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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) and how the rhizodeposits are used in the soil, still remain unanswered. Shields and Paul (1973) and Jenkinson (1977) demonstrated by field experiments, that decomposition of ^{14}C-labelled plant material is substantially lowered in the presence of cultivated plants or under natural grassland when compared to bare soil. In these field experiments the reduction in the decomposition rate is essentially explained by the modification of soil water balance by plant transpiration, lowering microbial activity. In addition to this indirect effect, nutrient uptake by plants, modifying the soil nutrient balance and subsequent N-mediated microbial processes, is another plant-induced modification. Thus Merckx et al. (1985, 1987) demonstrated that in N poor soils, the rhizosphere microbial biomass was controlled by N-limitation, despite the supply of available C derived from the roots. This illustrates the complexity of the response of soil net C and N mineralisation rates to the presence of active roots, resulting from the link between the C and N cycles and involving (1) the active roots as a net C source and net N sink, (2) decomposing dead plant material as a labile C supply and (3) the stabilised humus as a probable N source. In this system, the microbial biomass is the key pool linking the C and N cycles. Thus the still controversial question is: how the root and rhizosphere activity directly affects soil organic matter decomposition, modifying the energy input and nutrient balance.

In the present work, ^{14}C- and ^{15}N-labelled plant material was incubated in two contrasting soils over 2 years in pots under controlled laboratory conditions. Half of the pots were cropped with wheat, 11 times in succession, whereas the other half was treated as uncropped control bare soils. A carbon decomposition model was fitted to the results of both treatments. The aim was to describe and predict the effect of roots during a long-term incubation, involving the initial fast phase of fresh labelled plant material decomposition and the later slower phase, when the ^{14}C derived from the plant material was stabilised in humus compounds.

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 Pansu et al. (1998). Briefly, two Mediterranean soils from southern France were selected, differing mainly by their texture and organic matter content: soil 1, a clay soil (C 1.2%; N = 0.12%; clay content = 29%; total sand = 27%; pH(H_2O) = 7.9); and soil 2, a sandy soil (C = 2.7%; N = 0.20%; clay content = 11%, total sand = 66%; pH(H_2O) = 6.5). After drying, sieving (5 mm mesh) and homogenisation, the soils were split into 18 portions of 800 g dry soil. Each portion was mixed with 7 g of mature uniformly ^{14}C- and ^{15}N-labelled wheat straw (stems + leaves; C = 46%; N = 1.0%; specific activity 2.59 MBq g^{-1} C), cut in about 1–2-cm pieces and placed in 10×10×12 cm plastic pots. The pots were installed in a ventilated growth chamber with 16 h light (25±4 °C) and 8 h dark (15±3 °C), at ambient atmosphere. Half the pots were cropped 11 times in succession with spring wheat (*Triticim aestivum*, cultivar 'Florence Aurore', six seedlings to each pot). After 1.5–2 months of growth, the plants were harvested close to earing time and the roots were removed from the soil by sieving and hand sampling. The next culture started 2–5 days after each harvest, using 4–7-day-old pre-germinated seedlings. Thus in the planted pots, the soil was constantly occupied by active roots (from seedling to earing). The experiment was performed without fertilisation. The wheat variety (an old cultivar) was chosen for its low nutrient requirement. The other half of the pots remained unplanted. In all pots with or without plants, soil moisture was maintained at 75±15% of the WHC by weight adjustment. In order to reduce evaporation, soil surface was covered with a perforated aluminium sheet covering 80% of the soil surface area. At each remoistening, pots were randomly replaced in the growing chamber. Pots without plants were treated in the same ways as pots with plants, especially for the soil mixing when the roots were removed. Between harvest of culture 3 and new seeding for culture 4 and again between growth 8 and 9, all the pots were kept bare for 80 days without moistening. The soils dried out progressively.

During the 2 years of experiment, eight samplings of one paired bare and cultivated pots were collected. After harvest of plants and removal of roots, the

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.

