms [6, 21, 25]. For most microorganisms the portion of substrate carbon that will be incorporated into cell carbon does not exceed 50%. It can be accepted that this coefficient is about the same for most microorganisms from different soils because the parameters "use efficiency" is relatively constant independent of the environment [20] and dependent essentially on the investigated substance. Hence, we use the mean use efficiency of microorganisms from the investigated soils for the following calculations. This procedure leads to an increase of the significance of another model parameter calculated by the non-linear regression. The average values of Y (0.47 for glucose and 0.31 for glycine) were used to calculate the remaining four model parameters in the last step. They are presented in Table 2.

Figure 2 shows the curves corresponding to the regression model with the calculated coefficients. The initial decomposition rates of [2-^{14}C]-glucose calculated according to the suggested model were lower then those of [2-^{14}C]-glycine.

According to their decomposition constants (k) we calculated half-life periods ($T_{1/2}$) of the initial substance, substance bound in microbial biomass and adsorbed substance as follows:

$$T_{1/2} = \frac{\ln(2)}{k} \quad (10)$$

This is necessary in order to be able to compare the calculated results with the other data presented in the literature. The calculated half-life periods are presented in Table 3.

Table 3 Calculated half-life periods of free and adsorbed glucose and glycine, and of microbial biomass

formed from these substances

	[2-^{14}C]-glucose			[2-^{14}C]-glycine		
	$T_{1/2}a$	$T_{1/2}b$	$T_{1/2}g$	$T_{1/2}a$	$T_{1/2}b$	$T_{1/2}g$
Sample	(h)	(days)	(days)	(h)	(days)	(days)
1, Fallow	4.3	3.3	130	0.38	0.76	87
2, Rye	0.52	2.9	110	0.38	0.62	77
3, Rotation	1.6	4.4	200	0.64	3.4	124
4, Forest	2.4	4.3	165	1.1	3.8	145
Mean	2.2	3.7	150	0.62	2.1	109

$T_{1/2}a$, half-life period for free substance;

$T_{1/2}b$, half-life period for substance fixed in microbial biomass;

$T_{1/2}g$, half-life period for adsorbed substance

The calculated half-life periods of the substances (free glycine and glucose, substance fixed in microbial biomass and adsorbed on humus and clay minerals) are similar to previously reported decay rates of soil microorganisms, obtained by other methods [8, 15, 23, 28]. However, the decomposition rates of amino acids decomposed in soils at 20 °C obtained by [5] were considerably slower. The calculated half-life periods of microbial soil biomass ($T_{1/2}b$; Table 3) are similar to some data of soil bacteria lifecycles, obtained with others methods. However, big differences exist between turnover rates of soil microorganisms reported in the literature. Babjeva and Senova [4] reported that during one vegetation period, 30–40 soil bacteria generations are changed in a Podzoluvisol. The turnover rates of microbial soil biomass calculated by [25] are between 0.25 and 3^{-1} year, which corresponds to half-lives of 2.8–0.2 years. We suppose that the data reported in this paper and in [4] correspond only to the potential turnover rate of microbial soil biomass, especially of soil bacteria, by sufficient amount of easily decomposable organic substrate. These fast turnover rates of microbial biomass are impossible in natural soils if only average amounts of available substrate are present.

The achieved model parameters for glucose correlate with the parameters of glycine for the different soil samples (Table 2). The highest correlation coefficients were found for parameters that depend on soil properties, such as the adsorption capacity (H), the soil biochemical activity (b) and the decomposition rates of humic substances (g). It is likely that the present model can be used to characterise biological activity of soils and their adsorption capacity to low molecular organic substances.

The maximal decomposition rates for glycine and glucose were obtained from the soil with eternal rye and without fertilisers. The quantity of microorganisms (colony form units) in this soil is 2.5 times as high as that of eternal fallow soil [26]. The data of [26] found in the past can be used for our soil samples taken in 1993 because most of the parameters of microbial biomass and soil organic matter are in steady state after 30–40 years in the long field experiments. The whole quantity of soil microorganisms with crop rotation is 3 times as high as those of the eternal fallow soil [26], but probably mineralisation activity of microorganisms is not higher than that of the soil with eternal rye and without fertilizers. Other authors [25] have found that the average turnover rates of microbial biomass of the fallow soil are 1.5–2 times faster than in plots of the 2-year crop rotation, and the turnover rates of the 2-year crop rotation are 1.5 times faster than those of the 5-year rotation. Biederbeck et al. [7] concluded that the larger amount of microbial biomass in soils under continuous rotation must be less active than the smaller amount of microbial biomass in fallow soils. Turnover of microbial biomass requires sufficient C input for growth and turnover. Therefore, less microbial biomass in a dystric soil has shorter half-life periods than a larger amount in a soil with a high quantity of available C.

The portion of glucose incorporated into humus substances and clay minerals (Table 2) corresponds to the clay content of soil (Table 1). For glycine, however, this relation is not significant. Dashman and Stotzky [12]

have shown that glycine is the only amino acid that is not adsorbed onto different clay minerals.

The suggested model also allows us to describe the dynamics of ^{14}C incorporation in microbial biomass (Fig. 3). The experimental estimation of ^{14}C incorporation is rather difficult because of the absence of the methods permitting the complete extraction of microorganisms from soil without destruction of their structure. The theoretical curves of ^{14}C incorporation from glucose and glycine into soil biomass have a maximum , on the first day (Table 4). The location of this maximum on the time axis is completely determined by the soil type as a ratio of the constants of decomposition, a, b and g. A maximal amount from 12 to 22% of ^{14}C input activity is incorporated into microbial biomass depending on the soil and investigated substances (Table 4).

