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Modelling the effect of active roots on soil organic matter turnover

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Abstract

The aim of this experiment was to study the effect of living roots on soil carbon metabolism at different decomposition stages during a long-term incubation. Plant material labelled with ^{14}C and ^{15}N was incubated in two contrasting soils under controlled laboratory conditions, over two years. Half the samples were cropped with wheat (*Triticum aestivum*) 11 times in succession. At earing time the wheat was harvested, the roots were extracted from the soil and a new crop was started. Thus the soils were continuously occupied by active root systems. The other half of the samples was maintained bare, without plants under the same conditions. Over the 2 years, pairs of cropped and bare soils were analysed at eight sampling occasions (total-, plant debris-, and microbial biomass-C and -^{14}C). A five compartment (labile and recalcitrant plant residues, labile microbial metabolites, microbial biomass and stabilised humified compounds) decomposition model was fitted to the labelled and soil native organic matter data of the bare and cropped soils. Two different phases in the decomposition processes showed a different plant effect. (1) During the initial fast decomposition stage, labile ^{14}C-material stimulated microbial activities and N immobilisation, increasing the ^{14}C-microbial biomass. In the presence of living roots, competition between microorganisms and plants for inorganic N weakly lowered the measured and predicted total-^{14}C mineralisation and resulted in a lower plant productivity compared to subsequent growths. (2) In contrast, beyond 3–6 months, when the labile material was exhausted, during the slow decomposition stage, the presence of living roots stimulated the mineralisation of the recalcitrant plant residue-^{14}C in the sandy soil and of the humified-^{14}C in the clay soil. In the sandy soil, the presence of roots also substantially stimulated decomposition of old soil native humus compounds. During this slow decomposition stage, the measured and predicted plant induced decrease in total-^{14}C and -C was essentially explained by the predicted decrease in humus-^{14}C and -C. The ^{14}C-microbial biomass (MB) partly decayed or became inactive in the bare soils, whereas in the rooted soils, the labelled MB turnover was accelerated: the MB-^{14}C was replaced by unlabelled-C from C derived from living roots. At the end of experiment, the MB-C in the cropped soils was 2.5–3 times higher than in the bare soils. To sustain this biomass and activity, the model predicted a daily root derived C input (rhizodeposition), amounting to 5.4 and 3.2% of the plant biomass-C or estimated at 46 and 41% of the daily net assimilated C (shoot + root + rhizodeposition C) in the clay and sandy soil, respectively.

Introduction

There is a substantial body of information reviewed by Wipps (1990) on the amounts and quality of root-derived organic compounds released in the rhizosphere and defined as rhizodeposition. More recently the effect of plant below-ground activity on nutrient mobilisation has raised new interest as a response to atmospheric CO_2 increase (Rogers et al., 1994; Van Noordwijk et al., 1998; Van Veen et al., 1991). The release of organic compounds in the rhizosphere is recognised as a major energy input to the soil, provid-

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ing an essential driving force for microbial mediated processes: carbon mineralisation–humification, nutrient mobilisation, mineralisation and immobilisation, denitrification (Quian et al., 1997) and maintenance of soil structure. However some essential questions on how the root and rhizosphere activity positively or negatively affects decomposition (Dormaar, 1990)

Materials and methods

Data acquisition

Data were obtained from an incubation experiment carried out under controlled laboratory conditions and previously described by Sallih and Pansu (1993) and

soil was immediately divided into several portions for analyses. The following analyses previously described (Pansu et al., 1998; Sallih and Pansu, 1993) were performed: C and ^{14}C of (1) the whole soil, (2) the undecomposed labelled plant debris separated from the soil by flotation and wet sieving, (3) the microbial biomass determined by the fumigation–incubation technique (Jenkinson and Powlson, 1976), and (4) the plant materials (shoots and roots) of the 11 wheat crops. The cumulated total loss of soil ^{14}C adhering to the roots at plant harvests did not exceed 4% of the initial ^{14}C. The statistical analyses are described in Sallih and Pansu (1993).