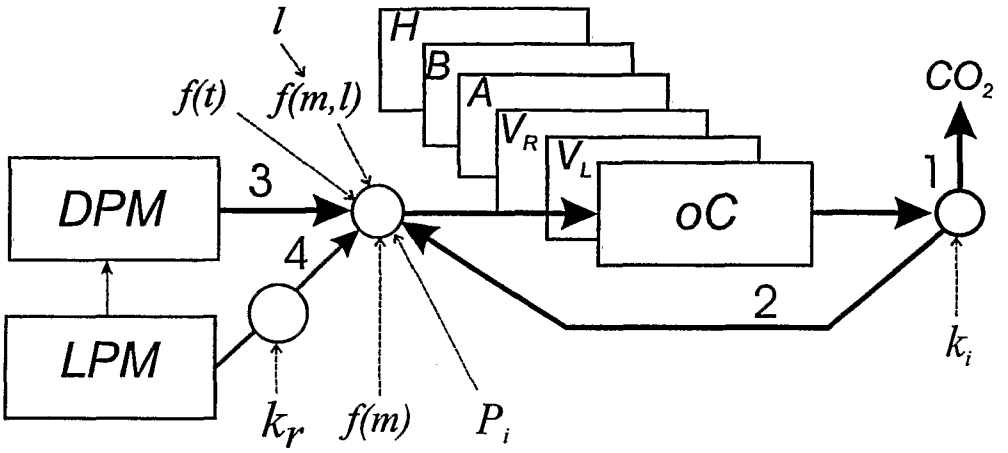


Figure 1. The MOMOS-C model. Five soil organic carbon (oC) compartments (V_L, labile plant material; V_R, resistant plant material; A, labile metabolites; B, microbial biomass; H, stable humified material). Two plant material compartments (DPM, dead plant material = above ground and root litter; LPM, 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).

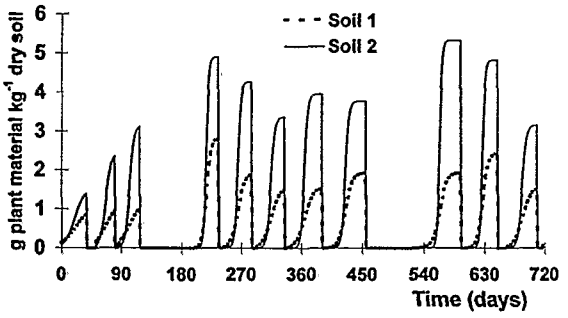


Figure 2. Simulated production of plant material over the eleven successive wheat growths (see Eq. (2)). LPM_{max} was set to the measured plant dry weight at each harvest.

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 soil only once, at the beginning of incubation (70% directed into V_L and 30% into V_R).

The numerical integration was performed using Euler's method and the parameter optimisation using Powell's method, by minimising the following criterion:

