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Contribution of *Lolium perenne* rhizodeposition to carbon turnover of pasture soil

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Abstract

Carbon rhizodeposition and root respiration during eight development stages of *Lolium perenne* were studied on a loamy Gleyic Cambisol by $^{14}CO_2$ pulse labelling of shoots in a two compartment chamber under controlled laboratory conditions. Total $^{14}CO_2$ efflux from the soil (root respiration, microbial respiration of exudates and dead roots) in the first 8 days after ^{14}C pulse labelling decreased during plant development from 14 to 6.5% of the total ^{14}C input. Root respiration accounted for was between 1.5 and 6.5% while microbial respiration of easily available rhizodeposits and dead root remains were between 2 and 8% of the ^{14}C input. Both respiration processes were found to decline during plant development, but only the decrease in root respiration was significant. The average contribution of root respiration to total $^{14}CO_2$ efflux from the soil was approximately 41%. Close correlation was found between cumulative $^{14}CO_2$ efflux from the soil and the time when maximum $^{14}CO_2$ efflux occurred (r=0.97). The average total of CO_2 efflux from the soil with *Lolium perenne* was approximately 21 μg C-CO_2 d^{-1} g^{-1}. It increased slightly during plant development. The contribution of plant roots to total CO_2 efflux from the soil, calculated as the remainder from respiration of bare soil, was about 51%. The total ^{14}C content after 8 days in the soil with roots ranged from 8.2 to 27.7% of assimilated carbon. This corresponds to an underground carbon transfer by *Lolium perenne* of 6–10 g C m^{-2} at the beginning of the growth period and 50–65 g C m^{-2} towards the end of the growth period. The conventional root washing procedure was found to be inadequate for the determination of total carbon input in the soil because 90% of the young fine roots can be lost.

Introduction

The intensity of underground turnover of organic matter is often measured by the total CO_2 efflux from the soil surface. In this case the soil is usually covered with a vessel and the CO_2 is trapped in an alkaline or other CO_2 sorbent. In most cases the green plants growing under the vessel will be cut off and removed from the surface to exclude the assimilation of CO_2. The roots are remaining in the soil and continue to contribute to the CO_2 efflux measured on the surface. This contribution from plants (carbon rhizodeposition and root respiration) to the measured CO_2 efflux is very important because the root respiration does not affect the turnover of soil organic matter and only interferes with the picture of turnover of organic matter. The rhizodeposition on root exudates (easily available carbon source) greatly influence carbon (C) turnover in soils and can lead to C accumulation or C consumption due to influence on the microbial activity in the rhizosphere. The contribution of both C flows (carbon rhizodeposition and root respiration) to total CO_2 efflux is essentially unclear and varies in literature from 19% (Warembourg and Paul, 1977) to 80% (Martin and Merckx, 1992).

Labelling of plants with ^{14}C has been widely used to quantify rhizodeposition as it allows one to distinguish between root-derived organic carbon and native soil organic carbon (Whipps, 1990). Two varieties

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of ^{14}C labelling are commonly used: continuous labelling and pulse labelling. Pulse labelling with ^{14}C compared to continuous labelling has the advantage of being easier (Whipps, 1990), gives more information on photosynthate distribution at specific development stages of the plants (Meharg and Killham, 1990) and can be used for kinetic investigation of $^{14}CO_2$ evolution from soil (Warembourg and Billes, 1979). In addition, pulse labelling can help distinguish between different stages of $^{14}CO_2$ efflux from soil. Results about the contribution of agricultural plants (wheat, barley and maize) to carbon accumulation and turnover of soil organic matter showed that agricultural plants seldomly transfer more than 33% of assimilated carbon into the soil (Swinnen et al., 1995; Zagal et al., 1993). More than half of this carbon can be respired by roots and microorganisms in the first days after $^{14}CO_2$ assimilation (Cheng et al., 1993; Gregory and Atwell, 1991; Swinnen, 1994; Swinnen et al., 1995).

Although pasture plants are often used for soil reclamation, there is little information about their contribution particularly to carbon accumulation in soil and turnover of soil organic matter. Pasture plants can differ from annual agricultural crops such as wheat, barley or maize, with which most of the investigations about rhizodeposition were carried out. This is because agricultural grain plants were selected and cultivated to maximise the harvest index while the breeding of pasture grasses is aimed at maximising floor yield. This leads to differences in partitioning of assimilates from photosynthesis.

This paper presents attempts to quantify root respiration and total carbon rhizodeposition of *Lolium perenne* under laboratory conditions.

Materials and methods

We studied the C rhizodeposition and root respiration of *Lolium perenne* on a fine loamy Gleyic Cambisol by means of $^{14}CO_2$ pulse labelling of shoots in eight development stages in a two compartment chamber (Martin and Merckx, 1992; Merbach, 1992; Warembourg and Kummerow, 1991) under controlled laboratory conditions.

