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SOIL CHEMISTRY

Tracer Studies of Carbon Translocation by Plants from the Atmosphere into the Soil (A Review)

Ya. V. Kuzyakov

Institute of Soil Science and Land Evaluation, University of Hohenheim, Emil-Wolff-Strasse 27, D-70599 Stuttgart, Germany

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Abstract—The research data on the translocation of carbon assimilated by plants from the atmosphere into the soil are reviewed. The most correct method for quantification of carbon flows in the atmosphere–plant–soil system is the tracer method with the use of ^{14}C, ^{13}C, or ^{11}C. Specific features of carbon translocation to the soil by different types of plants (agricultural cereals, meadow plants, and trees) are shown. Wheat and barley translocate about 20–30% of assimilated carbon to the soil. Half of it is used for root growth; one third is used for root respiration and root exudates that will be actively decomposed by rhizosphere microorganisms. Meadow plants translocate about 30–50% of assimilated carbon, and the relationship between the translocation fluxes is nearly the same as that for agricultural cereals. The amounts of carbon translocated by trees to the soil are low in comparison with those translocated by grasses. These differences are connected with peculiarities of water consumption and mineral nutrition of trees. Three methods for distinguishing between root respiration and microbial respiration are discussed. The problems of efficient carbon use by microorganisms and the priming effects in the rhizosphere are analyzed.

INTRODUCTION

In spite of a large body of statistical information about the state, reserves, and composition of organic compounds in plants, plant litter, and in the soils of different ecosystems [1, 2, 5, 6, 96], little is known about the influx of organic compounds and their transformation in soil. Organic substances arrive in the soil from three main sources: (1) root residues and organic fertilizers, (2) aboveground residues and litter, and (3) root exudates.

The total transportation of carbon compounds by plants from the atmosphere to the soil will be referred to in this review as carbon translocation.

Abundant data on the amounts of organic compounds coming into the soils of different ecosystems from root residues, organic fertilizers, over-ground residues, and litter, as well as their decomposition rates, are available in the literature. A large body of information has been accumulated on the degradation of most plant residues (especially of agricultural crops) and organic fertilizers under various conditions: at different temperatures, moisture content, acidity (pH), soil type, and the amount and comminution degree of plant residues. These results, in a formalized form, are successfully used in most models of soil carbon and nitrogen cycles [27, 98].

The third source, root excretions from living plants (exudates, secretions, lysates, etc.), is still little understood. This is primarily associated with two methodological problems: the low concentration of exudates in the soil (especially in mixed averaged soil samples) and their rapid decomposition by rhizospheric microorganisms to CO_2. Root excretions contain components significantly differing in physicochemical properties, decomposition rate, and contributions to the energy and matter budgets and the total soil respiration [42, 115]. One specifies the following main components of carbon translocation from plants into the soil: (1) roots themselves (alive and dead), a permanent pool of organic matter relatively slowly degrading in the soil, (2) root excretions (high- and low-molecular), a relatively rapidly degrading carbon pool in the soil with a very intensive cycle, and (3) root respiration, which exerts no direct effect on the pool of organic compounds in the soil, but forms an essential part of the CO_2 flux from the soil to the atmosphere. The sum of the second and third fluxes is referred as the total rhizosphere respiration.

The aim of this review is to summarize the results of studies on the structure of translocation fluxes of organic substances by plants from the atmosphere into the soil. This knowledge significantly enlarges the concepts of the soil segment of the carbon cycle, the carbon budget in an ecosystem, and the soil as a source or sink of carbon. We shall enlarge upon two less understood components of carbon translocation (root excretions and root respiration), because there are rich experimental data on this topic: root atlases [56, 114], data on the biomass of root residues [2], their profile distribution for different soils and plants, etc. Special attention will be paid to the methodological problems of studying the total translocation volumes and the structure of carbon fluxes translocated by plants into the soil.

METHODS OF STUDYING THE CARBON TRANSLOCATION BY PLANTS INTO THE SOIL AND THE SCOPE OF THE TRACER METHOD

The methods of studying carbon translocation by plants to the soil may be classified into two groups, those with and without C isotopes. Most results have been obtained using traditional techniques, without the application of isotopes. These methods involve the determination of root weight (root washing, observation of the growth of roots throughout the soil profile, and weight calculation from the shoot-to-root ratio), without accounting for root excretions and root respiration. The traditional methods give significantly underestimated results for the weight of roots and root residues and especially for root excretions, as compared to C pulse-labeling techniques [94]. This is associated with the formation of CO_2 during the microbial degradation of organic substances transferred by plants into the soil during the whole vegetation period, as well as with the impossibility of determining the root excretions and root respiration under soil conditions by traditional techniques. The root weight, as determined using the ^{14}C tracer, is higher by 20–60% (depending on species and plant age) than that found by traditional root washing [94]. The possibility of evaluating the total amount of readily decomposed exudates and root respiration represents the special advantage of the ^{14}C or ^{13}C pulse labeling techniques. From the results of experiments with a ^{14}C tracer, the concentration of readily decomposable carbon compounds in the rhizosphere is about 20–100 times larger than their concentration used in some rhizosphere models based on the results of traditional methods [18].

