Archives of Agronomy and Soil Science, February 2004, Vol. 50, pp. 115–132 Taylor & Francis Taylor & Francis Group

REVIEW OF ESTIMATION OF PLANT RHIZODEPOSITION AND THEIR CONTRIBUTION TO SOIL ORGANIC MATTER FORMATION

ÜBERBLICK ÜBER DIE ABSCHÄTZUNG DER RHIZODEPOSITION VON PFLANZEN UND IHREN BEITRAG ZUR BILDUNG DER ORGANISCHEN BODENSUBSTANZ IM BODEN

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(Received 22 August 2003)

The methods used for estimating rhizodeposition of plants (carbon (C) deposition of living roots), and the results obtained for different plant species are reviewed. Three tracer techniques using C isotopes to quantify rhizodeposition are discussed: pulse labelling, continuous labelling, and natural ^{13}C abundance. Only the tracer methods provided adequate results for the whole rhizodeposition. The differences in the below-ground C translocation pattern between cereals and grasses are discussed. Cereals (wheat and barley) transfer 20–30% of total assimilated C into the soil. Half of this amount is subsequently found in the roots and about one-third in CO_2 evolved from the soil by root respiration and microbial utilization of root-borne organic substances. The remaining part of below-ground translocated C is incorporated into the soil microorganisms and soil organic matter (SOM). The portion of assimilated C allocated below the ground by cereals decreases during growth and by increasing N fertilization. Pasture plants translocated about 30–50% of assimilates below-ground, and their translocation patterns were similar to those of crop plants. On average, the total C amounts translocated into the soil by cereals and pasture plants are approximately the same (1.5 Mg C ha^{-1}; calculated for the productivity of about 6 Mg grain yield), when the same growth period is considered. However, during one vegetation period the cereals and grasses allocated beneath the ground about 1.5 and 2.2 Mg C ha^{-1}, respectively. Finally, a simple approach is suggested for a rough calculation of C input into the soil and for root-derived CO_2 efflux from the soil. Contribution of C_4 carbon (from maize and some C_4 grasses) to turnover of SOM (C_3 soils) estimated by natural ^{13}C abundance is reviewed. In average for Ap horizons, the portion of maize derived carbon increases of about 0.98% of SOM content per year. Factors influencing the contribution of maize-derived carbon to soil organic carbon are discussed. The contribution of maize derived carbon decreases with soil depth, without fertilization, after removal of above ground biomass, and with soil tillage.

Keywords: Rhizodeposition; Soil organic matter; Below-ground C translocation; C turnover and balance; Rhizosphere; Root respiration

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ISSN 0365-0340 print; ISSN 1476-3567 online
DOI: 10.1080/03650340310001627658

1. INTRODUCTION

All of the organic carbon (C) found in the soil is primarily plant derived. Basing on the life cycle of plants, two main sources of C input in the soil can be distinguished:

(1) Root and shoot remains contributing to the accumulation of soil organic matter (SOM) due to humification after plant death.
(2) Root exudates and other root-borne organic substances released into the rhizosphere during the plant growth, as well as root hairs and fine roots sloughed by root elongation.

The first source (root and shoot residues) of the C input into soils is well investigated, and the results for different ecosystems are summarized by Rodin and Basilevich (1965), Basilevich and Rodin (1971), Schlesinger (1977), Titlyanova and Tesarzheva (1991). Chemical composition of the entire plant residues, their decomposition rates and biochemical transformation chains in the soil during the humification are also known (Redmann, 1992; Paul and Clark, 1996; Kögel-Knabner, 2002).

The second source, including all organic carbon released by living roots into the soil, will be referred to as rhizodeposits, and the process of their release as rhizodeposition. We will describe the total amounts of C recovered in the rhizodeposits, in the root-tissue, and in CO_2 derived from rhizosphere respiration (root respiration and microbial respiration of the rhizodeposits) as root-derived C.

The second source of C input into the soil – the amount of rhizodeposits – has not been sufficiently investigated. The main problem is that profound results observed in plant physiology of root exudations can only partially be used under real soil conditions. The interactions of the roots with the mineral soil matrix and the soil microorganisms lead to the different C allocation and sequestration by roots when compared with the nutrient solution culture (Schönwitz and Ziegler, 1988; Meharg and Killham, 1991) or sterile soil (Warembourg, 1975; Merbach *et al.*, 1990, 1991). Unfortunately, the wide spectrum of methods developed in plant physiology for investigations of root-derived organic substances in nutrient solutions and artificial substrates cannot be directly applied to native soils. Consequently, our knowledge on the C input by roots into the soil is still incomplete. There are four main reasons causing this deficiency:

(1) Low concentration of root-derived organic substances in the soil in comparison to the content of other organic substances.
(2) Fast decomposition ($T_{\frac{1}{2}} = 0.5-10$ days) by soil microorganisms of all organic substances released from roots.
(3) Appearance of the rhizodeposits in a narrow zone of soil adhering the root surface.
(4) Difficulties in distinguishing between organic substances derived by SOM decomposition and microbial turnover and those released by roots.

The application of C isotopes (^{14}C and ^{13}C) in rhizosphere studies has led to significant progress in the understanding of the C cycling within the rhizosphere. The results of experiments, in which plants were labelled, have shown that the amounts of root-derived C are 3–7 times higher than observed with root washing methods or

root growth estimation. For example, root weight estimated by means of ^{14}C was about 20–60% higher than by means of root washing (Sauerbeck and Johnen, 1976). Exudate concentrations obtained with ^{14}C tracer technique were 20–100 times higher (Cheng *et al.*, 1993) than the concentrations calculated according to the exudation rates of roots in nutrient solution studies (Newman and Watson, 1977; Darrah, 1991a,b).

Whipps (1990) summarized estimates of C input by plants into the soil obtained in experiments with continuous labelling. In the last decade new methods were suggested for the estimation and partitioning of below-ground C input, and new results were obtained. These results and methods have not yet been reviewed.

The present review is directed at below-ground C translocation by living plants under natural soil conditions. Only the results obtained by using different C tracer techniques are reviewed here. This is because traditional methods considerably underestimate the rhizodeposition and do not allow for a partitioning of the translocated C. Special attention is given to the applied tracer methods. The contribution of plant derived organic substances to the SOM turnover obtained with ^{13}C natural abundance is also reviewed.

2. CARBON TRACER TECHNIQUES FOR ESTIMATION OF RHIZODEPOSITION

Currently, three tracer methods are commonly used for the estimation of C input into the soil by plants: (1) pulse labelling, (2) continuous labelling, and (3) ^{13}C natural abundance. The first two methods are based on the artificial labelling of plants. Shoots are exposed to CO_2 in an atmosphere labelled with ^{14}C, ^{13}C or ^{11}C. The shoots assimilate the label and translocate a part of it into soil. This C is incorporated into the root tissue, exuded as high and low molecular organic substances, sloughed as cell tissue by root elongation, and released as CO_2 derived from root respiration. Hence, the entire labelled C later found in all soil pools or evolved as CO_2 from the soil is plant-derived. This allows the calculation of C input by plants into the soil on the background of soil organic C, which remains unlabelled.