Mathematical model

The MOMOS-Carbon model describing C-transfer in the soil organic matter, has been previously presented by Sallih and Pansu (1993) and extended to N-transfers (MOMOS-N, Pansu et al., 1998). Five organic compartments were defined: (Figure 1): V_L, V_R are labile and resistant plant residues; A is labile microbial metabolite; B is microbial biomass; and H is stable humified materials. In the present model, two additional compartments describe the plant carbon: (1) dead plant material entering the soil (Dead Plant Material, DPM) and (2) living plant material (Living Plant Material, LPM, Fig. 1). The organic carbon (oC) dynamics of a given compartment m in relation with i compartments is given by:

$$\frac{doC_m}{dt} = -k_m oC_m + P_m \sum_i k_i oC_i + f(t)f(m,l) DPM + f(m)k_r LPM \quad (1)$$

The first (1 in figure 1) and second (2 in figure 1) terms previously described in Pansu and Sallih, 1993) of Eq. (1) indicate a first-order kinetics decrease in each soil compartment with kinetic constants k_i (T^{-1}, with $k_A = k_{V_L}$); P_m (dimensionless) represents the proportion of carbon input from compartments i to the compartment m (with $P_{V_L} = P_{V_R} = 0$). The metabolised material (balance between total ^{14}C minus plant debris-^{14}C minus microbial biomass-^{14}C) could not be described with only one first-order kinetic compartment H (HUM of the model of Jenkinson, 1990). Thus compartment A was integrated as labile metabolites. The predicted total ^{14}C and microbial biomass-^{14}C were more sensitive to changes of P parameters than changes in k parameters, especially for P_A which regulates the greatest C flow. Modification of P_H (the lowest P parameter influenced only predicted total ^{14}C at the end of experiment. Changes in any k parameter modified first the C content of the corresponding compartment. The effect of k_H modifications on total ^{14}C were weak during the years of experiment but it becomes important for long-term predictions.

The third (3 in figure 1) term ($f(t)f(m,l)DPM$) defines the C of dead plant material (DPM, g C kg^{-1} dry soil day^{-1}) entering the soil. The DPM flow is distributed into V_L and V_R by the Boolean function $f(t)$ (with $f(t) = 1$ when t = the input time, else $f(t) = 0$) and a distribution function $f(m,l)$ (with $f(m,l) = 0$ for $m \in \{A, B, H\}$, $f(m,l) = l$ for $m = V_L$, $f(m,l) = 1 - l$ for $m = V_R$; l = labile fraction of DPM input set at 0.7 from plant debris ^{14}C data).

The last (4 in figure 1) term of equation 1 ($f(m)k_r LPM$) expresses the rhizodeposition, that is the C input derived from living roots (Living Plant Material = LPM, g plant-dw kg^{-1} dry soil) regulated by a distribution function $f(m)$ (with $f(m) = 0$ for $m \in \{V_L, V_R, B, H\}$, and $f(m) = 1$ for $m = A$). The constant k_r, defining the proportion of C derived from living roots and entering the soil was calculated in two ways: (1) at any time during plant growth, k_r (g C g^{-1} plant-dw day^{-1}) is considered as a constant proportion of plant-dw (shoots + roots; equation 1); (2) k_r (g C g^{-1} plant-dw) is a constant proportion of the plant daily net production (shoots + roots). In Eq. (1), replace LPM by d(LPM)/dt (= Eq. (1′)).

In the model, the living root effect is based on two assumptions: (1) during the active root phase (in this experiment from seedling to earing time), the C-input from roots is a constant (k_r) proportion of LPM (Eq. (1)) or d(LPM)/dt (Eq. (1′)); (2) C input derived from living roots is essentially composed of labile compounds (Wipps, 1990). This material is directly incorporated into compartment A (labile metabolites). Sensitivity test showed that 10% change in k_r values induced a corresponding linear modification in predicted total- (3%) and microbial biomass-C (10%).