$$SSK = \sum_q w_q^2 \sum_r (y_{qr} - \hat{y}_{qr})^2 \qquad (3)$$

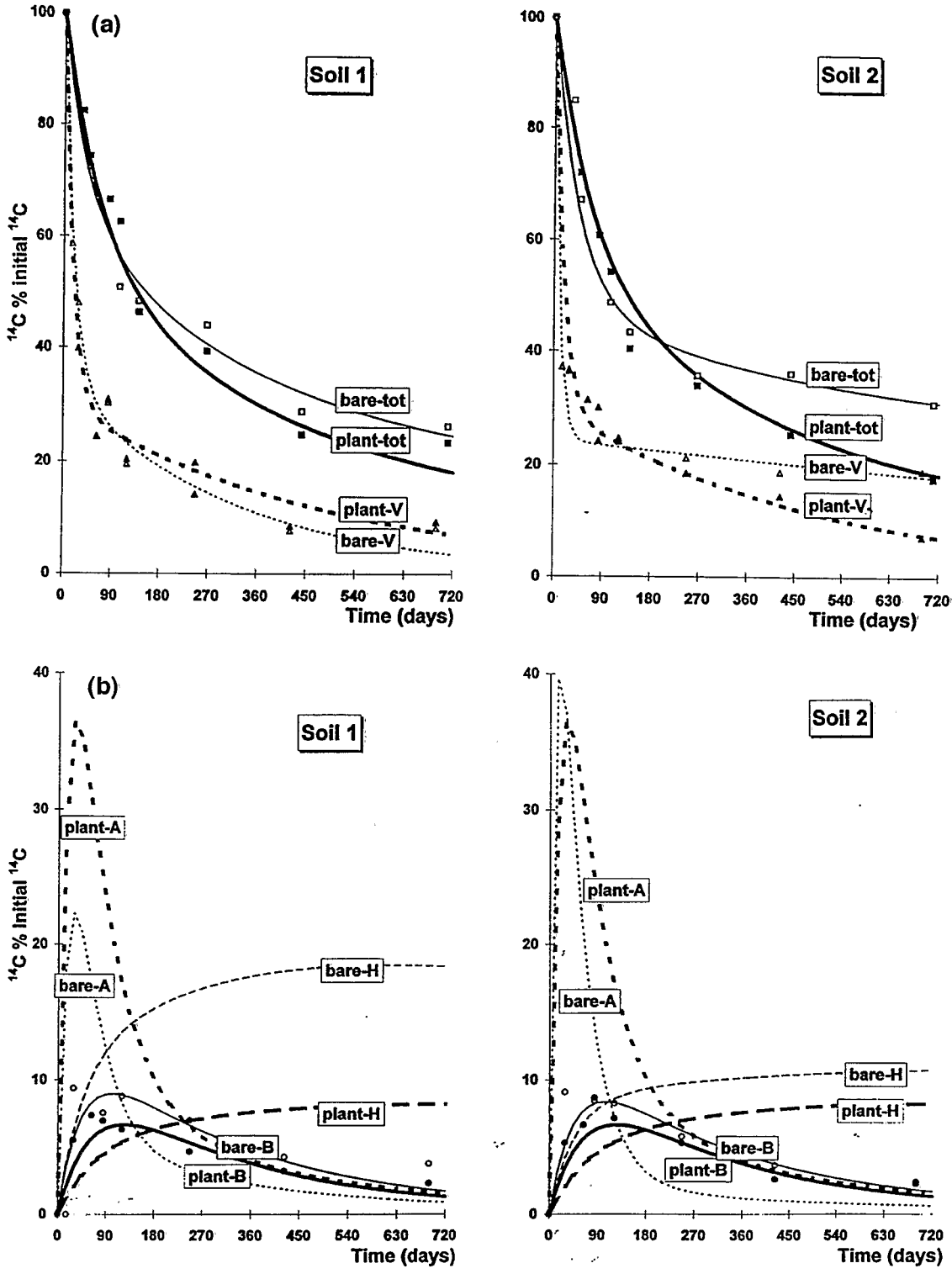
where r identifies the number of sampling points; q is the number of data series and y_{qr} and $\hat{y}_{qr}$ are the measured and the predicted value of each data point respectively; w_q are weight coefficients for each data series. For these data, w_q was set at 0.3, 0.3 and 1 for total-, plant material- 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 availability of labile labelled plant material stimulated the microbial activity and N immobilisation (Pansu et al., 1998). This active decomposition stage is illustrated by (1) high total-^{14}C mineralisation rates (Fig. 3A), (2) increasing microbial biomass-^{14}C, reaching maximum levels after 3–4 months (Fig. 3B) and (3) high microbial metabolic quotients for labelled CO_2 (qCO_2-^{14}C, Bottner et al., 1988). In the presence of living plants, the competition between roots and active micro-organisms for inorganic N lowered the total-^{14}C



ure 3. Measured and predicted ^{14}C distribution (in percent of total initial ^{14}C) in the soil compartments in bare and cultivated soils 1 and 2.

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.

mineralisation rates. This explanation is supported by the observations of Merckx et al. (1985, 1987) showing that in nutrient limited soils the N deficiency in the rhizosphere reduces the C metabolism. Thus the depletion of mineral nutrients by plants may limit microbial activity during active decomposition stages. The competition between micro-organisms and plants occurring during the initial decomposition stage, also resulted in a lower plant productivity (Fig. 2). The dry weight of plant material produced during the three first growths was lower than subsequent growths.

In contrast, beyond 3 or 6 months, the measured and predicted total-^{14}C mineralisation was significantly increased in both cultivated soils compared to the bare soils (Fig. 3A). The total-^{14}C remaining in the soils at the end of the experiment was 18% of the initially added ^{14}C in both cultivated soils, compared to 25 and 31% for bare soils 1 and 2, respectively. Thus, during the low activity stages, when the labile ^{14}C-compounds were exhausted, the presence of active roots stimulated the mineralisation of the more resistant ^{14}C-compounds. A similar stimulation of total-^{14}C mineralisation was observed by Cheng and Coleman (1990) as evidenced by a higher CO_2-^{14}C release and interpreted as resulting from a higher microbial metabolism.

In addition to the total-^{14}C mineralisation, the model predicts root-induced modifications of some measurable and unmeasurable organic matter compartments. In bare soils, the plant debris-^{14}C (V_L + V_R, Fig. 3A) remaining at the end of experiment was 4 and 18% of the initial ^{14}C in soil 1 and 2, respectively. In cultivated soils, this proportion was not significantly modified for soil 1, but greatly decreased to 7% for soil 2 (Fig. 3A). Thus, in soil 2 the roots accelerated the decomposition of the stable labelled plant debris, explaining partly the plant induced stimulation of total-^{14}C mineralisation.