Soil

The soil, a fine loamy Gleyic Cambisol (FAO-UNESCO, 1990), was taken from the top 10 cm (Ah horizon) of a pasture in Allgäu (South Germany, Kleber, 1997, HFV plot), air dried, mixed and passed through a 5-mm sieve (Table 1). Each pot was filled with 3.1 kg of air dried soil.

Chamber and labelling

The two compartment Plexiglas chamber consists of 1) a lower part (Ø138 mm and height 220 mm) for the soil and plant roots and 2) an upper part (Ø138 mm and height 300 mm) for the shoots and $^{14}CO_2$ generation. Both parts are separated from each other by a Plexiglas lid with drill holes (Ø= 6 mm) for plants. One day before labelling, each hole with a plant was sealed with Silicon paste NG 3170 of Fa. Thauer & Co. Dresden (Gregory and Atwell, 1991; Swinnen et al., 1995).

340 kBq of ^{14}C as $Na^{14}CO_3$ solution was put in a 2-ml Eppendorf micro test tube in the upper compartment of the chamber, the chamber was then closed and 1 ml of 5 *n* H_2SO_4 was added to the $Na^{14}CO_3$ solution in the microtest tube through a pipe on the upper chamber part. This allowed complete evolution of $^{14}CO_2$ into the chamber atmosphere.

The labelling took place at 8 different growth stages (plant heights from 7 to 35 cm, comp. Table 2). Plants in different chambers were used for labelling at different development stages.

Growing conditions

Nine non-vernalized seedlings of *Lolium perenne*, spec. Gremie, were grown in each pot. The distance between every two plants was about 3.5 cm. The plants were grown at 26–28 °C day and 22–23 °C night temperature with a day-length of 14 h and light intensity of approximately 400 μmol m^{-2} s^{-1} at the top of the canopy. The soil water content of each chamber was measured gravimetrically and was adjusted daily to about 60% of the available field capacity.

To compare total unlabelled CO_2 evolution with and without *Lolium perenne*, the soil was also incubated in the same pots and under the same conditions.

Sample analysis

During the experiment, the CO_2 evolving from upper and lower chamber compartment was trapped separately in 20 ml of 0.5 *n* NaOH solution by continuously pumping (100 cm^3 min^{-1}) with a membrane pump. Labelling took place within 8 hours after the pulsing of $^{14}CO_2$ and trapping of CO_2 from the upper chamber

Table 1. Basic characteristics of the Ah horizon of the fine loamy Gleyic Cambisol from an Allgäu pasture (south Germany) used in the experiment (Kleber, 1997, HFV)

pH($CaCl_2$)	Corg	Nt	C/N	Clay	Silt	Sand	FC[1]	AWC[2]	$CaCO_3$
	%	%		<2μm	2–63μm	63–2000μm	%	%	%
5.2	4.7	0.46	10	28.4	47.1	24.5	50	230	

FC[1] and AWC[2]: field capacity (pF = 1.8) and available water capacity (pF 1.8 - pF 4.2).

Table 2. Plant height, days after sowing and development stages of *Lolium perenne* at which ^{14}C labelling was conducted

plant height (cm)	7	13	15	19	22	24	30	35
days after sowing	45	57	59	63	66	69	77	95
development stage	emergence	tillering begin		tillering middle			tillering end	

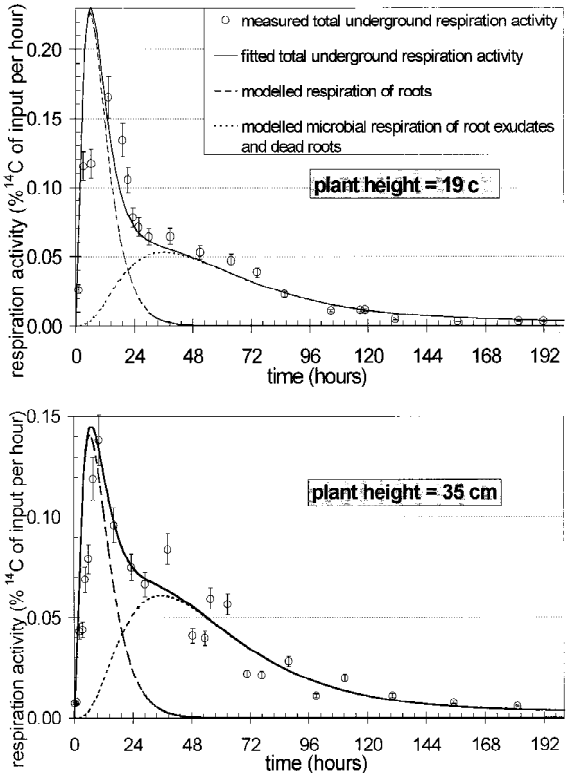

Figure 1. Measured and fitted $^{14}CO_2$ efflux from the soil and differentiation between root respiration and microbial respiration of root exudates and dead roots. $^{14}CO_2$ efflux at plant height 19 cm (at the top) and at plant height 35 cm (at the bottom) is shown. (Each point of $^{14}CO_2$ efflux is placed in the center between two neighboring points of NaOH exchange.)

compartment was then started to remove the remaining unassimilated $^{14}CO_2$.

