Carbon input by plants into the soil. Review

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Summary – Zusammenfassung

The methods used for estimating below-ground carbon (C) translocation by plants, and the results obtained for different plant species are reviewed. Three tracer techniques using C isotopes to quantify root-derived C are discussed: pulse labeling, continuous labeling, and a method based on the difference in ^{13}C natural abundance in C3 and C4 plants. It is shown, that only the tracer methods provided adequate results for the whole below-ground C translocation. This included roots, exudates and other organic substances, quickly decomposable by soil microorganisms, and CO_2 produced by root respiration. Advantages due to coupling of two different tracer techniques are shown.

The differences in the below-ground C translocation pattern between plant species (cereals, grasses, and trees) 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 rootborne organic substances. The remaining part of below-ground translocated C is incorporated into the soil microorganisms and soil organic matter. 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 (1500 kg C ha^{-1}), when the same growth period is considered. However, during one vegetation period the cereals and grasses allocated beneath the ground about 1500 and 2200 kg 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.

Key words: soil organic matter / below-ground C translocation / C turnover and balance / rhizosphere / root respiration / exudation / assimilate allocation / ^{14}C / ^{13}C

Kohlenstoffeintrag in Böden durch Pflanzen

In diesem Review werden Methoden zur Einschätzung der Translokation von Kohlenstoff (C) in Böden durch Pflanzen und entsprechende Ergebnisse für unterschiedliche Pflanzengruppen diskutiert. Drei Methoden unter Verwendung von C-Isotopen als Tracer für wurzelbürtigen C werden vorgestellt: Pulsmarkierung, kontinuierliche Markierung und die Methode, die auf dem Unterschied in der natürlichen ^{13}C-Abundanz von C3- und C4-Pflanzen basiert. Es wird gezeigt, dass nur die Tracer-Methoden adäquate Ergebnisse zur unterirdischen Translokation des gesamten wurzelbürtigen Kohlenstoffs liefern. Die Vorteile der Kopplung von zwei unterschiedlichen Tracer-Methoden werden gezeigt.

Die Unterschiede im Muster der unterirdischen C-Translokation zwischen den Pflanzengruppen (Getreide, Weidegräser und Bäume) werden untersucht und in Tabellen zusammengefasst. Getreide (Weizen und Gerste) bringen 20%–30% des gesamten assimilierten C unter die Bodenoberfläche. Die Hälfte dieser Menge wird anschließend in den Wurzeln wiedergefunden. Ein Drittel verlässt den Boden als CO_2, das durch Wurzelatmung und mikrobielle Veratmung der wurzelbürtigen organischen Substanzen entsteht. Der Rest des durch die Wurzeln in den Boden eingebrachten C wird in die mikrobielle Biomasse und in die organische Bodensubstanz eingebaut. Der Anteil des assimilierten C, der in den Boden durch Getreide eingebracht wird, verringert sich im Laufe der Pflanzenentwicklung und mit steigender N-Düngung. Die Weidegräser transportieren sogar 30%–50% des assimilierten C in den Boden, aber die Relation zwischen den einzelnen Pools bzw. Flüssen ist ähnlich wie beim Getreide. Sowohl Getreide als auch Weidegräser transportieren durchschnittlich ca. 1500 kg C ha^{-1} in den Boden bei Voraussetzung gleich langer Wachstumsperioden. Bei Berücksichtigung einer vollen Vegetationsperiode transportieren die Weidegräser ca. 600 kg C ha^{-1} mehr in den Boden als Getreidekulturen. Eine einfache Methode zur groben Kalkulation der durch Pflanzen in den Boden eingebrachten C-Mengen und des wurzelbürtigen CO_2-Effluxes aus dem Boden wird vorgeschlagen.

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

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in the soil during the humification are also known. *Redmann* (1992) has reviewed data concerning the grassland ecosystems, while *Paul* and *Clark* (1996) have summarized some results on the C input by other agricultural plants.