LPM (shoots + roots) was simulated at each cultivation (Fig. 2) from the harvested plant material dry weight by a classical logistic function (Eq. (2)):

$$LPM^j = \frac{LPM^J_{\max}}{1 + e^{\alpha LPM^j_{\max}(t^j - t^j_{1/2})}} \quad (2)$$

where $LPM^j_{\max}$ is total dry matter of the harvest j, t^j is growth time since planting of the seedlings, j, $t^j_{1/2}$ is half of the growth period, α is growth kinetic parameter set at 0.001 day^{-1} to simulate the wheat growth.

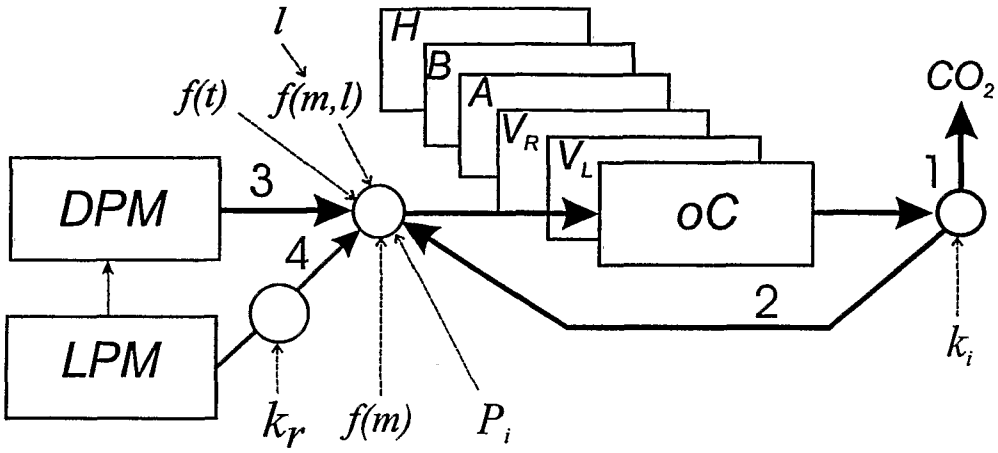


Figure 1. The MOMOS-C model. Five soil organic carbon (oC) compartments (V_L, labile plant material; V_R, resistant plant material; A, labile metabolites; B, microbial biomass; H, stable humified material). Two plant material compartments (DPM, dead plant material = above ground and root litter; LPM, living plant material). The numbers correspond to the terms in Eq. (1): 1, carbon mineralisation; 2, humification; 3, dead plant material-oC input (litter); 4, oC input from living roots (rhizodeposition). The parameters are defined in Eq. (1).

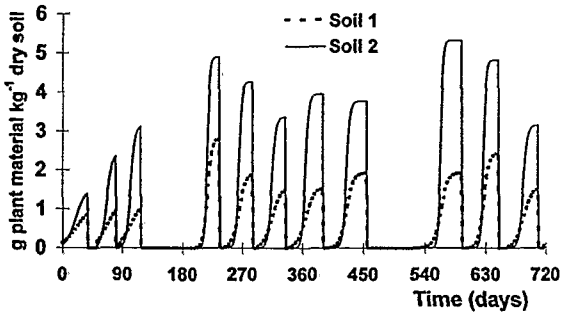


Figure 2. Simulated production of plant material over the eleven successive wheat growths (see Eq. (2)). LPM_{max} was set to the measured plant dry weight at each harvest.