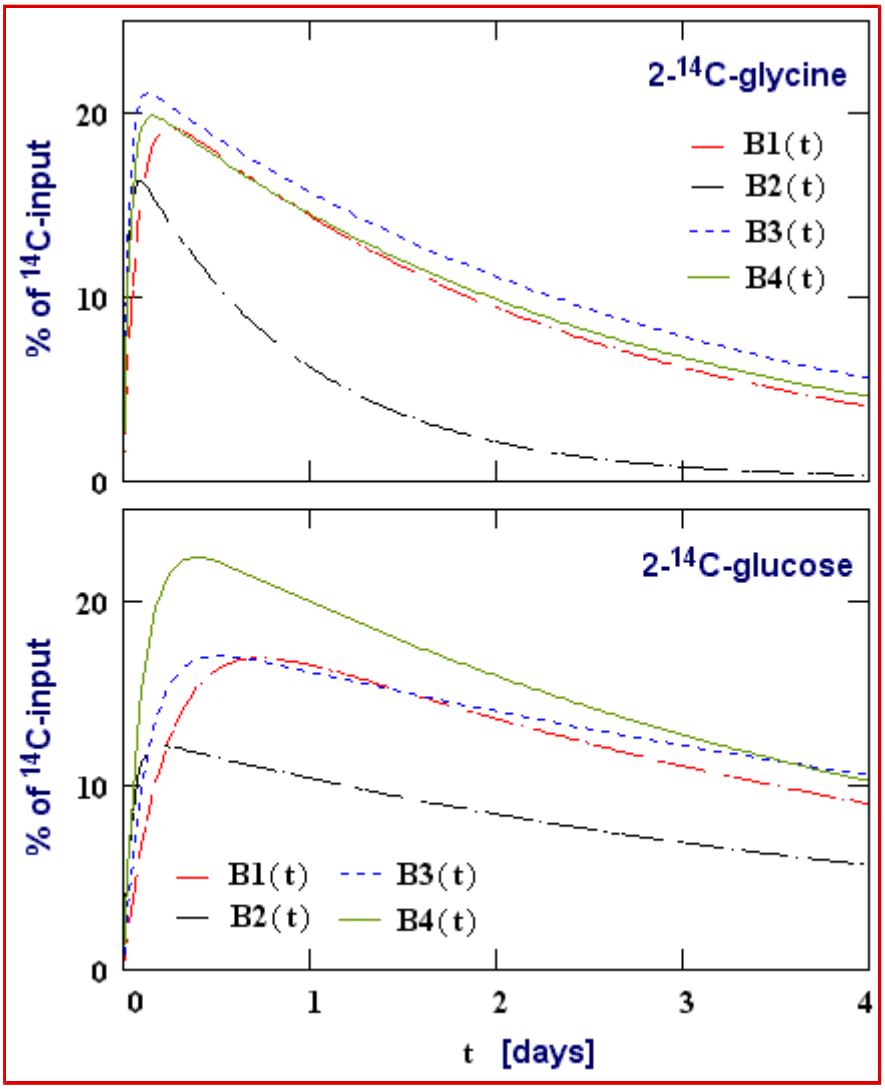

Fig. 3 Expected use of ^{14}C by biomass (*B1–B4*) in four different soils (*1–4*) after pulse addition of [2-^{14}C]-glucose (*above*) and [2-^{14}C]-glycine (*below*). Soil samples as in Fig. 2. ^{14}C use in percentage of input

Table 4 Indices of [2-^{14}C]-glucose and [2-^{14}C]-glycine carbon utilisation by soil microorganisms

	[2-^{14}C]-glucose			[2-^{14}C]-glycine		
	t_{max}	B_{max}	I	T_{max}	B_{max}	I
Sample	(h)	(%)	(% day^{-1})	(h)	(%)	(% day^{-1})
1, Fallow	18	17	138	6.1	19	60

2, Rye	4.9	12	122	2.1	16	23
3, Rotation	12	17	177	3.1	21	71
4, Forest	9.3	22	138	3.7	20	63

t_{max}, Time (in hours) of maximal ^{14}C incorporation into soil microbial biomass;

B_{max}, maximal incorporation of ^{14}C into soil microbial biomass (% of input activity);

I, area below calculated curve of substances used by soil microbial biomass (% of ^{14}C input day^{-1})

The presented results correspond well to the experimental curve of the formation and the decay of the isotope-labelled microbial biomass during the decomposition of ^{14}C and ^{15}N-labelled plant material [18].

The area under the corresponding curve (Fig. 3), i.e. integral of function B(t) with time, can be calculated as the direct index of carbon utilisation by soil microorganisms. This parameter is the product of the part of the added substance and its utilisation time by microbial biomass. It shows which part of the added substance was used by microorganisms and for how long. So the use of the second carbon atom from glucose by soil microorganisms is approximately 2–5 times higher than from glycine (Table 4).

The microbial oxidation of glucose and that glycine adsorbed on the surface of humic substances is approximately equal. Hence, the investigated substances (glucose and glycine) have similar accessibility to soil microorganisms even after their incorporation into the soil organic matter.

Conclusions

The presented model describes the experimental curve of CO_2 efflux from soil by decomposition of low molecular organic substances like glycine and glucose. It has five model coefficients, each with a clear physical meaning. The parameters of the model can be directly estimated by using the routine non-linear regression method. The calculated values of the decomposition rates of glycine and glucose correspond well to other data of mineralisation of low molecular organic substances in the literature.

Therefore the model can be used:

1. to calculate decomposition rates and half-life periods of free and adsorbed substances, and also to calculate microbial biomass formation from use of the supplied substances;
2. as a component part in a general model of substance transformation in soil;
3. to characterise biological activity of soil samples.

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