The trap for $^{14}CO_2$ evolved from the soil was changed every hour immediately after labelling, but after 5 days only twice daily. 8 days after labelling the chamber was opened, each plant cut at the base, each root-soil column pulled out, and roots were washed from the soil by hand on a 0.5-mm sieve. Shoots, roots and soil were dried at 60 °C. Dry samples of shoots, roots and soil were pulverized in a ball mill prior to analysis for radioactivity.

Radioactivities of shoots, roots and soil samples were measured with the scintillation cocktail Permafluor E^+ (Canberra Packard) by a Liquid Scintillation Counter Tri-Carb 2000CA (Canberra Packard), after combustion of 1 g of sample within an oxidizer unit (Canberra Packard), Model 307.

^{14}C in CO_2 collected in NaOH solution was measured with the scintillation cocktail Rothiscint-22x of Roth Company on 1-ml aliquots of NaOH after the decay of chemiluminiscence. The ^{14}C counting efficiency was about 89% and the ^{14}C-activity measurement error did not exceed 2%. The absolute ^{14}C-activity was standardized by addition of NaOH solution as quencher to the scintillation cocktail and using a two channel ratio method of extended standard (tSIE).

$^{14}CO_2$ effluxes from the soil were measured with two replications. Variability between the replications did not exceed 15%. ^{14}C measurements of shoots, roots and soils were conducted with four replications.

Total content of CO_2 collected in NaOH solution was measured by titration with 0.2 *n* HCl against phenolphtalein after addition of 0.5 *n* $BaCl_2$ solution (Black, 1965).

Total C content in shoots and roots was considered to be 40% of dry mass.

Results and discussion

Lolium perenne assimilated during the first eight hours practically all the total $^{14}CO_2$ input given to the shoot. Only 0.015 – 4.3% of $^{14}CO_2$ input remained in the upper compartment (trapped in NaOH after 8 hours). For this reason, all results about the distribution of ^{14}C are presented as per cent of ^{14}C total input.

Total $^{14}CO_2$ efflux from the soil

The beginning of $^{14}CO_2$ efflux from the soil was recorded within the 1^{st} hour after labelling the shoots of *Lolium perenne*. Cheng et al. (1993) found the beginning of $^{14}CO_2$ evolution from soil with winter wheat and rye to be within 30 minutes after pulse labelling. These results and some other investigations (Gregory and Atwell, 1991) show that assimilation of CO_2 and the downward transport of C in plants are very rapid processes. $^{14}CO_2$ evolution reached its maximum within the 1^{st} day (Figure 1), and the time taken to reach this maximum decreased during plant development (Figure 2). Young plants transport C downwards more slowly than old plants. The time of maximum $^{14}CO_2$ evolution was highly correlated ($r=0.97, \alpha<0.001$) with cumulative $^{14}CO_2$ efflux from the soil during the first 8 days after labelling (Figure 2, the inset). The more $^{14}CO_2$ evolved from the soil the later the maximum $^{14}CO_2$ respiration activity was detected. We can not explain the reasons for this phenomenon, therefore additional investigations are necessary.

Total $^{14}CO_2$ efflux from the soil in the first 8 days after ^{14}C pulse labelling decreased from 14 to 6.5% of ^{14}C input during plant development (Figure 2). Total root activity at the beginning of development is obviously much higher than during the latest development stages.

Separating root respiration and microbial respiration of rhizodeposits

Total $^{14}CO_2$ efflux from the soil comprises of 1) root respiration, 2) microbial respiration of root exudates and 3) microbial respiration of dead roots and root parts (Helal and Sauerbeck, 1991; Whipps, 1990). Sterilisation of soil with roots used in some experiments is insufficient to separate root respiration from microbial respiration of rhizodeposits because of stimulation of root exudation and development by soil microorganisms. Meharg and Killham (1995) showed that some microorganisms could increase the root exudation of *Lolium perenne* 34-times in comparison with sterile soil. Merbach and Ruppel (1992) found a 13-fold increase of root exudation by wheat.

Two other different approaches based on the isotope dilution method were used to separate root respiration from microbial respiration of rhizodeposits (Cheng et al., 1993; Swinnen, 1994). These experiments showed, however, highly varying results: Cheng et al. (1993) found that root respiration of 3-week-old wheat plants is about 41% of the total respiration of rhizosphere. Swinnen (1994) estimates the contribution of root respiration of 30-day-old wheat and barley plants to total rhizosphere respiration to be 89–95%.

In order to separate the processes of root respiration, microbial respiration of root exudates and of dead roots and root parts we have developed a simple model for $^{14}CO_2$ efflux from soil after $^{14}CO_2$ pulse labelling of shoots. The model describes separately only the underground flows of labelled carbon and can divide total $^{14}CO_2$ efflux from soil into the 3 fluxes named above.