The tracer technique allows not only the comprehensive assessment of the overall budget for plant-assimilated carbon, but also the determination of losses (e.g., the losses of root residues and other organic substances in the course of their washing to remove soil). The composition of the overall budget is based on the known total content of C tracer introduced into an atmosphere–plant–soil system and the content of C tracer in each separate pool of the system, regardless of the total unlabeled C in the system or its separate parts. Thus, the most correct method for the determination of carbon translocation by plants is the measurement of ^{14}C, ^{13}C, or ^{11}C assimilated by the aboveground plant organs and translocated into the soil [115].

The principle of the method is the following: the aboveground parts of plants are exposed to an atmosphere of labeled carbon dioxide, which is absorbed by the leaves and is transformed in the course of photosynthesis to low-molecular organic compounds. They spread as saccharose throughout the plant and, particularly, are transported via the phloem to roots [72, 82]. Saccharose and attendant compounds are consumed by plants for the growth of their aboveground and underground organs, for respiration, and for root exudates. When the aboveground parts of plants are isolated from the soil by a gas-proof partition, the totality of labeled C contained in the soil or released from it as CO_2 passes through the plant, i.e., is transferred by the plant from the soil. Different modifications of this method and corresponding installations are described in a number of publications [18, 45, 50, 94, 97, 100, 103, 107, 108, 110, 116].

Two methods are used for the application of labeled carbon: pulsed (single) and continuous supplies of labeled CO_2. The pulsed labeling (the single short-term exposure of plants to the atmosphere of labeled CO_2) is the simplest and least expensive method. The pulsed administration of labeled atoms allows the determination of the distribution and translocation of assimilates at specific stages of plant development. A disadvantage of the method is the impossibility to correctly quantify the carbon included into different plant organs, because the isotopic ratio in the formed and translocated metabolites continuously changes in the course of metabolism and carbon transportation throughout the plant. In addition, the tracer partitioning at the time of the experiment can differ from its distribution over a long time period. At the pulsed tracer administration, only an approximated weight of carbon released with exudates or root respiration can be calculated [59, 60].

This disadvantage can be avoided, when continuous labeling is used: plants are exposed to an atmosphere of labeled CO_2 with a constant specific activity (or a constant ratio of carbon isotopes) for a sufficiently long time, generally for the whole period of plant development. This results in the constant isotopic ratio in all metabolites (continuous enrichment with ^{13}C, or constant specific activity when ^{14}C is used). The ratio between the soil and rhizospheric CO_2 can be calculated from the decrease in specific activity (or enrichment) of CO_2 released from the soil, as compared to the CO_2 from the artificial atmosphere. In addition, comparing the amounts of soil CO_2 in the pots with and without plants, one can calculate the additional mineralization of humus caused by the presence of plants (see below).

A method was proposed recently for determining the carbon translocation by plants and for separating the overall soil respiration into the CO_2 of rhizosphere and the CO_2 of the humus substances themselves. This method is based on the natural fractionation of ^{13}C by plants during photosynthesis [17]. Because of the different isotopic discrimination of $^{13}CO_2$ by rubisco (ribulose-biphosphate carboxilase) enzymes (C3 plants) and phosphoenolpyruvate carboxylase (C4 plants), plants with the C3 photosynthesis type are more depleted in ^{13}C ($\delta^{13}C \approx -27‰$). The $\delta^{13}C$ value of soil organic matter resulting from plant residues corresponds to the $\delta^{13}C$ of the plant type. Isotopic effects are minor ($\delta^{13}C$ = 1–3‰) or absent under humification conditions. The method for the separate determination of the contributions of humus and plants to the CO_2 flux from the soil is based on growing C3 plants (e.g., wheat) on

Table 1. Results of experiments (with pulsed labeling) on the total carbon translocation by wheat from the atmosphere into nonsterile soil* (in percentage of assimilated labeled carbon)