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 amount 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 between the roots, 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 three 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. There are SOM, plant residues, intermediates of SOM decomposition, and products of soil biota metabolism. This problem is particularly noticeable when the samples of rhizosphere soil and bulk soil are taken together and mixed before analysis.
2) Fast decompostion ($T_{1/2}$ = 0.5–10 days) by soil microorganisms of all organic substances released from roots (*Paul* and *Clark*, 1996; *Kuzyakov*, 1997; *Kuzyakov* and *Demin* 1998).
3) Appearance of the rhizodeposits in narrow zone of soil adhering the root surface.

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 labeled 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 measured with tracer techniques were 20–100 times higher (*Cheng* et al., 1993) than the concentrations calculated according to the exudation rates of roots (*Newman* and *Watson*, 1977; *Darrah*, 1991a, b). This is due to high losses during the root washing (*Swinnen* et al., 1994; *Kuzyakov* et al., 1999) and fast microbial utilization of organic substances released by the roots (*Paul* and *Clark*, 1996; *Kuzyakov*, 1997; *Kuzyakov* and *Demin* 1998). *Whipps* (1990) summarized estimates of C input by plants into the soil. However, he only reviewed the results of experiments with continuous labeling. 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 towards looking at below-ground C translocation by living plants under natural soil conditions. Only the results obtained by using 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 chemical composition and transformation of root-derived C and the localization of exudates in rhizosphere or along the roots are not reviewed.

2 Tracer techniques for estimation of below-ground C translocation

Currently, three tracer methods are commonly used for the estimation of C input into the soil by plants: (1) pulse labeling, (2) continuous labeling, and (3) ^{13}C natural abundance.

The first two methods are based on the artificial labeling of plants. Shoots are exposed to CO_2 in an atmosphere labeled 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 labeled 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 unlabeled.

In the case of the pulse labeling, the shoots assimilate the labeled CO_2 for only a short period, and only once during the whole plant growth. By continuous labeling the plants assimilate labeled CO_2 over a long period, and mostly between the emergence of the first leaf and the sampling time. Different experimental systems for pulse and continuous labeling 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*, 2000; *Stewart* and *Metherell*, 2000).

Although both methods only differ in the duration of the exposure period to the labeled CO_2, they are used for different aims. Pulse labeling, compared with continuous labeling, has the advantage of being easier to handle (*Whipps*, 1990), provides more information on the recent photosynthate distribution at 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; *Kuzyakov* et al., 1999; 2000a; 2000b; *Nguyen* et al., 1999). The results obtained by pulse labeling correspond to the relative distribution of assimilated C at the moment of labeling. The distribution of labeled C does not correspond to the distribution of total unlabeled C in different plant parts, but rather to the product of total C in the plant part multiplied by its growth rate at the moment of labeling. The total amount of C assimilated by plant is unknown and can be calculated only roughly. For pulse labeling, all three C isotopes can be used: ^{14}C, ^{13}C or ^{11}C. The pulse labeling was used in most studies conducted up to now.

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 labeling is that

Table 1: Below-ground translocation of carbon by wheat into non-sterile soil (expressed as percent of assimilated carbon). Experiments have been carried out with pulse labeling method of tracer supplying.
Tabelle 1: Translokation von Kohlenstoff in nicht sterilen Boden durch Weizen (in % von der C-Gesamtassimilation) (nur die Experimente mit Pulsmarkierung sind zusammengefasst).