The model consists of seven ^{14}C labelled compartments (Figure 3):

$^{*}CO_2$: $^{14}CO_2$ that was introduced in the upper chamber part at labelling begin (is equal to 100% of ^{14}C activity at t = 0), glucose: photosynthetically assimilated ^{14}C, shoot and root: ^{14}C incorporated in shoots and roots after photosynthesis, exudate: ^{14}C in easily available deposits exudated from roots, microb. biomass: ^{14}C incorporated in soil microorganisms by mineralisation of roots and exudates,

CO_2: $^{14}CO_2$ evolved from soil.

All ^{14}C flows in the model (microbial decomposition of root exudates and of dead roots and root parts) are described with 1^{st} order kinetics (Van Veen et al., 1985). The rate constants used for calculations in the model were taken from previous investigations and this experiment too (Table 3). Most of the rate parameters: microbial decomposition rate of exudates, microbial respiration, dead root decomposition rates, ^{14}C transport rate of photosynthate in the root, except for rate of root respiration and exudation were introduced into the model for different development stages of *Lolium perenne* as constants. The parameters: rate of root respiration and exudation were estimated by fitting modelled $^{14}CO_2$ efflux to measured $^{14}CO_2$ efflux. The fitting occurs by minimising of least squares using

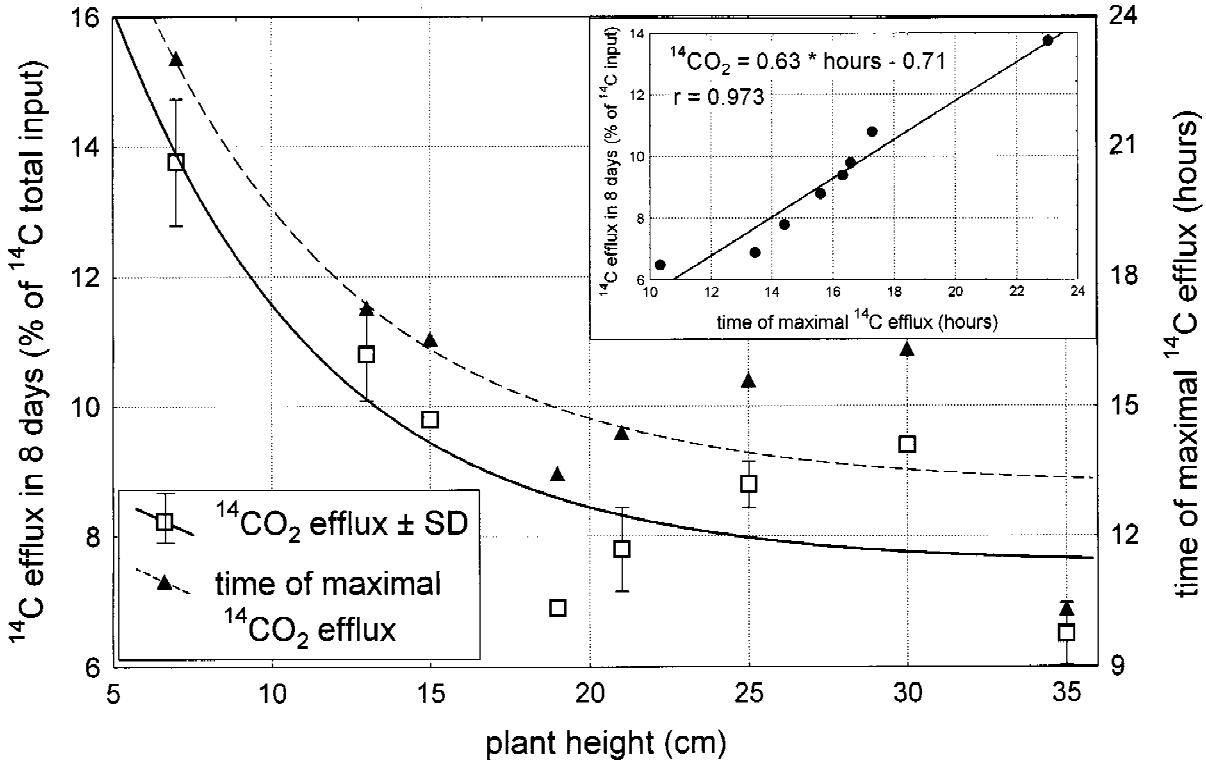

Figure 2. $^{14}CO_2$ efflux from the soil (means ± standard deviation) in the first 8 days after ^{14}C pulse labelling as part of total assimilated C and the time when maximum $^{14}CO_2$ evolution was attained in relation to plant height. The inset presents the relationship between the two parameters.