The daily net plant production was simulated by the differential form of Eq. (2), giving Eq. (2′):

$$\frac{d(LPM^j)}{dt} = \alpha LPM^j \left(1 - \frac{LPM^j}{LPM^j_{\max}}\right) \qquad (2')$$

In the experiment and for the simulation, the dead (labelled) plant material (DPM) was introduced in the

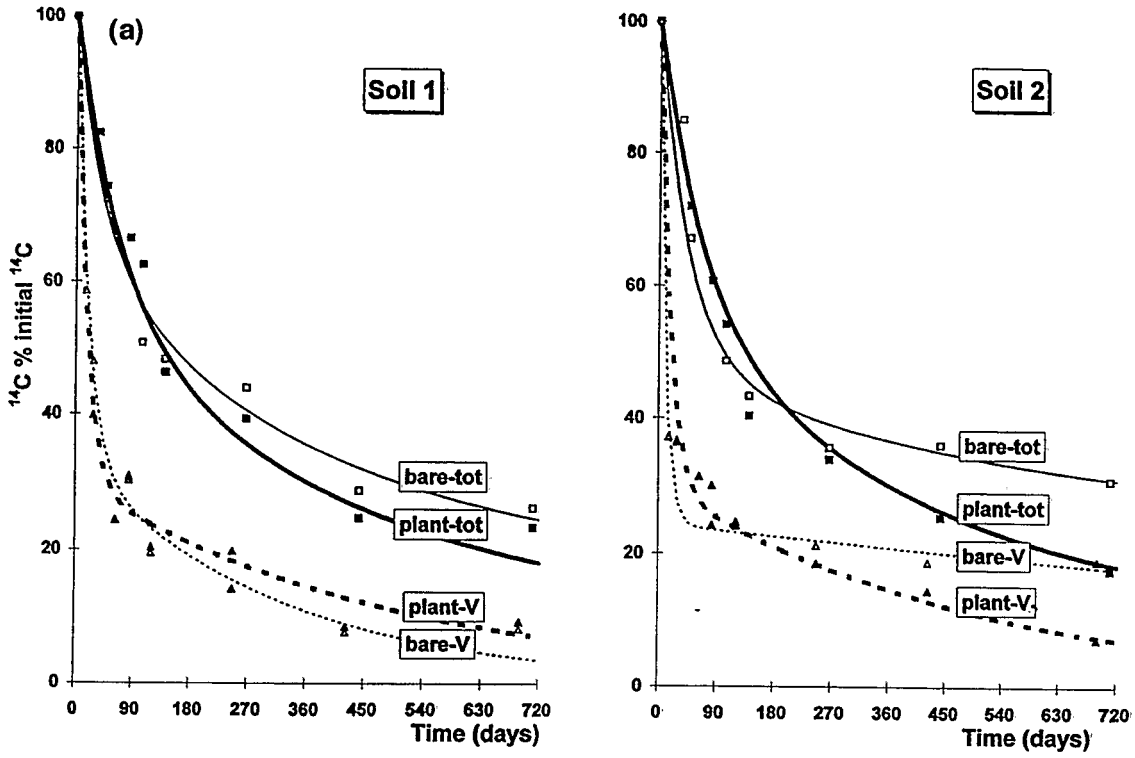
where r identifies the number of sampling points; q is the number of data series and y_{qr} and $\hat{y}_{qr}$ are the measured and the predicted value of each data point respectively; w_q are weight coefficients for each data series. For these data, w_q was set at 0.3, 0.3 and 1 for total-, plant material- and microbial-^{14}C, respectively.

Results and discussion

Mineralisation and humification of labelled plant material

The respective parameters describing the ^{14}C dynamics were different for the two bare soils. In contrast when the two cultivated soils are compared, the parameters were similar (Table 1).

The presence of living plants lowered the measured and predicted total ^{14}C mineralisation during the first 3 (soil 1) or 6 (soil 2) months (Fig. 3A). Nevertheless the retarding effect was weak, especially in soil 1. During the initial decomposition stages, the


(a)
Soil 1
Soil 2
^{14}C % initial ^{14}C
Time (days)
bare-tot
plant-tot
plant-V
bare-V
0
20
40
60
80
100
0
90
180
270
360
450
540
630
720