Stage of plant growth at the time of labeling	Soil texture	Total below-ground 1+2+3+4	Converted to CO_2 1+2	Root respiration 1	Exudates/ microbial respiration 2	Roots 3	Soil 4	References
28 d	Sandy	40	5.8			33	0.8	*Palta* and *Gregory,* 1998
36 d		41	5.0			35	0.7	
43 d		41	17			23	1.4	
51 d		42	15			25	1.4	
64 d		26	7.7			17	0.8	
In whole vegetation	Loamy	19	14–15	6.4	5	7		*Swinnen* et al., 1995
30 d	Loamy	36	21	19–21	1–2	12	3.1	*Swinnen*, 1994
22 dc		46	17	7–15	2–10	20	19	
58 dc		8.5	3.3	2.7–3.2	0.1–0.5	3.7	1.5	
81 dc		8	3.6	2.8–3.5	0.1–0.8	2.4	2.0	
	Sandy	25			22		3.5	*Merbach* and *Ruppel*, 1992
49 d		55	25			28	2	*Gregory* and *Atwell*, 1991
70 d		15	4			10	1	
105 d		5	2			3	0.2	
126 d		4	2			2	0.2	
In whole vegetation		48	13			33	1.6	
Straw emergence		39	14–16			15–18	4–9	*Swinnen* et al., 1994
earring		23	9–12			8–13	3–6	
blooming		23	9–10			5–6	4–9	
milk ripeness		15	7			2–3	5–6	
wax ripeness		17	9			2–6	5–8	
4–6 leaves		39		14	22		3.4	*Merbach* et al., 1990
21 d	Loamy	40	30	12	18	9.4		*Cheng* et al., 1993
Median		**26**	**10**	**7**	**2**	**7**	**3.5**	**Median**
Arithmetical average		**29**	**11**	**10**	**9**	**14**	**3.4**	**Average**

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 labeling pulses applied at regular intervals during plant growth have been found to provide a reasonable estimate of the cumulative below-ground C input (*Gregory* and *Atwell*, 1991; *Keith* et al., 1986; *Jensen*, 1993; *Swinnen* et al., 1994; *Kuzyakov* et al., 1999, 2000a).

In case of continuous labeling, the total amount of assimilated C is known. In addition, the distribution of labeled 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; the isotopic effects are not considered here). Therefore continuous labeling is particularly appropriate for the estimation of the amount of total C transferred by the plant into the soil and below-ground pools during the labeling period (*Meharg*, 1994). Continuous labeling is also useful for the separation of root-derived and SOM-derived CO_2 (*Johnen* and *Sauerbeck*, 1977; *Whipps*, 1987).

Continuous labeling 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 labeling chamber. These facilities are expensive and limited to a few places in the world. For both pulse and continuous labeling 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 labeling so far. This preferential use of ^{14}C is based on the high sensitivity, lower costs of the purchase and analyses, and easier sample preparation compared with ^{13}C or ^{11}C. Since ^{11}C has a short half-lifetime (20.4 min) only ^{14}C and ^{13}C are appropriate for

Table 2: Below-ground translocation of carbon by barley into non-sterile soil (expressed as percent of total assimilated carbon). (Experiments with only pulse labeling are reviewed).
Tabelle 2: Translokation von Kohlenstoff in nicht sterilem Boden durch Gerste (in % von der C-Gesamtassimilation). (nur die Experimente mit Plusmarkierung sind zusammengefasst).

Stage of plant growth at the time of labeling	Soil texture	Total below-ground	Converted to CO_2	Root respiration	Exudates/ microbial respiration	Roots	Soil	References
		1+2+3+4	1+2	1	2	3	4	
30 d	Sandy	26	11			12	2.2	*Zagal* et al.,
38 d		28	12			12	3.1	1993
46 d		33	18			13	2.9	
In whole vegetation	Loamy	26–33	22–27	13–14	5–6	9–14		*Swinnen* et al., 1995
30 d	Loamy	42	24	21–23	1–3	13	4.8	*Swinnen*, 1994
22 dc		64	36	32–35	0.5–4	22	6.3	
58 dc		13	5.8	5.1–5.7	0.1–0.7	4.5	2.3	
81 dc		4.4	2.3	1.7–2.2	0.1–0.6	1.1	1.0	
50 d		23	16			17	0.4	*Gregory* and
71 d		28	5			22	1.4	*Atwell*, 1991
106 d		9	3			6	0.1	
120 d		8	3			5	0.2	
cumulatively		58	24			32	2.4	
Median		**17**	**14**	**13.5**	**0.9**	**12.5**	**2.3**	**Median**
Arithmetical average		**28**	**14**	**15**	**2**	**13**	**2.3**	**Average**

d – days; dc – Decimal Code of plant development.