Table 3. Rate constants (r) used in the model to describe $^{14}CO_2$ efflux from the soil after $^{14}CO_2$ pulse labelling of shoots

Model parameters:	r (h^{-1})	The parameter was taken based on:
Photosynthesis	0.2	diminishing rate of $^{14}CO_2$ from the upper chamber part
Shoot growth	0.113	the relation between shoot growth and root growth was chosen to be equal to the ^{14}C incorporation in shoots and roots
Transport	1	very high transport rates of assimilated ^{14}C measured, (compare with Cheng et al., 1993)
Root respiration	0.003 – 0.01	fitted on experimental $^{14}CO_2$ efflux rates from soil at each development stage of *Lolium perenne* investigated separately
Root growth	0.05	see shoot growth
Mineralisation of roots	0.0001	Whitmore and Groot, 1994; Kuzyakov et al., 1997
Exudation	0.003 - 0.012	fitted on experimental $^{14}CO_2$ efflux rates from soil at each development stage of *Lolium perenne* investigated separately
Mineralisation of exudates	0.07	Kuzyakov 1993; 1997
Respiration of microbial biomass	0.03	Kuzyakov 1993; 1997

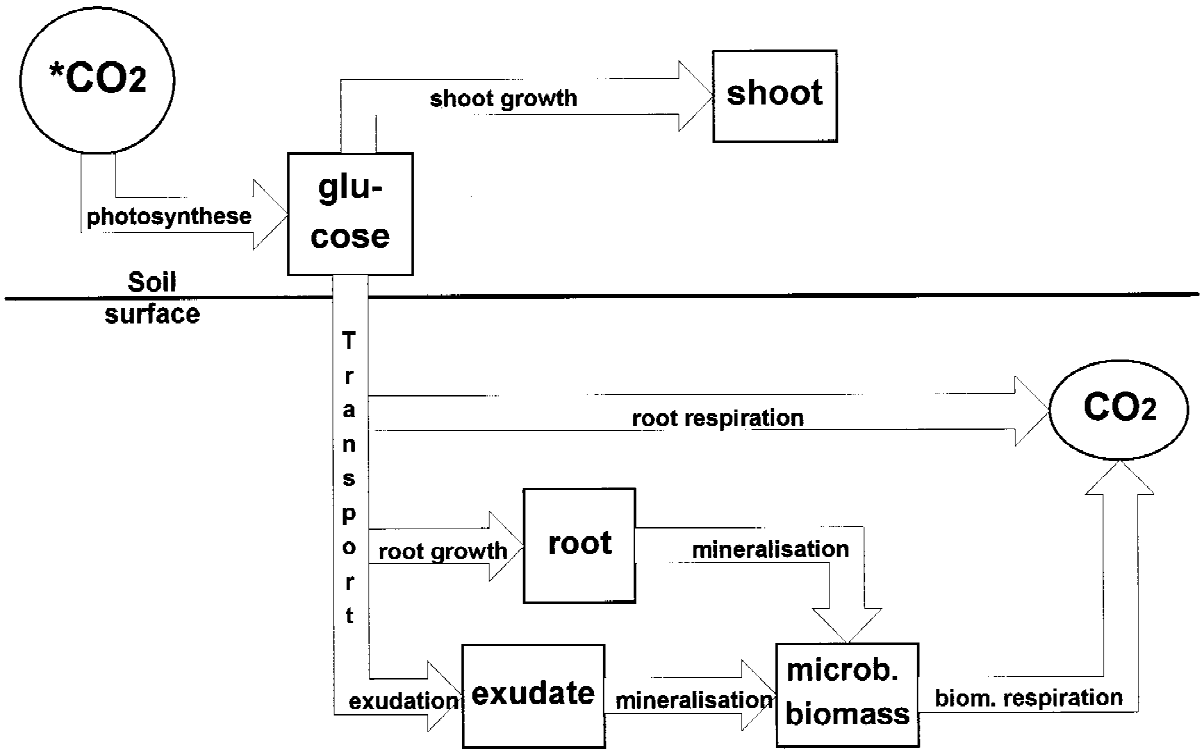

Figure 3. Simplified scheme of the model for $^{14}CO_2$ efflux from the soil after $^{14}CO_2$ pulse labelling of shoots.

the Marquardt method. We have fitted the model with the measured $^{14}CO_2$ efflux dynamics at each development stage of *Lolium perenne* investigated separately (Figure 1).

The separation of CO_2 efflux coming from different flows is based on the assumption that these three processes occur at different rates: the most rapid process is CO_2 efflux from root respiration. The CO_2 evolution by microbial respiration of root exudates is a slower process than root respiration because it consists of a chain of successive processes: exudation from the root, intake by microorganisms and respiration of microorganisms (Figure 3). The microbial respiration of dead roots is very slow and, therefore, it has only a negligible contribution to the total $^{14}CO_2$ efflux from soil in the first days after pulse labelling. This modelling approach allows the separation of different rate stages of $^{14}CO_2$ efflux and can only be used by pulse labelling. The fitted curve (Figure 1) and the subdivision in 1) root respiration and 2) microbial respiration of root exudates and dead roots for two of the development stages investigated (19 and 35 cm height) substantiate the assumptions.