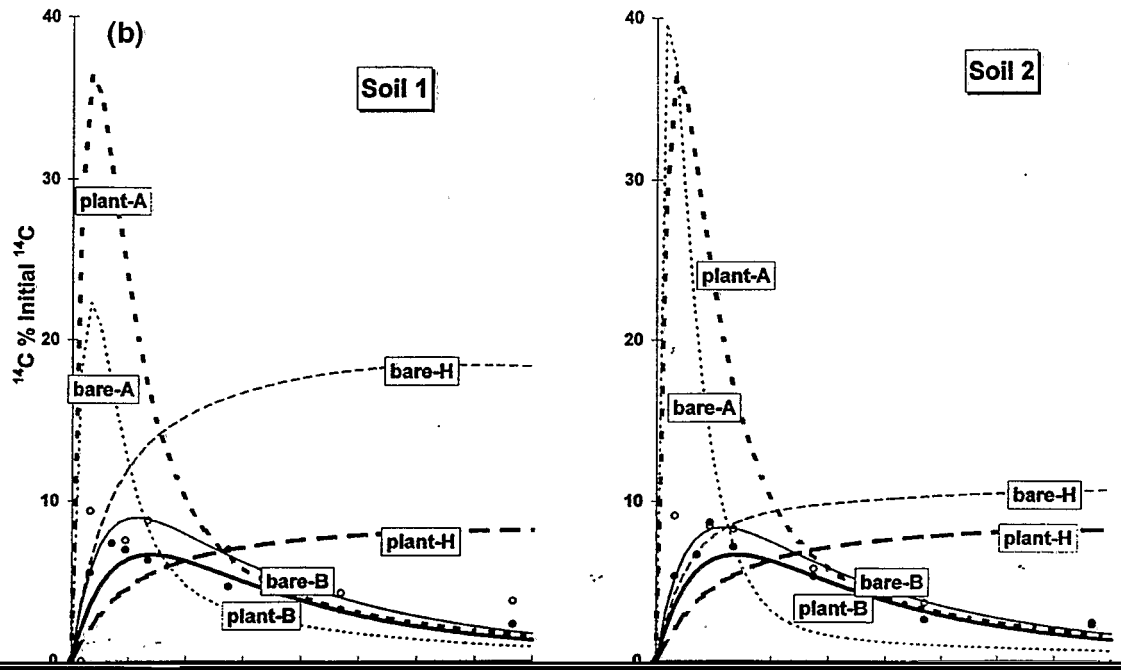

(b)
Soil 1
Soil 2
^{14}C % Initial ^{14}C
plant-A
bare-A
bare-H
plant-H
bare-B
plant-B
0
10
20
30
40

Table 1. Optimised model parameters for bare and cultivated soils

Compartment	Bare soil 1		Bare soil 2		Culivated soils 1 and 2	
	k_i	P_i	k_i	P_i	k_i	P_i
V_L	0.05	0.0	0.1	0.0	0.06	0
V_R	0.0031	0.0	0.00043	0.0	0.002	0
A	0.05	0.58	0.1	0.79	0.06	0.77
B	0.006	0.08	0.004	0.033	0.006	0.037
H	0.0004	0.08	0.0001	0.025	0.00025	0.02

K_i, kinetic constants (day^{-1}); P_i, proportion of compartment input. For the cultivated soils the parameters were similar.

partly became dormant by exhaustion of available ^{14}C-substrate. In the planted systems, part of the microbial biomass, stimulated by the input of labile C derived from the roots, remained active and ^{14}C was progressively replaced by unlabelled C derived from the roots. The qCO_2-^{14}C values (microbial metabolic quotient for CO_2-^{14}C) calculated by Bottner et al. (1988) for both systems, revealed that in the rooted soils the labelled biomass was smaller but more active than in the bare soils. Thus during the slow decomposition phases, the presence of roots accelerated the turnover of the portion of microbial biomass which previously used the labelled plant material as substrate. In Table 1 for soil 1, k_B (k_i for compartment B) is similar in bare and cultivated soil, but P_B in the planted soil is half that of bare soil, illustrating the higher turnover of C in compartment B of the planted soil.