continuous labeling. It is important that, although the application of ^{11}C is much more troublesome than of ^{14}C it has some fundamental advantages. For example, the detection limit of ^{11}C is about 10^{-19} mol compared to 10^{-13} mol for ^{14}C, or 10^{-7} mol for ^{13}C. These detection limits are given for simple analysis using conventional sample preparation and measurement techniques. In addition, the same plants can be labeled with ^{11}C many times during the growth as though each labeling is new. A very high detection limit of ^{11}C allows the labeling of the leaf part only, and traces of assimilated C in all other plant compartments (*Keutgen* et al., 1995). Using ^{11}C, *Farrar* et al. (1994) showed the stimulation of photoassimilate translocation into the roots by galactose. However, both experiments with ^{11}C were conducted in nutrient solutions.

An important advantage of the described tracer techniques compared with traditional methods is that the amount of tracer 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 estimate the system losses. Traditional methods are more inaccurate 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 labeling.

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 C3 plants leads to the ^{13}C depletion of about –27‰ (–35‰ $\leq \delta\ ^{13}C \leq$ –20‰) when compared with atmospheric CO_2. Phosphoenol pyruvate carboxylase (C4 plants) results in the depletion of about –13‰ (–15‰ $\leq \delta^{13}C \leq$ –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 though to be negligible. Therefore, the soils developed under C3 or C4 vegetation contain SOM with $\delta^{13}C$ = –27‰ or –13‰, respectively (*Cheng*, 1996). The method is based on cultivation of C3 plant on a C4 soil, or vice versa, and the estimation of rhizodeposition according to the $\delta^{13}C$ value in soil pools or CO_2 evolved from soil. This method can be considered as a variation of the continuous labeling, because the plants and soil are permanently labeled. However, the labeling of plant and soil occur naturally, not artificially, as is the case of pulse or continuous labeling methods described above. The use of ^{13}C natural abundance technique for the estimation C translocation by plants, and for the separation of CO_2 emission from soil into several fluxes, began only five years ago (*Cheng*, 1996). This method can easily be used under field conditions (*Rochette* and *Flanagan*, 1998) because special equipment for plant labeling 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. The situations where the C3 plants grow on a C4 soil, or vice versa, are unnatural. Hence, the application of this method is restricted to places where soils developed under C3 vegetation allow the growth of C4 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 ±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.

In most studies, only one of the tracer techniques was used. However, a combination of two different tracer techniques, or two isotopes in one experiment, could lead to significant progress in the understanding of interactions between plants and soil. *Johansson* (1993) combines continuous ^{13}C labeling before cutting with continuous ^{14}C labeling after cutting and during the regrowth of *Festuca pratensis* L. He found that 21%

Table 3: Comparison of below-ground carbon translocation by different pasture plants (as percent of assimilated ^{14}C-CO_2).
Tabelle 3: Vergleich der Translokation von Kohlenstoff in den Boden durch unterschiedliche Wiesengräser (in % des assimilierten ^{14}C-CO_2).