In the case of the pulse labelling, the shoots assimilate the labelled CO_2 for only a short period, and only once during the whole plant growth. In contrast to this, in the case of continuous labelling, the plants assimilate labelled CO_2 over a long period, mostly between the emergence of the first leaf and the sampling time. Different experimental systems for pulse and continuous labelling of plants are described in many publications (e.g. Warembourg, 1975; Sauerbeck and Johnen, 1976; Johnen and Sauerbeck, 1977; Warembourg and Billes, 1979; Whipps and Lynch, 1983; Warembourg and Kummerow, 1991; Shepherd and Davies, 1993; Cheng *et al.*, 1993; Jensen, 1993; Swinnen, 1994; Swinnen *et al.*, 1995; Siniakina and Kuzyakov, 2002; Stewart and Metherell, 2000).

Although both methods only differ in the duration of the exposure period to the labelled CO_2, they are used for different aims. Pulse labelling, compared with continuous labelling, has the advantage of being easier to handle (Whipps, 1990), provides more information on the recent photosynthate distribution at a specific developmental stages of plants (Meharg and Killham, 1990; Swinnen *et al.*, 1994), and can be used for kinetic investigations of $^{14}CO_2$ evolution from the soil (Warembourg and Billes, 1979; Swinnen *et al.*, 1994; Nguyen *et al.*, 1999; Kuzyakov *et al.*, 1999, 2000,

2001). The results obtained by pulse labelling correspond to the relative distribution of assimilated C at the moment of labelling and does not reflect the distribution of total unlabelled C in different plant parts, but correspond rather to the product of total C in the plant part multiplied by its growth rate at the moment of labelling. The total amount of C assimilated by the plant is unknown and can be calculated only roughly.

As partitioning patterns change during plant growth, the ^{14}C distribution at one stage of development cannot be applied to another or to a whole growth period. The most important limitation of the pulse labelling is that the results of C allocation observed for a specific growth stage can not be directly transferred for the whole growth period. However, a series of labelling pulses applied at regular intervals during plant growth have been found to provide a reasonable estimate of the cumulative below-ground C input (Keith *et al*., 1986; Gregory and Atwell, 1991; Jensen, 1993; Swinnen *et al*., 1994; Kuzyakov *et al*., 1999, 2001; Warembourg and Esterlich, 2000).

In the case of continuous labelling, the total amount of assimilated C is known. In addition, the distribution of labelled C corresponds to the distribution of total C, as long as it was applied from first leaf emergence to harvest time (the specific ^{14}C activity or ^{13}C abundance is equal in all plant parts). Therefore continuous labelling is particularly appropriate for the estimation of the amount of total C transferred by the plants into the soil and below-ground pools during the labelling period (Meharg, 1994). Continuous labelling is also useful for the separation of root-derived and SOM-derived CO_2 (Johnen and Sauerbeck, 1977; Whipps, 1987).

Continuous labelling requires special equipment for exposing the plants over a long period to $^{14}CO_2$ with constant ^{14}C specific activity or $^{13}CO_2$ with ^{13}C enrichment. In addition, the air temperature and moisture conditions must be controlled inside the labelling chamber. For both pulse and continuous labelling methods, special airtight equipment is necessary to separate the soil air and the atmosphere.

From the different C isotopes, the radioactive ^{14}C have been used in most studies with pulse and continuous labelling so far. This preferential use of ^{14}C is based on the high sensitivity, the lower costs for purchase and analyses, and easier sample preparation compared with ^{13}C or ^{11}C. Since ^{11}C has a short half-life (20.4 min), only ^{14}C and ^{13}C are appropriate for continuous labelling.

An important advantage of the described tracer techniques compared with traditional methods is that the amount of tracer which entered the system is exactly known. After the partitioning of assimilates, it is possible to calculate the balance of the C in the atmosphere – plant – soil system, as well as to estimate the system losses. Traditional methods are less accurate and can be used only to calculate the distribution of C between the measured C pools. Meharg (1994) published a more detailed review on the features and applications of pulse and continuous labelling.

The third method, ^{13}C natural abundance, is based on the discrimination of ^{13}C and ^{12}C isotopes during CO_2 assimilation by plants with different photosynthesis types. Enzyme Rubisco in C_3 plants leads to a ^{13}C depletion of about $-27‰$ ($-35‰ \leqslant \delta^{13}C \leqslant -20‰$) when compared with atmospheric CO_2. Phosphoenol pyruvate carboxylase (C_4 plants) results in a depletion of about $-13‰$ ($-15‰ \leqslant \delta^{13}C \leqslant -7‰$). The $\delta^{13}C$ values of different plants are reviewed by Farquhar *et al*. (1989) and Boutton *et al*. (1998). The effects of humification and other microbial-related processes on $\delta^{13}C$ are thought to be negligible. Therefore, the soils developed under C_3 or C_4 vegetation contain SOM with $\delta^{13}C = -27‰$ or $-13‰$, respectively (Cheng, 1996). The method is based on cultivation of C_3

plant on a C_4 soil, or *vice versa*, and the estimation of rhizodeposition according to the $\delta^{13}C$ value in soil C pools or CO_2 evolved from soil. This method can be considered as a variation of the continuous labelling, because the plants and soil are permanently labelled. However, the labelling of plant and soil occur naturally, not artificially, as is the case of pulse or continuous labelling methods described above. This method can easily be used under field conditions (Rochette and Flanagan, 1998) because special equipment for plant labelling and separation from the atmosphere is not necessary. The last feature and the future development of mass-spectrometry will promote the use of this method in forthcoming investigations.

The limitations of the ^{13}C natural abundance method are caused by soil–plant pairs. Situations where C_3 plants grow on a C_4 soil, or *vice versa*, are unnatural. Hence, the application of this method is restricted to places where soils developed under C_3 vegetation allow the growth of C_4 plants and *vice versa*. Additionally, the high-resolution and high-sensitive mass-spectrometry is necessary for ^{13}C analyses because a maximal range of only 14‰ is available for all variations of the $^{13}C/^{12}C$ ratio. At the same time, the variability of $\delta^{13}C$ value in soil or plant is about $\pm$ 1–2‰ (Cheng, 1996). For the last two reasons mentioned only a rough estimation of rhizodeposition in the soil and in the pools with high C exchange rates with the root-derived C (e.g. microbial biomass, dissolved organic C, active pools of SOM, etc.) is possible.

The results of the relative and total C translocation by wheat and barley (representative for agricultural ecosystems) and some grasses (representative for natural grassland ecosystems) are reviewed in the following sections.

3. BELOW-GROUND CARBON TRANSLOCATION BY DIFFERENT PLANT SPECIES

3.1. Below-ground C translocation and partitioning by wheat and barley

Most studies of the below-ground C translocation and partitioning have been conducted on cereals, mainly on wheat and barley. The summarized results concerning C partitioning by cereals obtained in pulse-labelling experiments in the last 10 years are presented for wheat and barley in Table I. After recalculations of original results, the data are expressed as a percentage of total assimilated ^{14}C. The data obtained in continuous labelling experiments concerning the below-ground carbon partitioning by crop plants growing in the soil were reviewed earlier (Whipps, 1990). Direct comparisons between the data collected by Whipps (1990) and Table I is difficult, because he presented the results as a percentage of net fixed C. The net fixed C (Whipps, 1990) does not take into consideration the part of C respired during shoot respiration, although this C can reach 40% of total assimilated C and even more (Warembourg and Morral, 1978; Swinnen *et al*., 1994; Kuzyakov *et al*., 2001). As a result, it is not possible to make any realistic balance of C partitioning within the plant–soil system. Also it should be taken into consideration that experimental systems used in different laboratories have different recovery rates of introduced ^{14}C as shown by Saggar *et al*. (1997).