In the Rothamsted model, Jenkinson (1990) described the effect of living plants by multiplying the first order kinetic constants by a constant factor ('retainment' factor). The present experiment shows that (1) the multiplication factor of k_i (Table 1) cannot be constant and (2) the plant effect varied positively or negatively depending on the decomposition phases, as illustrated by the total ^{14}C mineralisation and the plant debris-^{14}C decomposition (Fig. 3A). In bare soils, the model parameters (k_i and P_i, Table 1) varied according to the soil properties. In contrast for the planted soils, the model parameters were found to be similar for both soils. Thus, the plant effect could not be described by simply multiplying each bare soil parameter by a constant factor. The solution was to run the model for both treatments and to compare the re-optimised parameters of each treatment (Table 1). Nevertheless in a strictly mechanistic way, this procedure is not satisfying, since the plant effect could not be intrinsically described.

Total carbon transfers

Total-C was simulated using: (1) parameters defined

ment A. Thus A is defined by two origins: (1) labile microbial metabolites derived from the decomposing (labelled) plant material. In both bare soils, these transient compounds appear in small amounts essentially during the initial active decomposition phase (Fig. 4B), (2) labile material derived from active roots (rhizodeposits). The second origin is quantitatively greater than the first (compare bare to cultivated soils, in Fig. 4B), explaining the high fluctuation of simulated A related to the successive crops.

In the unplanted soils, the microbial biomass-C decreased from the beginning to the end of experiment, by a factor of 2.5–3 for both soils (compartment B, Fig. 4B), as a result of the progressive exhaustion of labile C (Sallih and Pansu, 1993). In contrast, with plants present, the measured and predicted microbial biomass-C remained at a relatively high level until the end of the experiment, illustrating the supply to micro-organisms of labile carbon derived from the living roots (A compartment). Nevertheless, the fluctuations of B are greatly attenuated compared to A. As a matter of fact, in the model 70% of A is directly mineralised and used as energy source and only 20% is used to build new microbial biomass. At the end of experiment, bare soil microbial biomass was 3 times lower than in the cultivated soils, illustrating the C and energy input derived from the roots.

The predicted H compartment (the stabilised humus, Fig. 4A) remained relatively stable in soil 1 under both bare and cultivated soil conditions. In contrast, in soil 2 the predicted H decreased substantially in the presence of plants. Thus the presence of living roots stimulated the mineralisation of the stabilised unlabelled soil native humus. In cultivated soil 2, when the k_H value of 0.00025 obtained from the ^{14}C data was used (as for the other k_i and P_i parameters, Table 1), the predicted H values were too high to properly describe the total-C dynamics. A new optimisation gave $k_H = 0.0007$. Thus in this cultivated soil 2, the parameters describing the ^{14}C dynamics could not be used to describe the unlabelled H compartment, indicating