Plant	Period[1)]	Experimental conditions[2)], soil	Total below-ground 1+2+3+4	Converted to CO_2 1	Root exudates 2	Roots 3	Soil 4	References
Lolium perenne	36 d	Laboratory,	36	14	8.0	6.8	22	*Kuzyakov* et al.,
	49 d	Loamy, p	39	11	6.7	1.3	28	1999
	51 d		23	9.8	3.3	1.5	13	
	55 d		31	6.9	4.0	2.4	24	
	58 d		16	7.8	2.0	0.9	8.2	
	61 d		35	8.8	4.7	3.2	26	
	68 d		29	9.4	7.3	3.4	20	
	87 d		15	6.5	4.5	1.4	8.6	
Lolium perenne	52 d	Laboratory,	5	2.7		0.8	1.8	*Kuzyakov* et al.,
	55 d	Loamy, p	12	6.0		1.8	4.2	2000a
	76 d		12	8.0		1.3	2.4	
	89 d		17	10		1.8	4.9	
	103 d		17	11		2.0	4.6	
Lolium perenne	28 d	Laboratory, Sandy, p	28	1.6		26	0.6	*Griffiths* et al., 1998
Lolium perenne	79 d	Laboratory, sandy, c	39–52	9		29–40	2.3	*Van Ginkel* et al., 1997
Lolium perenne	41 d	Laboratory,	49	16		29	3.0	*Zagal*
	62 d	loamy, c	65	21		40	2.4	1994
Lolium *perenne*	23 d	Laboratory,	28	22		6		*Meharg* and *Killham*
	30 d	sandy,	28	24		4		1990
	37 d		20	12		8		
	51 d		27	18		9		
	65 d		8	4		4		
Lolium perenne	4 w	Field, sandy	67	43		24		*Meharg* and *Killham*,
	8 w		28	16		12		1990
	12 w		15	6		9		
	16 w		44	14		29		
	20 w		37	14		24		
	24 w		14	8		6		
Lolium perenne	14 d	Nutrient solution, laboratory, p	33		1.8	32		*Meharg* and *Killham*, 1991
Median			**28**	**10**	**4.6**	**6**	**4.9**	**Median**
Average			**32**	**13**	**4.7**	**14**	**13**	**Arithmetical average**
Festuca arundinacea	3 w	Loamy				2.5		*Cheng* et al., 1994
Festuca pratensis	29 d ^{14}C	Mollic Gleysol,	22	10		9	3.4	*Johansson*,
	29+15 d ^{13}C	loamy, c	>20	11		9		1993
Festuca pratensis	10 d	Mollic Gleysol, loamy, c	44–49	25–31		28	4	*Johannson*, 1991; 1992
Bromus madritensis	3 w	Laboratory, c	69–75					*Warembourg* et al.,
	15 w		60–64	24–26				1990
	23 w		30–42					
	29 w		8–12	5–8				
Bromus erectus	3 w	Laboratory, c	70					*Warembourg* et al.,
	15 w		59–79	18–24				1990
	23 w		50–66					
	29 w		38–58	15–23				

Table 3: continued
Tabelle 3: Fortsetzung

Plant	Period[1)]	Experimental conditions[2)], soil	Total below-ground 1+2+3+4	Converted to CO_2 1	Root exudates 2	Roots 3	Soil 4	References
Agropyron Koeleria		Field, Chernozem	35–50	9–15				*Warembourg* and *Paul*, 1977
Bouteloua Buchloe		Field	80					*Sims* and *Singh*, 1971
Median			**50**	**17**		**9**	**3.7**	**Median**
Average			**49**	**17**		**12**	**3.4**	**Arithmetical average**

[1)] d – days; w – weeks [2)] p/c – pulse-/continous-labeling

of residual plant ^{14}C at cutting was in the new shoot biomass after regrowth. However, unlike the shoots, half of the roots formed during regrowth were reassimilated after the cutting and the other half before the cutting. Combining ^{13}C natural abundance with ^{14}C pulse labeling, *Kuzyakov* and *Cheng* (2000, unpublished) have shown that in the absence of light, wheat used recently assimilated C for root respiration and exudation instead of the C reserves. In the absence of light, the diurnal changes in efflux intensity of the root-derived CO_2 were recorded with both methods. As well as this, wheat cultivation led to the increase of turnover intensity of SOM.

The results of the relative and total C translocation by living plants are reviewed in the following sections. We summarize the studies according to the three most important types of the ecosystems: cereals (representative for agricultural ecosystems), pasture plants (representative for natural grassland ecosystems), and trees (representative for forests).

3 Below-ground C translocation and partitioning by cereals

Most studies of the below-ground C translocation and partitioning have been conducted on cereals, mainly on wheat and barley. The results concerning C partitioning by cereals obtained in pulse-labeling experiments in the last 10 years are summarized for wheat in Table 1 and for barley in Table 2. All data are expressed as a percentage of total assimilated ^{14}C. Some recalculations of original results were necessary because many authors published their results calculated as a percentage of recovery. The data obtained in continuous labeling experiments were reviewed earlier (*Whipps*, 1990). He has summarized results concerning the below-ground carbon partitioning by crop plants growing in the soil and presented them as a percentage of net fixed C. Direct comparisons between the data collected by *Whipps* (1990) and Tables 1 and 2 are difficult, because different calculation methods are used. 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 (*Waremboug* and *Morral*, 1978; *Swinnen* et al., 1994; *Kuzyakov* et al., 2000a). 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).