The portion of C translocated below-ground by cereals and used for root growth, respiration and exudation decreases during plant development (Keith *et al*., 1986; Swinnen *et al*., 1994; Steingroever, 1981; Lambers *et al*., 1981).

TABLE I Below-ground translocation of carbon by wheat, barley and pasture grasses into non-sterile soil (expressed as percentage of total assimilated carbon). Summary of 28 experiments carried out with ^{13}C or ^{14}C pulse labelling (from Kuzyakov and Domanski, 2000, changed)

Plants and average method	*Total below-ground 1 + 2 + 3 + 4*	*Converted to CO_2 1 + 2*	*Root respiration 1*	*Exudates/microbial respiration 2*	*Roots 3*	*Soil 4*
Wheat Median	26	10	7	2	7	3.5
Average*	29	11	10	9	14	3.4
Barley Median	17	14	13.5	0.9	12.5	2.3
Average	28	14	15	2	13	2.3
Lolium perenne Median	28	10	–	4.6	6	4.9
Average	32	13	–	4.7	14	13
Different grasses Median	50	17	–	–	9	3.7
Average	49	17	–	–	12	3.4

*Arithmetical average
– no data

Arithmetical average shows that wheat and barley transported about 30% of assimilates into soil (Table 1). However, most of the studies have been carried out on young plants, when the relative translocation was higher than during subsequent stages of growth. Weighted averages would be much more appropriate for the estimation of C partitioning based on experiments with ^{14}C. Taking this into consideration, we calculated the median as a parameter more appropriate than the arithmetical average. According to the medians wheat transfers 26% and barley 17% of total assimilated C into soils.

According to the summarized results this below-ground translocated C is used for (Table I):

- Root growth (7–13% of total assimilated C); this part of C was found in roots after the experiments.
- Rhizodeposition: exudates, secretes, root hairs and fine roots (1–2% of total assimilated C), which were decomposed by microorganism to CO_2 shortly after they appear in the rhizosphere. A part of this C remains adsorbed on clay minerals and SOM (2–4%), or is incorporated in rhizosphere microorganisms (0.8–3.2%, Kuzyakov *et al*., 2000a; ca. 2%, Van Ginkel *et al*., 2000; Domanski *et al*., 2001).
- Root respiration amounts to 7–14% of total assimilated C.

Here it is important to note that in many studies microbial respiration by decomposition of rhizodeposits (rhizomicrobial respiration) is also accounted as root respiration. Therefore in the presented summary, the rhizodeposition is strongly underestimated and root respiration is strongly overestimated.

The variations between different studies are very high. Therefore, this partitioning between the pools and flows named above cannot be accepted as fixed. Until new experimental results on the below-ground C allocation the following rough relationship can be used:

- about half of the below-ground translocated C is incorporated in root tissue
- one third is respired by roots and rhizosphere microorganisms utilizing exudates and fine roots and is evolved as CO_2 during few days after assimilation
- the rest remains in soil and microorganisms.

Mineral fertilization changes the amounts of C allocated beneath the ground as well as C in individual soil pools. In studies of wheat (Liljeroth *et al*., 1990), maize (Merckx *et al*., 1987), and horticultural plants (Siniakina and Kuzyakov, 2002) it was observed that the relative amount of C translocated below-ground decrease due to N fertilization. This indicates that measures to optimize above-ground plant growth and total fixed C (total dry mass production) result in a decrease of below-ground translocated portion of assimilated C, although the amount of total assimilated C increase.

3.2. Below-ground C translocation and partitioning by pasture plants

Although pastures are more closely to the natural ecosystems, there is much less information regarding the C translocation by grasses compared to cereals. Nowadays, this situation has changed because pastures have been found to be a significant sink for

atmospheric CO_2. Despite the fact that most pasture plants and the crop cereals have similar origins, some differences in C translocation patterns can be expected because:

(1) Most pasture plants ($\approx 80\%$) are perennial and have well developed root systems that are used as a C storage for new growth in spring or after grazing (mowing).
(2) Long and intensive breeding of cereals has led to the preferential allocation of assimilates in the above-ground parts, especially in the grains when compared to their natural relatives.
(3) Intensive and accurate fertilization of crops significantly decreases the inefficient loss of assimilates necessary for the uptake of nutrients by roots from the soil. In addition, well-balanced relationships between individual nutrients decrease the respiration losses during assimilation and growth.

All three points indicate that the relative below-ground translocation of assimilated C is higher for pasture plants than for cereals. Previous studies have shown that the C translocation by pasture plants can reach up to 80% of assimilates (Sims and Singh, 1971; Dormaar and Sauerbeck, 1983; Zagal, 1994). The extent of rhizodeposition varies widely, from as low as 8% (Meharg and Killham, 1990) to $> 65\%$ of assimilated C (Meharg and Killham, 1990; Zagal, 1994). In summary, the relative C translocation of pasture plants into soil is about $1.5-2$ times higher than that of cereals (Table 1). Nevertheless, the ratios of C partitioning between main below-ground fluxes remain approximately the same: about 50% of C translocated below the soil surface have been found in roots, more than 30% in root exudates and root-derived CO_2, and the remainder in SOM and microorganisms.

Most authors reported a decrease of below-ground C deposition during plant development (Brouwer, 1983; Kuzyakov *et al*., 1999). However, some results have shown the opposite trend (Zagal, 1994; Kuzyakov *et al*., 2002). It was suggested that the changes in the translocation pattern of Lolium could be connected with the vernalization of seedlings (Kuzyakov *et al*., 2002). As for cereals, an increasing N fertilization level decreased the relative amounts of the below-ground translocated C in pasture plants (Kuzyakov *et al*., 2002).

3.3. Total C input by plants into soil

In most studies related to C balance and C turnover in soils, mass units are important and not only the relative values reported above. We compiled C inputs by some agricultural plants and grasses into soils on the basis of mass units (Table II). The results vary widely both within (i.e. for wheat between 0.48 and 2.3 Mg C ha^{-1} yr^{-1}) (Martin and Puckridge, 1982; Knof, 1985; Whipps, 1990) and across species (Swinnen *et al*., 1995; Saggar *et al*., 1997; Van Ginkel *et al*., 1997).