In the presence of roots, the model predicts a decreased accumulation of the stabilised humus-^{14}C (H in Fig. 3B) especially in soil 1. At the end of incubation, the net ^{14}C accumulation in compartment H amounted to 8% of the total-^{14}C initially added for both cultivated soils, compared to 18% and 11% in bare soils 1 and 2, respectively. Thus, in soil 1, the lower total-^{14}C remaining at the end of the incubation in the cultivated soil (18%, Fig. 3A) compared to the bare soil (25%), is essentially explained in the model by a lower predicted (not measured) accumulation of stabilised humified-^{14}C in compartment H (Fig. 3B). For the bare soils, Sallih and Pansu (1993) explained the higher humification rates (accumulation in H) of the clay soil 1 (18%, Fig. 3B), compared to the sandy soil 2 (11%), by the properties of the clays to protect humified compounds (Merckx et al., 1985). The present simulation shows that this protecting effect may be counteracted in presence of roots. Thus the roots stimulate the mineralistion of recently stabilised humus fractions. Similarly, in a comparable experiment, Zagal (1994) demonstrated that the roots also liberated formerly stabilised ^{15}N compounds.

In both soils and both treatments, the microbial biomass-^{14}C increased during the initial active decomposition stage, in response to the availability of labile ^{14}C-material. Beyond this time, when the labile material was exhausted, the B compartment decreased slowly for both treatments, showing a typical shape of the microbial biomass curve (Fig. 3B) observed in many labelling experiments. Nevertheless the presence of roots slightly lowered the measured and predicted microbial biomass-^{14}C. Bottner et al. (1988) explained the ^{14}C decrease induced by the active roots by a stimulated C turnover in the microbial biomass. In the bare soils, beyond the active decomposition stage, the labelled portion of microbial biomass partly decayed (explaining the decrease of the curve) and

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 from ^{14}C data in cultivated soils (Table 1), (2) initial values of A, B and H compartments calculated in bare soils and (3) optimisation of the k_r parameter. Predicted values agreed closely with the experimental data (Fig. 4A, B).

The model predicted large fluctuations in compartment A (not measured), which were related to the successive plant growths (Figs. 2 and 4B). Indeed in the model, the labile C derived from the active roots (rhizosphere activity) was directed into the compartment 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 that roots probably stimulated the mineralisation of an extra-amount of old stabilised humus whose dynamics differ from those of recently formed stabilised humus. In soil 1, the predicted stimulation of H mineralisation was weaker (Fig. 4A). For both cultivated soils, the H compartment curve declined parallel to total C, illustrating that the dynamics of total-C are essentially explained by the dynamics of H. This compartment represents the major portion of organic matter. In cultivated soil 2, almost one-third of the total C was lost