Data from Tables 1 and 2 clearly show that C translocation depends on the stage of plant development, rather than on the plant species. The portion of C translocated below-ground by cereals and used for root growth, respiration and exudation decrease during plant development (Tables 1 and 2; *Keith* et al., 1986; *Swinnen* et al., 1994). Similar data have been reported earlier by *Steingroever* (1981) and *Lambers* et al. (1981).

Arithmetical average show that wheat and barley transported about 30% of assimilates into soil (Tables 1 and 2). 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. This, however, cannot be calculated because the total plant weight at the moment of labeling is not reported in most studies. Taking this into consideration, we calculated the median as a parameter more appropriate (but not optimal) than the arithmetical average. According to the medians wheat transfers 26% and barley 17% of total assimilated C into soils. According to the Tables 1 and 2 this below-ground translocated C is used for:

- Root growth (7%–13% of total assimilated C); this part of C was found in roots after the experiments.
- Exudates, secretes, root hairs and fine roots (1%–2% of total assimilated C), which were decomposed by micro-organism 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).
- Root respiration (7%–14% of total assimilated C), which is for maintenance, root growth and ion uptake.

A critical review of these data leads to the conclusion, that there are only a few publications that concern the whole partitioning of below-ground translocated C. For example *Rochette* and *Flanagan* (1998) reviewed detailed studies on the losses of assimilated C during root respiration and microbial respiration of root exudates.

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*, 2000) it was observed that the relative amount of assimilated C decreases 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 assimilated C increase. As a result, it is difficult to predict the general changes in total C input into the soil by intensification of crop production.

4 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 results for C translocation by grasses into the soil and the allocation of the root-derived C are presented in Table 3. The extent of rhizodeposition varies widely, from as low as 8% (*Meharg* and *Killham*, 1990) to >65% of assimilated C (*Zagal*, 1994; *Meharg* and *Killham*, 1990). In summary, the relative C translocation of pasture plants into soil is about 1,5–2 times higher than that of cereals (compare Tables 1, 2 and 3). 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.

Table 4: Amounts of below-ground translocated carbon by cereals and different grasses (only the results of tracer studies are summarized).
Tabelle 4: Mengen von C, die durch Getreidekulturen und unterschiedliche Gräser in den Boden eingebracht werden (nur die Ergebnisse der Experimente mit Tracern sind zusammengefasst).

Plants	Period	kg C ha^{-1}	References
Wheat	25 weeks	1300	*Keith* et al., 1986
Wheat	Vegetation period*	1000–1500	*Martin* and *Puckridge*, 1982
Wheat	63 d	1765	*Martin* and *Merckx*, 1992
	63 d	1790	*Martin* and *Merckx, 1993*
Wheat	153 d	2300	*Johnen* and *Sauerbeck*, 1977
Wheat	Vegetation period	1200–2900	*Whipps*, 1990
Wheat	Vegetation period	1000–1600	*Knof*, 1985
Wheat	167 d	480	*Gregory* and *Atwell*, 1991
Barley	167 d	580	
Wheat and barley	Vegetation period	1460–2250	*Swinnen* et al., 1995
Barley	127 d	1650	*Jensen*, 1993
Median	**All data**	**1520**	
Arithmetical average	**All data**	**1480**	
Arithmetical average	**Longer than 100 days**	**1500**	
Lolium perenne	112 d	2800	*Kuzyakov* et al., 2000a
Lolium perenne	95 d	500–650	*Kuzyakov* et al., 1999
Lolium perenne	Vegetation period	840–1660	*Van Ginkel* et al., 1997
Different kinds of grasses	Vegetation period	2451–4432	*Saggar* et al., 1997
Different kinds of grasses	5 months	1000	*Warembourg* and *Paul*, 1997
Median	**All data**	**1330**	
Arithmetical average	**All data**	**1790**	
Arithmetical average	**Longer than 100 days**	**2200**	

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

Detailed data concerning the effect of plant age on C translocation by *Lolium perenne* and other pasture grasses are compiled in Table 3. 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., 2000a). It was suggested that the changes in the translocation pattern of *Lolium* could be connected with the vernalization of seedlings (*Kuzyakov* et al., 2000a).