We calculated the arithmetical average for all data and it was 1.5 and 1.75 Mg C ha^{-1} yr^{-1} for cereals and grasses, respectively. These values were both close together and did not differ significantly. However, they gave only a rough estimation of C input into soil by agricultural and natural grass ecosystems of average productivity. Additionally, we calculated the C translocation based on the data from experiments longer than 100 days, because of the longer vegetation period of grasses compared to cereals. It showed significant differences between cereals and grasses (Table II). The longer vegetation

TABLE II Amounts of below-ground translocated carbon by cereals and different grasses (only the results of tracer studies are summarized)

Plants	*Period*	*Mg C ha^{-1}*	*References*
Wheat	25 weeks	1.3	Keith *et al.*, 1986
Wheat	Vegetation period*	1.0 – 1.5	Martin and Puckridge, 1982
Wheat	63 days	1.765	Martin and Merckx, 1992;
	63 days	1.79	Martin and Merckx, 1993
Wheat	153 days	2.3	Johnen and Sauerbeck, 1977
Wheat	Vegetation period	1.2 – 2.9	Whipps, 1990
Wheat	Vegetation period	1.0 – 1.6	Knof, 1985
Wheat	167 days	0.48	Gregory and Atwell, 1991
Barley	167 days	0.58	
Wheat and barley	Vegetation period	1.46 – 2.25	Swinnen *et al.*, 1995
Barley	127 days	1.65	Jensen, 1993
Median	All data	1.52	
Arithmetical average	All data	1.48	
Arithmetical average	Longer than 100 days	1.5	
Lolium perenne	112 days	2.8	Siniakina and Kuzyakov, 2002
Lolium perenne	95 days	0.5 – 0.65	Kuzyakov *et al.*, 1999
Lolium perenne	Vegetation period	0.84 – 1.66	Van Ginkel *et al.*, 1997
Different kinds of grasses	Vegetation period	2.45 – 4.43	Saggar *et al.*, 1997
Different kinds of grasses	5 months	1.0	Warembourg and Paul, 1977
Median	All data	1.33	
Arithmetical average	All data	1.79	
Arithmetical average	Longer than 100 days	2.2	

* – term used when enough data about vegetation period have been given.

period of grasses led to additional C allocation below the ground of about 0.6 Mg C ha^{-1} yr^{-1} when compared with cereals.

Although the relative C translocation into soil is higher for pasture plants than for cereals, the absolute C input is approximately the same when the same growth period is considered (Table II). The intensive agricultural cereals have a higher productivity per area and time unit when compared with grasses. Therefore, the lower relative below-ground C translocation by cereals compared to grasses is compensated by a higher total CO_2 assimilation from the atmosphere. As such, the pasture is a sink for atmospheric CO_2 only in the absence of a soil plough because the SOM decomposition is reduced, and not because of higher C input into the soil by pasture plants. In addition, extra C is assimilated by pasture because the vegetation period is usually longer than that of cereal crops.

Table II shows that results of C input into the soil obtained by using tracers are 3 – 7 times higher than those obtained with methods based on root growth estimation. For example, the data for barley based on the root growth estimation varied between about 0.2 and 0.6 Mg C ha^{-1} yr^{-1} (Hansson *et al.*, 1991, 1992; Kätterer *et al.*, 1993).

Such precise calculation of C input in the soil based on tracer techniques (Table II) is rare, and cannot be established for each plant – soil pair, different fertilization levels, etc. However, in many situations only a rough estimation of the annual C input in the soil is desirable and can be sufficient to approximate the C balance in the ecosystem. The use of the simple relationships named above can be helpful. For example (Table III), we tried to estimate the total C input into the soil and the root-derived CO_2 efflux

TABLE III Rough estimation of total C input in the soil and root-derived CO_2 efflux from the soil under wheat with 6 t ha^{-1} grain yield* and in a pasture of about 6 t ha^{-1} dry matter production

	% of total assimilated		*% of below-ground*		*t C ha^{-1}***	
	Wheat	*Pasture*	*Wheat*	*Pasture*	*Wheat*	*Pasture*
Shoot	50	30			4.8	2.4
Shoot CO_2***	25	30			2.4	2.4
Roots	13	20	52	50	1.2	1.6
Soil + MO****	3	5	12	13	0.3	0.4
Root CO_2*****	9	15	36	38	0.9	1.2
Below-ground	25	40	100	100	2.4	3.2
Total assim. C	100	100			10	8.0

*– it is accepted that total above-ground plant mass is two times higher than the grain yield
**– C content in dry mass of shoots and roots is accepted by 40%
***– shoot respiration
****– C remains in soil and microorganisms
*****– root-derived CO_2: the sum of root respiration and rhizomicrobial respiration of rhizodeposits

from the soil under wheat with 6 Mg ha^{-1} grain yield and in a pasture of about 6 Mg ha^{-1} dry matter production (three mows: 2.5 + 2 + 1.5 Mg DW ha^{-1} yr^{-1}). The portions of total assimilated C in Table III are close to the distribution of below-ground translocated C reported for wheat and pasture plants (see above). The C translocation was calculated according to the above-ground production and the portion of total assimilated C translocated below-ground. According to this very rough estimation of total C input, wheat and pasture translocate below-ground about 2.4 and 3.2 Mg C ha^{-1} per vegetation period, respectively. These amounts are higher than those measured by the tracer technique (Table II). After the root-derived CO_2 (9–15% of the assimilated C) is evolved from the soil, about 1.5–2.0 Mg C ha^{-1} remains. This rough calculation shows that the root-derived CO_2 efflux from soil is about 0.9–1.2 Mg C ha^{-1} yr^{-1} in both ecosystems.

4. CONTRIBUTION OF ROOT DERIVED ORGANIC CARBON TO TURNOVER OF SOIL ORGANIC MATTER ESTIMATED BY NATURAL ^{13}C ABUNDANCE

Beside using artificially labelled plants residues to quantify plant-derived carbon (C) in soil, different soil C pools and the rate of C turnover, natural ^{13}C abundance method can be used for this aims. Most investigations with artificially (^{14}C or ^{13}C) labelled plant residues lasted no longer than some years. To investigate C dynamics in soil over decades, the natural ^{13}C abundance method is more useful (Balesdent, 1996). In the following section results of several investigations using this approach are reviewed, the method itself is described above.

Principally, all soil–plant pairs could be used where a C_4 plant is grown on a soil developed under C_3 vegetation or the other way round. Because the natural vegetation under temperate conditions follows the C_3 photosynthetic pathway, all soils have C_3 isotopic composition. Therefore only pairs of C_4 plant and C_3 soil are possible under these conditions. Most studies are conducted with maize (C_4 plant) as it is an agriculturally important plant (for example Ludwig *et al.* (2003) and Puget *et al.*

(1995)) and only a few with other C_4 plants like Switchgrass (Garten and Wullschleger, 2000) or Miscanthus (Schneckenberger *et al*., 2003).

4.1. Annual plants: maize

Portions from maize derived carbon to soil organic carbon (SOC) vary greatly in different studies (Ludwig *et al*., 2003) (Table IV). For example, Gregorich *et al*. (1995) estimated portions of 25–35% of maize derived carbon to total organic carbon in the A_p horizon of a clay loamy soil after 25 years of continuous maize-cultivation in Canada, whereas in investigations by Flessa *et al*. (2000) in Germany only 15% of the total carbon content in a loamy sandy A_p horizon was maize-derived after even 37 years of maize cultivation. Silt loamy maize soils in France investigated by Puget *et al*. (1995) even contained 44% of maize derived carbon after only 23 years of cultivation.