In order to calculate separately the total root respiration and root exudation an integration of each function was performed. The calculated root respiration ranged from 1.5 to 6.5% and the microbial respiration of easily available rhizodeposits and dead root residues were between 2 and 8% of the total ^{14}C input (Figure 4). Both processes diminished during plant development, but the decrease in root respiration occurred faster and the parameters of the fitted exponential curve (Figure 4) were significant ($\alpha < 0.01$). The used separation between root respiration and microbial respiration show that the contribution of root respiration to the total $^{14}CO_2$ efflux from the soil fluctuated between 17 and 61% with an average of 41%. These results are similar to those of Cheng et al. (1993) found for 3-week-old wheat plants growing on an arable sandy soil using the isotope dilution method.

The separation of underground C flows in rhizodeposition and root respiration is very important because C rhizodeposition and root residues contribute to the C turnover of soil, especially to the microbial activity in the rhizosphere, thus completing the underground C stock. Root respiration does not affect the turnover

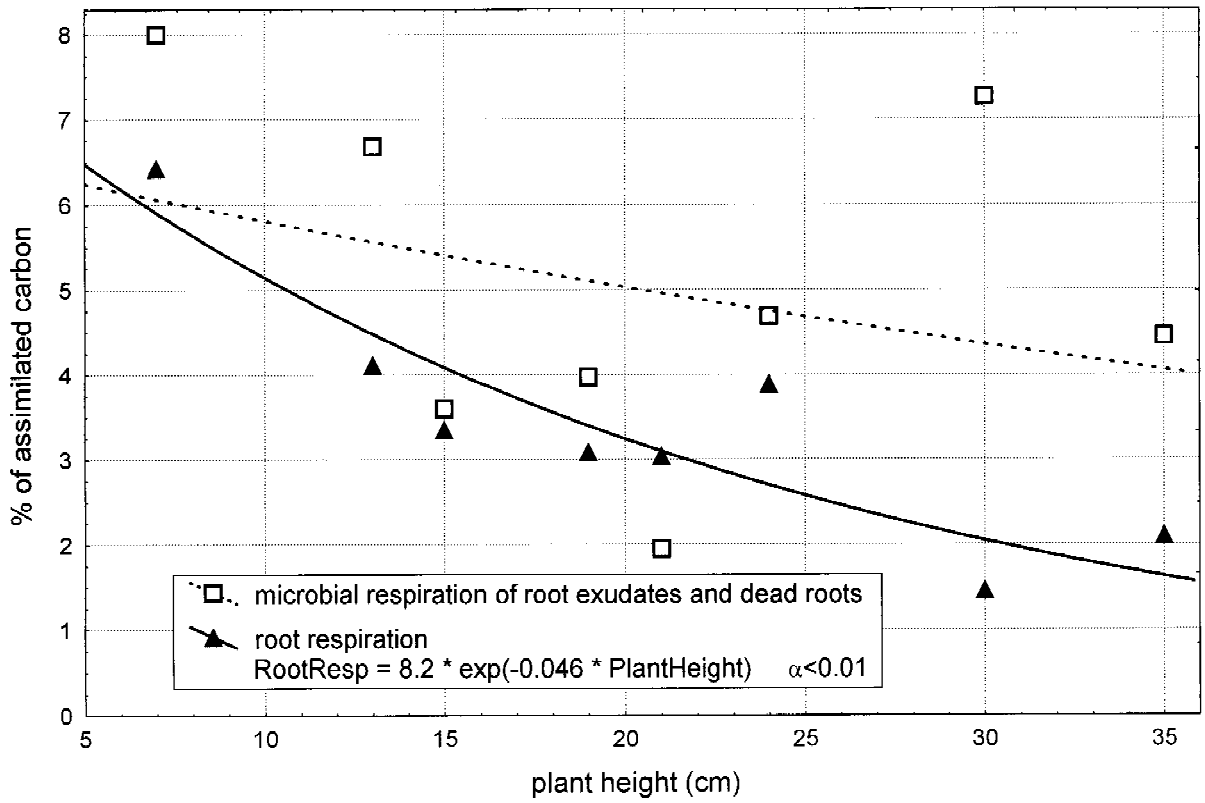

Figure 4. Calculated root respiration and microbial respiration of root exudates and dead roots during the development phase of *Lolium perenne*.

of organic matter but contributes to the total CO_2 evolution from the soil.

Contribution of Lolium perenne to the total CO_2 evolution from the soil

We compared the total unlabelled CO_2 evolution from the soil with plants and from the bare soil incubated under same conditions (the same soil amounts in the pot, the same soil moisture, the same air temperature and airflow). We calculated that the difference between CO_2 efflux from the soil with *Lolium perenne* and from the bare soil is equal to the contribution of plant roots to the whole CO_2 efflux. The average CO_2 efflux from the soil with *Lolium perenne* is about double that from the bare soil. The CO_2 evolution from bare soil was about 10.2 μg C-CO_2 d^{-1} g^{-1} and was nearly constant during the incubation (exception are the first 2-3 weeks after filling soil in the pots). The average CO_2 efflux from the soil with *Lolium perenne* was about 21.1 μg C-CO_2 d^{-1} g^{-1} and slightly increased during the plant development. The contribution of plant roots to the total CO_2 efflux from the soil (calculated as the difference) increased insignificantly during plant development and was about 51%. The soil used in the experiments had a very high total C content and therefore a high level of total CO_2 efflux. In soils with a lower total C content, the relative contribution of plants to the total CO_2 efflux from soil could be higher.