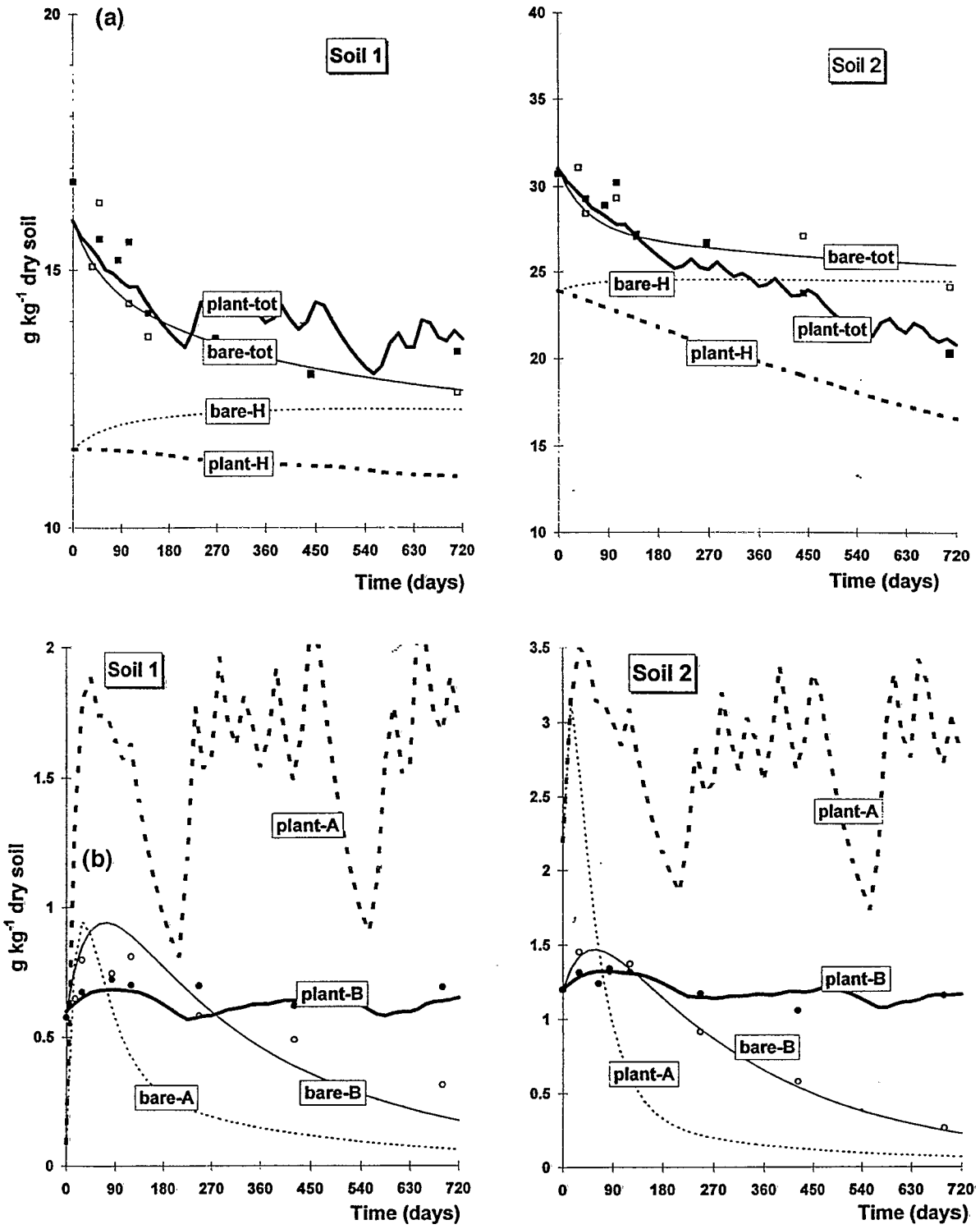


Figure 4. Measured and predicted total carbon distribution (g C kg^{-1} dry soil) in the soil compartments in bare and cultivated soils 1 and 2.

Conclusion

The present experiment investigated the effects of active roots on decomposition of labelled plant material, throughout a complete decomposition cycle, from very fast to slow stages dominated by dormant organisms. The root effect could not be described by simple multiplying factors. This illustrates the complexity of the root effect and the difficulty to parametrise the process, when multi-compartment models are fitted to measured soil carbon pools. Thus the plant effect cannot yet be easily extended to other soil and growth conditions. The generalisation of multi-compartment

from the root deposited carbon. During the slow decomposition phase, in the bare soils, the biomass decreased 2.5-to 3-fold by progressive energy exhaustion. By contrast in the cultivated soils, high biomass levels were maintained until the end of the experiment.

To maintain this high biomass level in the cultivated soils and to sustain its activity, the model predicts an input of labile C derived from the roots and related to the plant growth. This predicted organic rhizodeposition was described as a mean proportion of the living biomass: (shoots+roots) or as a mean proportion of the daily plant production. At each day, the mean

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