There are different reasons for these differences. The first important factor affecting the contribution of maize derived C to SOC is the time period after exchange of C_3 vegetation into maize cultivation. To compare results of different studies, we recalculate all the data for yearly contribution of maize derived carbon to total organic carbon (Figure 1). In this calculation we involuntarily accepted the linear increase of the contribution with time, because only one point is given in most publications. The yearly contributions vary between 0.08 and 1.91% maize C to total organic carbon. The

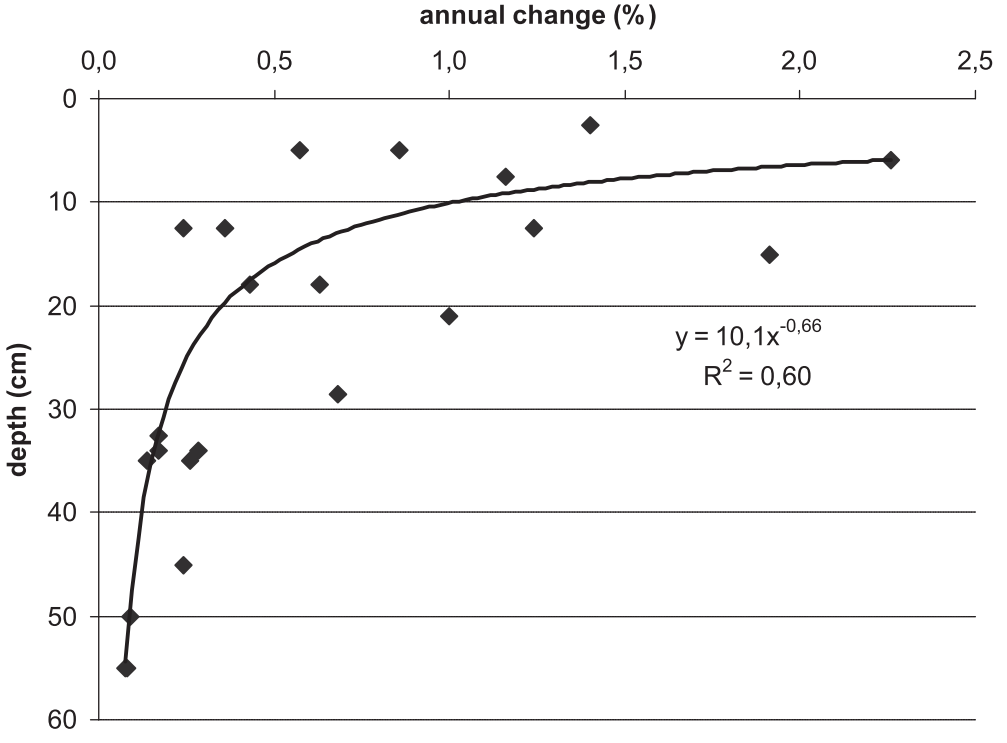

FIGURE 1 Annual increase of the contribution of maize-derived carbon to soil organic carbon in different soil depths (results from several investigations).

TABLE IV Contribution of C_4-plant derived carbon to soil organic carbon in A horizons estimated by natural ^{13}C abundance

Location	*Removal of litter*	*Tillage/ fertilization*	*Depth (cm)*	*C_4-C (%)*	*SOC- (%)*	*Years*	*Texture*	*Reference*
Studies with maize (Zea mays)								
Halle Germany	Yes	conv., NPK	0–25	15	1,3	37	loamy sand	Flessa *et al.* (2000)
Halle Germany	Yes	conv., NPK	0–25	14	1,3	39	loamy sand	Ludwig *et al.* (2003)
Halle, Germany	Yes	conv., not fertilized	0–25	9,5	1,0	39	loamy sand	
BoignevilleFrance	?	conv.	0–30	44	1,0	23	silt loam	Puget *et al.* (1995)
		superficial	0–12	52	1,3			
		no	2–3	72	2,5			
Woodslee Canada	No	conv., fertilized	0–10	30	2,2	35	clay loam	Gregorich *et al.* (1996)
			10–26	22	2,2			
Woodslee, Canada	No	conv., not fertilized	0–10	20	2,0		clay loam	
			10–26	15	2,0			
Winchester, Canada	No	conv.	0–5	35	2,0	25	clay loam	Gregorich *et al.* (1995)
			5–10	29	2,0			
			10–15	31	1,9			
			15–27	25	2,1			
Auzeville, France	No	conv.	0–30	22	0,9	13	silt clay	Balesdent and Mariotti (1987)
La Miniere, France	?	conv.	0–30	11	1	6	silt loam	Puget *et al.* (1995)
Studies with switchgrass (Panicum virgatum)								
Jackson, USA	Yes	no tillage, fertilized	0–10	22	0,6	5	fine–loamy	Garten and Wullschleger (2000)
			10–20	17				
			20–30	16				
Princeton, USA	Yes	no tillage, fertilized	0–10	32	0,6	5	fine–silty	
			10–20	20				
			20–30	16				
Knoxville, USA	Yes	no tillage, fertilized	0–10	43	0,8	5	fine–loamy	
			10–20	18				
			20–30	16				
Blacksburg, USA	Yes	no tillage, fertilized	0–10	40	0,8	5	clayey	
			10–20	25				
			20–30	22				

(*continued overleaf*)

TABLE IV (*continued*)

Location	*Removal of litter*	*Tillage/ fertilization*	*Depth (cm)*	*C_4-C (%)*	*SOC- (%)*	*Years*	*Texture*	*Reference*
Studies with Miscanthus × giganteus								
Stuttgart, Germany	No	no tillage, not fertilized	0 – 10	21	1,5	9	loamy	Schneckenberger *et al.* (2003)
			10 – 20	13	1,4			
			20 – 30	10	1,2			
			30 – 40	4	0,9			
			50 – 60	3	0,6			
			70 – 80	3	0,4			
			90 – 100	9	0,5			
Großbeeren, Germany	No	no tillage, not fertilized	0 – 10	17	1,51	10	sandy	Schneckenberger *et al.* (2003)
			10 – 20	8	1,28			

conv. = conventional tillage with ploughing

highest contributions were measured for A_p horizon (in average 0.98% of SOC content per year) and the contribution strongly decrease with the soil depth (in average 0.2% in deeper horizons) (Figure 1).

The second possible explanation for the differences described above is the remaining or removing of aboveground maize biomass. For example, in the investigation of Flessa *et al.* (2000) the aboveground biomass was removed for silage-making, which is in opposite to the study of Gregorich *et al.* (1996).

The next parameter is the soil tillage. Puget *et al.* (1995) investigated three maize plots under different tillage practices: (1) conventional tillage with ploughing (depth 30 cm), (2) superficial tillage and (3) without tillage. He recognized the highest portion of maize derived carbon in the plot without tillage (72% of total organic carbon was maize-derived, but only in the first 3 cm of soil profile) and the smallest one in the variant with conventional tillage (44% in A_p horizon (0 – 30 cm)) after 23 years of continuous maize cropping. Results of the plot with superficial tillage were placed between with 52% in first 12 cm. Obviously, the depth distribution of the maize derived carbon differs in different tillage practices. So, in the plot without any tillage most of the maize derived carbon is concentrated in the first few cm, while in the ploughed layer this C_4 carbon is distributed over the whole A_p horizon. Balesdent *et al.* (1990) sampled the same trials 6 years earlier and came to the same result. He mentioned that, regarded for the whole soil profile, accumulation of 'new' organic matter is markedly lower without tillage, because degradation of plant litter occurs mainly on the soil surface, where it cannot be protected by soil minerals as in the ploughed soil layer.