Turnover intensity of soil organic matter

The average CO_2 efflux from the bare soil was about 10.2 μg C-CO_2 d^{-1} g^{-1}. The content of organic carbon in the soil is 4.7%. On this basis we calculate the turnover intensity of soil organic matter as a mineralisation rate of total organic carbon. It is equal to 2.2 $\times$ 10^{-4} d^{-1}. Soil organic matter consists of both inert and microbially decomposable fractions (Körschens, 1993). Only the microbially decomposable fraction of soil organic carbon contributes to the turnover and CO_2 efflux from the soil. To calculate the content of the decomposable fraction the inert part must be subtracted from the whole carbon content of the soil. The amount of the inert fraction depends on the fine silt

and clay content and can be calculated for arable soils as follows (Körschens, 1993):

$$C_i = 0.04 \times (fine\,silt + clay)$$

where C_i is the inert carbon content. The soil investigated contains 40.6% fine silt and clay. Therefore the inert carbon content may be 1.62%. According to CO_2 efflux from the bare soil the mineralisation rate of the decomposable part of organic carbon is equal to 3.3 $\times$ 10^{-4} d^{-1}. The mineralisation rate of decomposable organic carbon for all European soils calculated by Franko (1995, 1997) is equal to 5.56 $\times$ 10^{-3} d^{-1}. This constant value was criticised by Rühlmann *et al.* (1997) who found an exponential dependence of the mineralisation rate on the content of decomposable organic carbon. Our soil has very high carbon content and therefore the lower mineralisation rate in comparison with that of Franko (1995, 1997) is explainable. When the turnover intensity of the soil organic matter is calculated based on the total CO_2 efflux from the soil with *Lolium perenne*, the turnover doubles.

Carbon transfer of Lolium perenne in the soil

The total ^{14}C content in the soil (soil and roots) after 8 days ranged from 8.2 to 27.7% of assimilated carbon. The data for ^{14}C incorporation in the roots of *Lolium perenne* reported by Meharg and Killham (1990, 1991) are of the same order (4–29%). However Zagal (1994) found that *Lolium perenne* transfers 32–42% of assimilated carbon under the soil surface for a long time. Only one tenth of this was in the soil and the rest in the roots. We found only between 1 and 6.8% of assimilated carbon in the roots after the root washing. We suppose that the finest roots contained most ^{14}C-radioactivity after the pulse labelling. These were lost during washing on a 1-mm sieve. The $^{14}CO_2$ evolution from the soil 8 days after the labelling was negligible ($< 0.4\%$ d^{-1}) because all labelled root exudates were decomposed and the labelled root respiration ended. Therefore most residual ^{14}C found in the soil was located in the roots. Accordingly, the relation between ^{14}C content in the soil with roots and ^{14}C content only in the roots, we have calculated that about 83–95% of finest roots were lost by the conventional root washing method. These fine roots make an essential contribution to the intensive underground carbon turnover.

For the estimation of carbon flows that *Lolium perenne* transfers below the soil surface at different development stages we used the following equation:

$$C_{UB}[g \cdot m^{-2}] = \frac{C_{shoots}[g \cdot m^{-2}] \times {}^{14}C_{UG}[\%]}{{}^{14}C_{shoots}[\%]}$$

where:
$C_{UG}[\ g \cdot m^{-2}]$: carbon amount transferred underground at each development stage
$C_{shoots}[g \cdot m^{-2}]$: carbon content in the shoots
$^{14}C_{UB}$ [%]: ^{14}C content in the soil 8 days after labelling
$^{14}C_{shoots}$[%]: ^{14}C content in the shoots 8 days after labelling Parameters $C_{shoots}[g \cdot m^{-2}]$, C_{UG}[%], $^{24}C_{shoots}$[%] were taken from the results of experiments and were different for each development stage investigated. This method allows only a rough estimation of the carbon amount transferred underground because C_{UG}[%] is equivalent to the growth rate of roots multiplied by the total root mass in the development stage investigated and not only to the whole root mass. The growth rates of roots and shoots at the same development stage must be equal for a precise underground carbon amount calculation according to the equation above.

According to the equation above, *Lolium perenne* transfers into the soil about 6–10 g m^{-2} C when growth begins (stage 1) and about 50–65 g C m^{-2} at growth stage 8. These correspond to 15–25 g m^{-2} organic matter and 160 g m^{-2} dry organic mater, respectively (Figure 5). This is equal to 0.61% of the C stock in the whole soil profile (0–100 cm) where the soil was taken from. The root mass may be a little higher than the calculated above because plants can transfer a part of assimilated carbon from the shoots to the roots later than 8 days after the labelling (Augustin, 1997, personal communication).