As for cereals, an increasing N fertilization level decreased the relative amounts of the below-ground translocated C in pasture plants (*Kuzyakov* et al., 2000a). In particular, a high N level in the soil reduced the "ineffective" C losses like root respiration and exudation.

5 Investigations of trees

Forest systems contain about 66% of the terrestrial above-ground C and 45% of the terrestrial soil C (*Dixon* and *Turner*, 1991; *Smith* et al., 1993). Additionally, *Dixon* et al. (1994) calculated the contribution of forest ecosystems on approximately 90% of the annual C flux between the atmosphere and terrestrial ecosystems. As a result, investigations on effects of trees on the C cycling are necessary, and of great importance. Nevertheless, there are only few papers that concern this topic (reviewed by *Grayston* et al., 1996; *Dixon*, 1995; *Vogt* et al., 1998). Results reviewed by *Grayston* et al. (1996), showed the large extent of below-ground C transfer by trees from 40% for *Liriodendron tulipitera* (*Edwards* and *Harris*, 1977) up to 60% for *Pinus sylvestris* (*Persson*, 1978) of assimilated C. *Kelting* et al. (1998) have investigated the CO_2 efflux from the soil with oak seedlings, but without application of a tracer. The calculated contributions of root respiration, microbial respiration of root exudates and microbial respiration of humus to total CO_2 efflux from soil have been estimated on 32%, 20% and 48%, respectively. Unfortunately, these results cannot be applied even for rough calculations of C partitioning within the system atmosphere-plant-soil because the amounts of assimilated C were not measured. We have found only a few papers in which the experiments with ^{14}C or ^{13}C devoted to quantification of rhizodeposition and C export to the roots have been described (*Norton* et al., 1990); *Horwath* et al., 1994; *Rygiewics* and *Andersen*, 1994; *Lacointe* et al., 1995; *Dyckmans* et al., 2000). *Rygiewics* and *Andersen* (1994) carried out studies on *Pinus ponderosa* seedlings and they found lower C translocation rate for these trees when compared to pasture or crop plants. In contrast, *Lacointe* et al. (1995) found for young walnut plants that the C translocation to the roots accounted for 48% and 40% of total assimilated C in August and October, respectively. Unfortunately, this study did not provide data on the contribution of the root respiration to total CO_2 efflux from the soil. This pool of C was studied by *Norton* et al. (1990) on 1-year-old *Pinus ponderosa* Laws. seedlings. Approximately 6% of the total ^{14}C was respired by the below-ground system during seven days chase period. The partitioning pattern of assimilated ^{14}C at the labeling day showed that about 60% of assimilated ^{14}C was allocated in the below-ground parts of the trees. Half of that carbon was found in the rhizosphere and bulk soil indicating high exudation rate of young pine trees.

The above results for C translocation into the soil by trees appears to be too high, because the main C sink in trees is the stem and not the root. Much lower assimilated export to the roots has been reported by *Dyckmans* et al. (2000). Using beech seedlings, they showed that growing leaves were the major sink for newly assimilated C. The leaves accounted for about 60% of this C, while only 10% was allocated to the roots. These last data are in accordance with the statement that the fastest growing organ is the biggest sink for assimilated C. In addition, and according to the tree physiology, the main C sink in trees is the stem. In contrast to grasses, most nutrients in trees are stored in the stem.

Table 5: 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.
Tabelle 5: Grobe Einschätzung des C-Gesamtinputs in den Boden und des wurzelbürtigen CO_2-Effluxes aus dem Boden unter Weizen mit 60 dt ha^{-1} Kornertrag und unter Wiese mit 60 dt ha^{-1} Trockensubstanzertrag.