All results mentioned above were observed on fertilized maize plots. But fertilization also affects soil organic matter turnover and maize residue C storage (Gregorich *et al.*, 1996). He evaluated in his investigation the differences of the portions of maize derived carbon between a fertilized and an unfertilized soil in Canada. The unfertilized soil contained less (15 – 20%) maize-derived C in the A_p horizon after 35 years of cultivation than the fertilized soil (22 – 30%). So, fertilization leads to an increasing contribution of maize-derived carbon to SOC. Content of C_3 carbon was similar in the fertilized and the unfertilized plot (Gregorich *et al.*, 1996), but whole SOC content was higher in the fertilized plots (22 mg kg^{-1} vs. 20 mg kg^{-1}). So, this difference must be a result of the higher amount of maize-derived C (Gregorich *et al.*, 1996), after Ludwig *et al.* (2003). The reason for this higher amount of maize C in fertilized soils is the greater biomass production caused by fertilization. Ludwig *et al.* (2003) corroborate results of Gregorich *et al.* (1996) for fertilized and unfertilized maize plots in Germany. These results confirm the statement mentioned above, that the increased total production caused by N fertilization compensates the decreasing portion of below-ground translocated C.

4.2. Perennial C_4-grasses

Compared with maize, there is much less information available for the distribution of new organic carbon under cultivated perennial C_4 grasses. These plants have got a high biomass production, a very well developed root system as C storage for winter and are cultivated for many years without soil tillage. Therefore, a differing distribution of new organic carbon in soil, compared with the annually ploughed maize that was selected for a high above ground biomass production, is expected.

Garten and Wullschleger (2000) investigated the distribution of 'new' derived carbon under Switchgrass (*Panicum virgatum* L.) on four different locations under different climatic conditions in the United States. They found very high portions of Switchgrass derived carbon (22–43% after just 5 years of cultivation) in the first 10 cm even though harvested biomass was removed from the field. In a depth of 30–40 cm, 13–19% of soil organic carbon was still derived from Switchgrass. Cumulative fractions of the Switchgrass derived C in the surface 40 cm of the soils were 19–31%.

Compared with results of our investigation with another perennial C_4 crop *Miscanthus* × *giganteus* (Schneckenberger *et al*., 2003), these results for Switchgrass are quite high (Tab. IV) because aboveground biomass was not totally removed in case of *Miscanthus* plots. For *Miscanthus* × *giganteus*, contribution of new derived carbon was 10–21% in the first 30 cm in Stuttgart-Hohenheim after 9 years of cultivation, and 17% (0–10 cm) and 10% (10–20 cm) in a soil near Berlin after nearly 10 years of cultivation. Perhaps these differences in C accumulation beneath Switchgrass and *Miscanthus* are caused by climate. Garten and Wullschleger (2000) note a 'more rapid rate of SOC sequestration beneath Switchgrass grown in warmer climates'. There was a linear positive relationship between mean annual temperature and the fraction of new C_4-derived carbon. Another explanation could be the relatively small contents of SOC in the Switchgrass soils (5.5–8.0 mg kg^{-1}). So relatively small amounts of new organic carbon is needed for a high proportion of new organic carbon.

5. CONCLUSIONS

The introduction of tracer techniques (^{14}C and ^{13}C) for labelling of root-derived C has led to significant progress in the estimation of C input by plants into the soil, and in the partitioning of the root-derived C. Three techniques using C isotopes as tracers for root-derived C were discussed: pulse labelling, continuous labelling, and method based on ^{13}C natural abundance in C_3 and C_4 plants.

Highly productive species such as cereals translocate a smaller portion of assimilated C than do less productive plants such as pasture plants. The higher intensity of CO_2 assimilation, higher efficiency of conversion of CO_2 into organic C, as well as smaller ineffective C losses (root respiration and exudation) by cereals level out their smaller relative C translocation into the soil when compared with grasses. As such, the total C amounts translocated into the soil by cereals and pasture plants are approximately the same (1.5 Mg C ha^{-1}), when the same growth period is considered. However, during one vegetation period the cereals and grasses allocated beneath the ground about 1.5 and 2.2 Mg C ha^{-1}, respectively. These values correspond to the same average productivity of both ecosystems (6 Mg ha^{-1}). The common methods for optimizing plant growth, such as N fertilization, lead to a decrease of the below-ground translocated portion of assimilated C, but increase the total fixed C, the total productivity per area, and therefore the total C input into soil.

Estimated by natural ^{13}C abundance (maize grown on C_3 soils), the average contribution of new plant derived C to SOM in A_p horizon is about 0.98% of SOC content per year. The contribution of 'new organic carbon' increases: (i) with decreasing soil depth, (ii) compared with missing fertilization, (iii) with soil tillage, (iv) without

removal of above ground plant residues. These parameters change both: the input of plant derived C and the stabilization of newly formed soil organic matter.

References

Balesdent, J. (1996) The significance of organic separates to carbon dynamics and its modelling in some cultivated soils. *Eur. J. Soil Sci.*, **47,** 485–493.

Balesdent, J. and Mariotti, A. (1987) Natural ^{13}C abundnace as a tracer for studies of soil organic matter dynamics. *Soil Biol. Biochem.*, **19,** 25–30.

Balesdent, J., Mariotti, A. and Boisgontier, D. (1990) Effect of tillage on soil organic carbon mineralization estimated from ^{13}C abundance in maize fields. *J. Soil Sci.*, **41,** 587–596.

Basilevich, N.I. and Rodin, L.E. (1971) Productivity and turnover of elements in natural and artificial phytocenosen (on example of USSR). [Russian]. In: Biological productivity and turnover of chemical elements in different vegetation communities. Nauka, Leningrad, pp. 5–32.

Brouwer, R. (1983) Functional equilibrium: sense or nonsense? *Neth. J. Agric. Sci.*, **31,** 335–348.

Boutton, T.W., Archer, S.R., Midwood, A.J., Zitzer, S.F. and Bol, R. (1998) $\delta^{13}C$ values of soil organic carbon and their use in documenting vegetation change in a subtropical savanna ecosystem. *Geoderma*, **82,** 5–41.

Cheng, W. (1996) Measurement of rhizosphere respiration and organic matter decomposition using natural ^{13}C. *Plant and Soil*, **183,** 263–268.

Cheng, W., Coleman, D.C., Carroll, C.R. and Hoffman, C.A. (1993) In situ measurement of root respiration and soluble C concentrations in the rhizosphere. *Soil Biol. Biochem.*, **25,** 1189–1196.

Darrah, P.R. (1991a) Models of the rhizosphere. I. Microbial population dynamics around a root releasing soluble and insoluble carbon. *Plant and Soil*, **138,** 187–199.

Darrah, P.R. (1991b) Models of the rhizosphere. II. A quasi three-dimensional simulation of the microbial population dynamics around a growing root releasing soluble exudates. *Plant and Soil*, **138,** 147–158.

Domanski, G. Kuzyakov, Y. Siniakina, S.V. and Stahr, K. (2001) Carbon flows in the rhizosphere of *Lolium perenne*. *J. Plant Nut. Soil Sci.*, **164,** 381–387.