The root mass obtained by means of conventional root washing procedure is equal to 150–290 g m^{-2} and was only slightly dependent on the plant development. This amount includes about 100–130 g m^{-2} of the old roots from the pasture where the soil was taken from.

As shown in Figure 5, the root development of *Lolium* is faster than the development of the shoots and it ends earlier than that of the shoots. The root growth rate reaches its maximum in the second month of plant development.

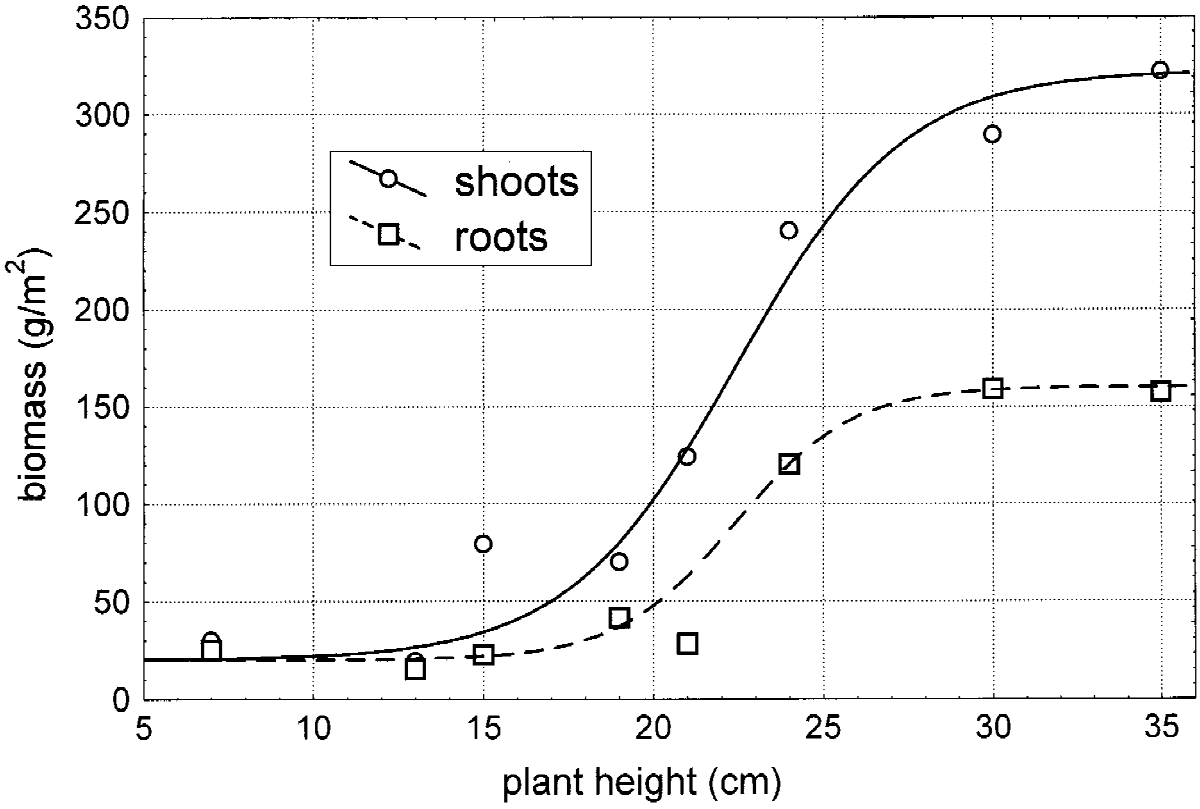

Figure 5. Measured development in shoots of *Lolium perenne* and development of its root biomass calculated as ^{14}C activity.

Conclusions

- The total $^{14}CO_2$ efflux from the soil (root respiration, microbial respiration of exudates and of dead roots) in the first 8 days after the ^{14}C pulse labelling decreased during plant development from 14 to 6.5% of the total ^{14}C input. Root respiration accounted for between 1.5 and 6.5% and microbial respiration of easily available rhizodeposits and dead root remains were between 2 to 8% of the ^{14}C input. The average contribution of root respiration to the total $^{14}CO_2$ efflux from the soil was approximately 41%.
- The average total unlabelled CO_2 efflux from the soil with *Lolium perenne* was about 21 μg C-CO_2 g^{-1} d^{-1} and slightly increased during plant development. The contribution of plants to the total CO_2 efflux from the soil calculated as a difference between the respiration of soil with plants and that of bare soil was about 51% of total CO_2 efflux from the soil with *Lolium perenne*.
- The total ^{14}C content in the soil with roots after 8 days ranged from 8.2 to 27.7% of carbon input. This corresponds to an underground carbon transfer by *Lolium perenne* of about 50–65 g m^{-2} C during three months of plant development.
- Conventional root washing procedure was found to be inadequate for the determination of total carbon input in particular of carbon turnover in the soil because 90% of the young fine roots can be lost.

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