	% 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 2 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

Therefore, the intensive acquisition of nutrients by the trees from the soil is of less importance when compared with grasses. For the same reason, the relative below-ground translocation of assimilated C must also be smaller. Since the productivity of forest ecosystems is higher than of grasslands, the total input of C by trees would be expected to be higher. In addition, the C translocated by roots of trees has longer mean residence time compared with the C translocated by grass roots, because it comprises more lignin and other slowly decomposable structural components.

Still, our knowledge on the below-ground C allocation of trees is incomplete because not only most of the previous studies were focused on the above-ground C part of forest ecosystems, they were carried out without the use of a tracer. Of course, artificial labeling of trees with ^{14}C or ^{13}C is very difficult, limited to young trees, and can be used only in a limited number of experiments. However, the use of ^{13}C natural abundance can lead to important progress in estimating root-derived C and its partitioning by trees, and could help to overcome the limitations of artificial labeling methods (*W. Cheng*, 1999, personal communication).

6 Total C input by plants into soil

In the previous three sections, we described the below-ground C translocations of plants as a part of total assimilated C. This corresponds to the partitioning of the labeled C after the pulse labeling, although the amount of total assimilated C remains unknown. However, in most studies related to C balance and C turnover in soils, the mass units are important. Therefore, we compiled C inputs by some agricultural plants and grasses into soils on the basis of

mass units (Table 4). The results vary widely both within (i.e. for wheat between 480 and 2300 kg C ha^{-1} yr^{-1}) (*Martin* and *Puckridge*, 1982; *Knof*, 1985; *Whipps*, 1990) and across species (*Saggar* et al., 1997; *Van Ginkel* et al., 1997; *Swinnen* et al., 1995).

We calculated the arithmetical average for all data and it was 1500 and 1750 kg 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. It showed significant differencs between cereals and grasses (Table 4). The longer vegetation period of grasses led to additional C allocation below the ground of about 600 kg C ha^{-1} yr^{-1} when compared with cereals.

Although the relative C translocation into soil is higher for pasture plants then for cereals, the absolute C input is approximately the same when the same growth period is considered (Table 4). 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 for 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 4 shows that results on 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 200 and 600 kg 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 4) is seldom, and cannot be established for each plant-soil pairs, 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 (Tables 1, 2 and 3) can be helpful. For example (Table 5), we tried to estimate the total C input into the soil and the 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 (three mows: 2.5 + 2 + 1.5 t DW ha^{-1} yr^{-1}). The portions of total assimilated C in Table 5 are close to the averages found average in the Table 1 for wheat and Table 3 for pasture plants. The C translocation was calculated according to the above-ground production and portion of total assimilated C translocated below-ground C. According to this very rough estimation of total C input, wheat and pasture translocate below-ground about 2.4 and 3.2 t C ha^{-1} per vegetation period, respectively. These amounts are higher than those measured by the tracer technique (Table 4). After the root-derived CO_2 (9%–15% of the assimilated C) leaves the soil, about 1.5–2.0 t C ha^{-1} remains. This rough calculation shows that the root-derived CO_2 efflux from soil is about 0.9–1.2 t C ha^{-1} yr^{-1} in both ecosystems.

7 Conclusions

The introduction of tracer techniques for labeling 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 labeling, continuous labeling, and method based on ^{13}C natural abundance in C3 and C4 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 (1500 kg C ha^{-1}), when the same growth period is considered. However, during one vegetation period the cereals and grasses allocated beneath the ground about 1500 and 2200 kg C ha^{-1}, respectively. These values correspond to average productivity of both ecosystems. 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.

Although forest systems are a considerable reservoir of the terrestrial above-ground and soil C, only a few studies using tracers have been devoted to C input in the soil. Of course, artificial labeling of trees with ^{14}C or ^{13}C is very difficult and is limited to young plants. However, the use of ^{13}C natural abundance can lead to important progress by estimating of root-derived C and its partitioning by trees.

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