Dormaar, J.F. and Sauerbeck, D. (1983) Seasonal effects on photoassimilated carbon-14 in the root system of blue grama and associated soil organic matter. *Soil Biol. Biochem.*, **15,** 475–479.

Farquhar, G.D., Ehleringer, J.R. and Hubick, K.T. (1989) Carbon isotope discrimination and photosynthesis. *Ann. Rev. Plant Physiol. Plant Mol. Biol.*, Palo Alto, California, Annual Reviews, Inc. **40,** 503–537.

Flessa, H., Ludwig, B., Heil, B. and Merbach, W. (2000) The origin of soil organic C, dissolved organic C and respiration in a long-term maize experiment in Halle, Germany, determined by ^{13}C natural abundance. *J. Plant Nut. Soil Sci.*, **163,** 157–163.

Garten, C.T. and Wullschleger, S.D. (2000) Plant and environment interaction–soil carbon dynamics beneath Switchgras as indicated by stable isotope analysis. *J. Environ. Qual.*, **29,** 645–653.

Gregorich, E.G., Ellert, B.H. and C.M., M. (1995) Turnover of soil organic matter and storage of corn residue carbon estimated from natural ^{13}C abundance. *Can. J. Soil Sci.*, **75,** 161–167.

Gregorich, E.G., Ellert, B.H., Drury, C.F. and Liang, B.C. (1996) Fertilization effects on soil organic matter turnover and corn residue C storage. *J. Soil Sci. Soc. Am.*, **60,** 472–476.

Gregory, P.J. and Atwell, B.J. (1991) The fate of carbon in pulse labelled crops of barley and wheat. *Plant and Soil*, **136,** 205–213.

Hansson, A.C., Andren, O. and Steen, E. (1991) Root production of four arable crops in Sweden and its effect on abundance of soil organisms. In Atkinson, D. (Ed.): *Plant Root Growth, an Ecological Perspective*. Blackwell, Oxford, pp. 247–266.

Hansson, A.C., Steen, E. and Andren, O. (1992) Root production of daily irrigated and fertilized barley investigated with ingrowth cores, soil cores and minirhizotrons. *Swed. J. Agric. Res.*, **22,** 141–152.

Jensen, B. (1993) Rhizodeposition by $^{14}CO_2$-pulse-labelled spring barley grown in small field plots on sandy loam. *Soil Biol. Biochem.*, **25,** 1553–1559.

Johnen, B.G. and Sauerbeck, D.R. (1977) A tracer technique for measuring growth, mass and microbial breakdown of plant roots during vegetation. In Lohm, U. and T. Persson (Eds.): Soil Organisms as Components of Ecosystems Ecological Bulletins, Stockholm, **25,** 366–373.

Keith, H., Oades, J.M. and Martin, J.K. (1986) Input of carbon to soil from wheat plants. *Soil Biol. Biochem.*, **18,** 445–449.

Kätterer, T., Hansson, A.C. and Andren, O. (1993) Wheat root biomass and nitrogen dynamics – effects of daily irrigation and fertilization. *Plant and Soil*, **151,** 21–30.

Knof, G. (1985) Eine Gerätekombination zur Bestimmung des Kohlenstoffs und seines 14C-Anteils in Wurzeln und anderen pflanzlichen Substanzen. *Arch. Acker-Pflanzenb. Bodenk.*, **29,** 23–30.

Kögel-Knabner, I. (2002) The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. *Soil Biol. Biochem.*, **34,** 139–162.

Kuzyakov, Y. and Domanski, G. (2000) Carbon input by plants into the soil. Review. *J. Plant Nut. Soil Sci.*, **163,** 421–431.

Kuzyakov, Y., Kretzschmar, A. and Stahr, K. (1999) Contribution of *Lolium perenne* rhizodeposition to carbon turnover of pasture soil. *Plant and Soil*, **213,** 127–136.

Kuzyakov, Y., Ehrensberger, H. and Stahr, K. (2001) Carbon partitioning and below-ground translocation by *Lolium perenne*. *Soil Biol. Biochem.* **33,** 61–74.

Kuzyakov, Y., Friedel, J.K. and Stahr, K. (2000) Mechanisms and quantification of priming effects. *Soil Biol. Biochem.* **32,** 1485–1498.

Lambers, H., Posthumus, F., Stulen, I., Lanting, L., Van de Dijk, S.J. and Hofstra, R. (1981) Energy metabolism of *Plantago major* ssp. major as dependent on the supply of mineral nutrients. *Physiol. Plant*, **51,** 245–252.

Liljeroth, E., Van Veen, J.A. and Miller, H.J. (1990) Assimilate translocation to the rhizosphere of two wheat lines and subsequent utilization by rhizosphere microorganisms at two soil nitrogen concentrations. *Soil Biol. Biochem.*, **22,** 1015–1021.

Ludwig, B., John, B., Ellerbrock, R., Kaiser, M. and Flessa, H. (2003) Stabilization of carbon from maize in a sandy soil in a long-term experiment. *Eur. J. Soil Sci.*, **54,** 117–126.

Martin, J.K. and Puckridge, D.W. (1982) Carbon flow through the rhizosphere of wheat crops in South Australia. In Galbally, I.E. and J.R. Freney (Eds.): The Cycling of Carbon, Nitrogen, Sulphur and Phosphorus in Terrestrial and Aquatic Ecosystems. Australian Academy of Science, Canberra, pp. 77–81.

Martin, J.K. and Merckx, R. (1992) The partitioning of photosynthetically fixed carbon within the rhizosphere of mature wheat. *Soil Biol. Biochem.*, **24,** 1147–1156.

Martin, J. K. and Merckx, R. (1993) The partitioning of root-derived carbon within the rhizosphere of arable crops. In Mulongoy, K. and R. Merckx (Eds.): Soil Organic Matter Dynamics and Sustainability of Tropical Agriculture, Wiley-Sayce Co-Publication, Leuven, pp. 101–107.

Meharg, A.A. (1994) A critical review of labelling techniques used to quantify rhizosphere carbon-flow. *Plant and Soil*, **166,** 55–62.

Meharg, A.A. and Killham, K. (1990) Carbon distribution within the plant and rhizosphere in laboratory and field grown *Lolium perenne* at different stages of development. *Soil Biol. Biochem.*, **22,** 471–477.

Meharg, A. A. and Killham, K. (1991) A new method of quantifying root exudation in the presence of soil microflora. *Plant and Soil*, **133,** 111–116.

Merbach, W., Knof, G. and Miksch, G. (1990) Quantifizierung der C-Verwertung im System Pflanze–Rhizosphäre–Boden. Tag.-Ber., Akad. Landwirtsch.-Wiss., Berlin. **295,** 57–63.

Merbach, W., Ruppel, S. and Rietz, C. (1991) Einfluss der Mikrobenbesiedlung auf die ^{14}C-Freisetzung durch Wurzeln unter Bodenbedingungen. *Ökophysiologie des Wurzelraumes*, **2,** 66–68.

Merckx, R., Dijkstra, A., den Hartog, A. and Van Veen, J.A. (1987) Production of root-derived material and associated microbial growth in soil at different nutrient levels. *Biol. Fertil. Soils*, **5,** 126–132.