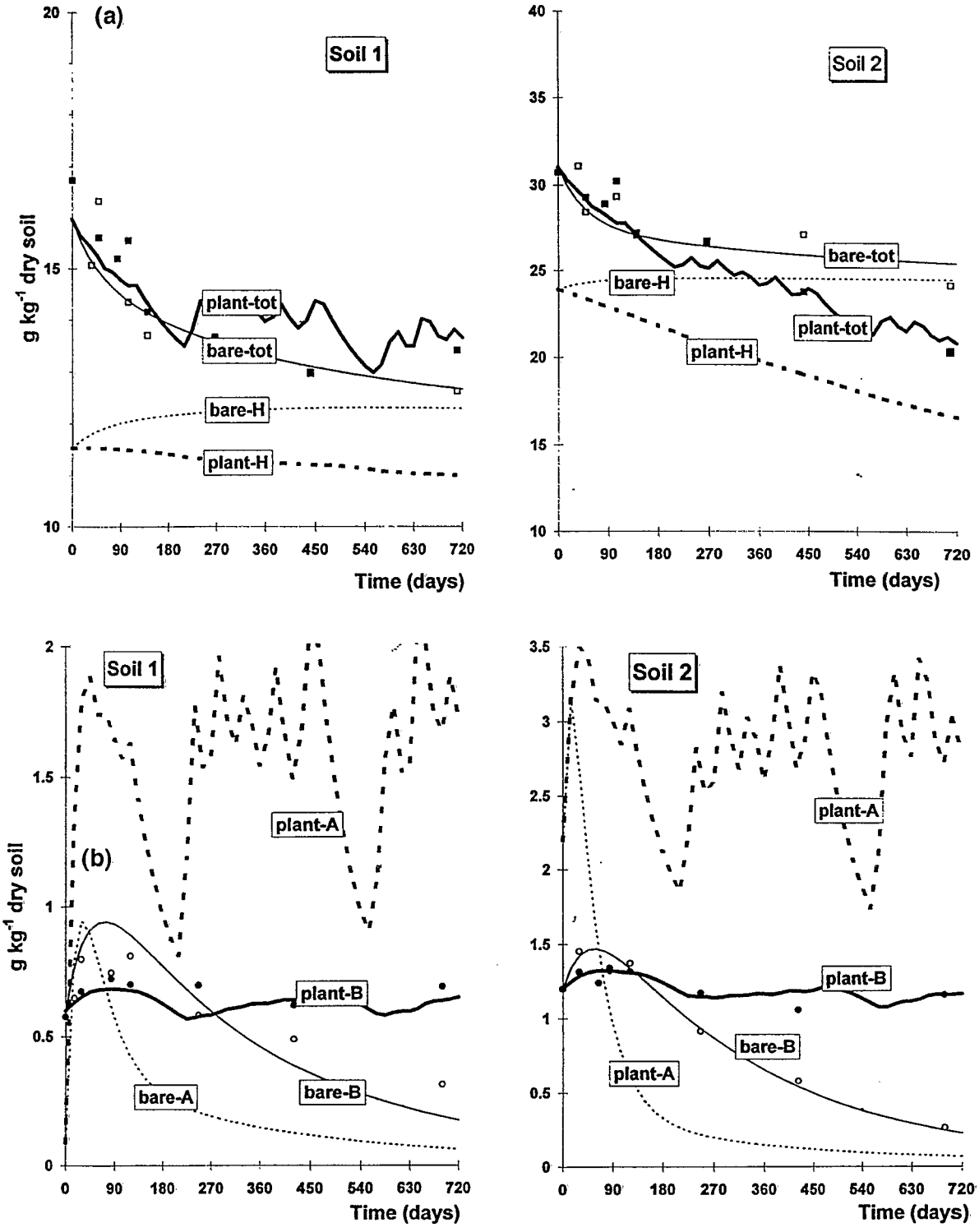


Figure 4. Measured and predicted total carbon distribution (g C kg^{-1} dry soil) in the soil compartments in bare and cultivated soils 1 and 2.

during the experiment, indicating a high instability under the experiment conditions, especially with plants (Fig. 4A).

Predicted rhizodeposition

Total N contents of soil 1 and 2 were 0.12 and 0.20%, respectively. Plant production of soil 1 was about half that of soil 2 (Fig. 2). Cumulative total N taken up by the plants of the 11 growths amounted to 173 and 366 mg N kg^{-1} dry soil for soils 1 and 2, respectively, 14 and 18% of the total soil N. The decline in productivity of both soils at the last growth (11th, Fig. 2) indicates nutrient exhaustion (this was confirmed by the 12th growth not used in the calculations). For each growth, LPM (shoots + roots) was simulated from the mass of harvested dry plant material and from a classical logistic function (formula 2; Fig. 2). Parameter k_r is the predicted proportion of C, which is derived from living roots and directed into the soil as labile material. In formula 1, k_r is defined as a constant proportion of the plant biomass (LPM) and was 0.025 and 0.015 g C g^{-1} plant dw day^{-1}, which is 0.054 and 0.032 g C g^{-1} plant-C day^{-1} (plant material-C = 46%) for soils 1 and 2 respectively. Thus the model predicts a lower proportion of labile C released from roots for the more productive soil 2 than in the less productive soil 1. Nevertheless, in absolute values, predicted C derived from roots was comparable for both soils. During the 11 growths, 10.7 and 13.8 g organic C kg^{-1} dry soil were released by plants into soils 1 and 2, respectively. The model prediction confirms results from many pulse-labelling and non-labelled experiments, pointing out an increased below ground translocation and rhizosphere activity with decreased N availability (Hansson et al., 1991). By contrast, Swinnen et al. (1995) in a pulse-labelling experiment, found that N fertilisation of a winter wheat had no effect on the proportion of ^{14}C which is translocated to the roots, calculated as a proportion of net assimilated ^{14}C. Unlike our results, Liljeroth et al. (1990) found that the proportion of net assimilated ^{14}C recovered in root/soil respiration and deposited in soil was higher with a high N fertilisation, compared to low N. These contradictory results illustrate that, beside the N fertility, other factors also control below-ground C translocation. Thus, a higher soil compaction in the clay soil 1 also may explain the higher proportion of ^{14}C released in the soil, since Barber and Gun (1974) observed a higher exudation rate in soils with increased physical resistance to roots.