Newman, E.I. and Watson, A. (1977) Microbial abundance in the rhizosphere: a computer model. *Plant and Soil*, **48,** 17–56.

Nguyen, C., Todorovic, C., Robin, C., Christophe, A. and Guckert, A. (1999) Continuous monitoring of rhizosphere respiration after labelling of plant shoots with $^{14}CO_2$. *Plant and Soil*, **212,** 191–201.

Paul, E.A. and Clark, F.E. (1996) Soil microbiology and biochemistry. London. Academic Press.

Puget, P., Chenu, C. and Balesdent, J. (1995) Total and young organic matter distributions in aggregates of silty cultivated soils. *Eur. J. Soil Sci.*, **46,** 449–459.

Redmann, R.E. (1992) Primary productivity. In: Coupland, R.T. (Ed): Natural grasslands. Introduction and western hemisphere, London, Elsevier, p. 75–93.

Rochette, P. and Flanagan, L.B. (1998) Quantifying rhizosphere respiration in a corn crop under field conditions. *Soil Sci. Soc. Am. J.*, **61,** 466–474.

Rodin, L.E. and Basilevich, N.I. (1965) Dynamics of organic matter and biological turnover in the most important vegetation types. [Russian]. Leningrad. Nauka.

Saggar S., Hedley, C. and Mackay, A.D. (1997) Partitioning and translocation of photosyntetically fixed ^{14}C in grazed hill pastures. *Biol. Fertil. Soils*, **25,** 152–158.

Sauerbeck, D. and Johnen, B. (1976) Der Umsatz von Pflanzenwurzeln im Laufe der Vegetationsperiode und dessen Beitrag zur „Bodenatmung“ *Z. Pflanzenernähr. Bodenk.*, **3,** 315–328.

Shepherd, T. and Davies, H.V. (1993) Carbon loss from the roots of forage rape (*Brassica napus* L.) seedlings following pulse-labelling with $^{14}CO_2$. *Ann. Bot.*, **72,** 155–163.

Schönwitz, R. and Ziegler, H. (1988) Interaction of maize roots and rhizosphere microorganisms. *Z. Pflanzenernähr. Bodenkd.*, **152,** 217–222.

Schlesinger, W.H. (1977) Carbon balance in terrestrial detritus. *Ann. Rev. Ecol. Syst.*, **8,** 51–81.

Schneckenberger, K., Reiher, W. and Kuzyakov, Y. (2003) Estimation of the distribution of ‘new’ organic carbon in soil under perennial energy plants (*Miscanthus x giganteus*) using natural ^{13}C abundance. Proceedings of ‘Mechanism and regulation of organic matter stabilization in soils’ Conference, Munich, Germany October 5–8, 2003, **127**

Sims, P.L. and Singh, J.S. (1971) Herbage dynamics and net primary production in certain ungrazed and grazed grasslands in North America. In French, N.R. (Ed.): Preliminary Analysis of Structure and Function in Grasslands. Range Science Department Series No. 10. Colorado State University, Fort Collins, Colorado, pp. 59–124.

Siniakina, S.V. and Kuzyakov, Y. (2002) The ^{14}C tracer study of carbon turnover in soil in a model experiment. *Euras. Soil Sci.*, **35**, 1287–1295.

Steingroever, E. (1981) The relationship between cyanide-resistant root respiration and the storage of sugars in the taproot in *Daucus carota* L. *J. Exp. Bot.*, **130,** 911–919.

Stewart, D.P.C. and Metherell, A.K. (2000) Carbon (^{13}C) uptake and allocation in pasture plants following field pulse-labelling. *Plant and Soil*, **210,** 61–73.

Swinnen, J. (1994) Evaluation of the use of a model rhizodeposition technique to separate root and microbial respiration in soil. *Plant and Soil*, **165,** 89–101.

Swinnen, J., Van Veen, J.A. and Merckx, R. (1994) ^{14}C pulse-labelling of field-grown spring wheat: an evaluation of its use in rhizosphere carbon budget estimations. *Soil Biol. Biochem.*, **26,** 161–170.

Swinnen, J., Van Veen, J.A. and Merckx, R. (1995) Carbon fluxes in the rhizosphere of winter wheat and spring barley with conventional vs. integrated farming. *Soil Biol. Biochem.*, **27,** 811–820.

Titlyanova, A.A. and Tesarzheva, M. (1991) Regimes of biological turnover. [Russian]. Nauka, Novosibirsk.

Van Ginkel, J.H., Gorissen, A. and Van Veen, J.A. (1997) Carbon and nitrogen allocation in *Lolium perenne* in response to elevated atmospheric CO_2 with emphasis on soil carbon dynamics. *Plant and Soil*, **188,** 299–308.

Van Ginkel, J.H., Gorissen, A. and Polci, D. (2000) Elevated atmospheric carbon dioxide concentration: effects of increased carbon input in a *Lolium perenne* soil on microorganisms and decomposition. *Soil Biol. Biochem.*, **32,** 449–456.

Warembourg, F.R. (1975) Application de techniques radioisotopiques a l'etude de l'activite biologique dans la rhizosphere des planes. *Rev. Ecol. Biol. Sol.*, **12,** 261–272.

Warembourg, F.R. and Paul, E.A. (1977) Seasonal transfers of assimilated ^{14}C in grassland: plant production and turnover, soil and plant respiration. *Soil Biol. Biochem.*, **9,** 295–301.

Warembourg, F.R. and Morral, R.A.A. (1978) Energy flow in the plant – microorganism system. In Dommergues, Y.R. and S.V. Krupa (Eds) *Interactions between non-pathogenic soil microorganisms and plants.* Elsevier, Amsterdam, pp. 205–242.

Warembourg, F.R. and Billes, G. (1979) Estimating carbon transfers in the plant rhizosphere. In: Harley, J.L. and Scott Russel, R. (Eds) *The soil–root interface*. Academic Press, London, pp. 183–196.

Warembourg, F.R. and Kummerow, J. (1991) Photosynthesis/translocation studies in terrestrial ecosystems. In: Coleman, D.C. and Fry, B. (Eds) *Carbon Isotope Techniques*. Academic Press, San Diego, pp. 11–37.

Warembourg, F.R. and Esterlich, H.D. (2000) Towards a better understanding of carbon flow in the rhizosphere: a time-dependent approach using carbon-14. *Biol. Fert. Soils*, **30,** 528–534.

Whipps, J.M. (1987) Carbon loss from the roots of tomato and pea seedlings grown in soil. *Plant and Soil*, **103,** 95–100.

Whipps, J.M. (1990) Carbon Economy. In Lynch, J.M. (Ed): *The Rhizosphere*. Wiley, Chichester, pp. 59–97.

Whipps, J.M. and Lynch, J.M. (1983) Substrate flow and utilization in the rhizosphere of cereals. *New Phytol.*, **95,** 605–623.

Zagal, E. (1994) Carbon distribution and nitrogen partitioning in a soil–plant system with barley (*Hordeum vulgare* L.), ryegrass (*Lolium perenne*) and rape (*Brassica napus* L.) grown in a $^{14}CO_2$–atmosphere. *Plant and Soil*, **166,** 63–74.