In formula (1′), k_r was defined as a constant proportion of the net daily production and was 0.43 and 0.35 g C g^{-1} plant dw or 0.93 and 0.76 g C g^{-1} plant-C for soils 1 and 2, respectively. If in our calculation the 'assimilated C' is defined as the sum of shoots-C +roots-C+the organic C released from the roots as rhizodeposition, then the model predicts that the organic C released from the roots represented 48 and 43% of this 'assimilated C'. These values are high, because in the calculation the direct root respiration-C (not measured nor predicted in this experiment) is not included in the 'assimilated C'. The estimated proportion of assimilated C translocated to the roots is controversial, with a large degree of uncertainty. Approximately 10–30% of the total assimilated C is lost by the roots as root respiration and organic C release (Van Veen et al., 1991). The estimated root respiration/microbial respiration ratio ranges from 1/1 (Warembourg and Billes, 1979) to 1/4 (Van Veen et al., 1991). When the means of these values are used, then the rhizodeposited-C in soils 1 and 2 amounts to 46% and 41%, respectively, in percent of the classically defined net assimilated-C (shoot+root+direct root respiration+root exudation). These values are still high. Except under sterile conditions, the techniques (pulse labelling) seldom allow direct measurement of organic C release from the roots. Microbial respiration cannot therefore be distinguished from root respiration. The fluxes are generally calculated indirectly. Reviewing the carbon economy in the rhizosphere, Wipps (1990) reported that the CO_2 produced by the micro-organisms utilising carbon sources derived from the roots varied from 7% to at least 30% of the total C fixed by the plant. The author concluded that the majority of below-ground CO_2 respired during the growth of wheat, was derived from the respiration of micro-organisms degrading root-derived material. In addition, the root exudation varies to a large extent, depending on the age of the plants (Meharg and Killham, 1990; Warembourg 1997). The present experiment was performed only with active root systems (until earing time), generating mean values calculated from the model prediction over the 11 growths. Finally, the relatively high k_r (Eq. (1′)) values may also be partly explained by a quantity of fine roots which remained in the soil after each plant harvest and root extraction, slightly overestimating the input of organic C derived from the living roots. The cumulated soil ^{14}C adhering to the roots at plant harvests did not exceed 4% of the initial total ^{14}C, but the cumulated proportion of roots remaining in soil was probably higher.

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 models supported by measured compartments is still questionable. The controversial response of the soil processes to the presence of living roots, pointed out by many authors, is in this experiment predicted by two main processes:

(1) The competition between plants and microorganisms for inorganic N explains the negative effect of plants on total C mineralisation rates, during the initial active decomposition stage, when available labile-C stimulates microbial activity. This effect is also reflected by lower plant productivity and lower plant N uptake during the active decomposition stages compared to the subsequent growths. Nevertheless this root-induced reduction of decomposition is relatively low.

(2) By contrast, the presence of living roots stimulates the total carbon mineralisation during the later decomposition stage. During this phase, the labile-C resources are exhausted, leading to low mineralisation rates. In bare soils, part of the microbial biomass decays, and most of the surviving organisms are dormant. In the presence of living roots, the model predicts the mineralisation of an extra amount of stabilised humus or recalcitrant plant debris. The protecting effect of clays and loam on recently formed labelled humus is partly counteracted by the presence of roots, stimulating its mineralisation. The model also predicts a stimulated mineralisation of old soil native stabilised organic fractions; they are not governed by the same mineralisation rates as the freshly formed compounds derived from the labelled material. The total soil native-C dynamics are essentially explained by the humus compartment, since this fraction is largely dominant. The presence of roots led to a progressive replacement of the labelled microbial biomass derived from the initial plant material by unlabelled microbial biomass derived 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 value of C released by the roots into the soil amounted to 5.4 and 3.2% of the plant biomass present or 48 and 43% of the daily plant 'net production' for soils 1 and 2, respectively. These calculated values are relatively high but within the range of some published data.

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