Age or development stage of plant at labeling	Soil horizon	Root respiration (1)	Exudates/microbial respiration (2)	Degraded to CO_2**, (1) + (2)	Roots (3)	Soil (4)	Total in the soil, (1)–(4)	Source
28 days	Loamy sand			5.8	33.1	0.8	39.7	[86]
36 days	Ah	***		5.0	35.5	0.7	41.1	
43 days				16.6	23.5	1.4	41.5	
51 days	^{13}C			15.3	25.2	1.4	41.9	
64 days				7.7	17.3	0.8	25.8	
Over the whole vegetation period	Loam	6.4	5	14–15	7		19	[103]
30 days	Loam	19–21	1–2	21	12	3.1	36	[100]
22 dc****	Calcaric	7–15	2–10	17	20	19	46	
58 dc	Fluvisol	2.7–3.2	0.1–0.5	3.3	3.7	1.5	8.5	
81 dc		2.8–3.5	0.1–0.8	3.6	2.4	2.0	8	
	Loamy sand		22			3.5	25	[79]
49 days	Sandy on clay			25	28	2	55	[31]
70 days				4	10	1	15	
105 days				2	3	0.2	5	
126 days				2	2	0.2	4	
Over the whole vegetation period				13	33	1.6	48	
Shooting	Loamy sand			14–16	15–18	4–9	39	[101, 102]
Heading	Calcaric			9–12	8–13	3–6	23	
Flowering	Fluvisol			9–10	5–6	4–9	23	
Milky maturity				7	2–3	5–6	15	
Waxy maturity				9	2–6	5–8	17	
4–6 leaves		14	22			3.4	39	[77]
21 days	Loamy sand	12	18	30	9.4		40	[18]
Median		7	2	10	7	3.5	26	
Arithmetic mean		10	9	11	14	3.4	29	

*The effect of soil types on carbon translocation cannot be analyzed for lack of experimental material.
**Calculated as the sum of root respiration and microbial CO_2 at the degradation of exudates or measured together.
***Blank cells mean the absence of data in the published source.
****(dc) Decimal Code of the stages of plant growth and development.

the soil originated under C4 plants (e.g., in savanna) and on measuring $\delta^{13}C$ of CO_2 released from the soil [17]. The method also works under the reverse conditions (C4 plants on C3 soil, e.g., growing corn on soils with original steppe vegetation) [91]. The method of evaluating carbon fluxes based on the natural isotopic fractionation has some advantages over the artificially labeled atom method. Both plants and humus are totally labeled; therefore, complex installations for the long-term exposition of plants to the labeled CO_2 atmosphere are not required. The method is suitable for field conditions [17, 91].

The estimates of the volume and relative contribution of rhizospheric CO_2 of the overall soil respiration differ widely, from 15 to 60% [94]. The estimates of the portion of root respiration in the overall rhizospheric CO_2 also vary from 40 [18, 59] to 90 [17] or even 95% [100]. Therefore, we shall consider the carbon translocation by different plant groups, as well as the methods for subdividing the rhizospheric respiration into components.

TRANSLOCATION OF CARBON INTO THE SOIL BY AGRICULTURAL CEREALS

The results of studying the translocation of labeled carbon by agricultural cereals (wheat and barley) into the soil using the pulsed tracer are summarized in Tables 1 and 2 (published data since 1990). Analogous reviews on the carbon translocation under continuous exposure to the labeled CO_2 atmosphere were published earlier [46, 115]. Most studies of organic com-

Table 2. Results of experiments (with pulsed labeling) on the total carbon translocation by barley from the atmosphere into nonsterile soil* (in percentage of assimilated labeled carbon)

Age or development stage of plant at labeling	Soil	Root respiration (1)	Exudates/microbial respiration (2)	Degraded to CO_2, (1) + (2)	Roots (3)	Soil (4)	Total in the soil, (1)–(4)	Source
30 days	Loamy sand			11	12	2.2	26	[199]
38 days				12	12	3.1	28	
46 days				18	13	2.9	33	
Over the whole vegetation period	Loam	13–14	5–6	22–27	9–14		26–33	[103]
30 days	Loam	21–23	1–3	24	13	4.8	42	[100]
22 dc	Calcaric	32–35	0.5–4	36	22	6.3	64	
58 dc	Fluvisol	5.1–5.7	0.1–0.7	5.8	4.5	2.3	13	
81 dc		1.7–2.2	0.1–0.6	2.3	1.1	1.0	4.4	
50 days	Sandy on clay			16	17	0.4	23	[31]
71 days				5	22	1.4	28	
106 days				3	6	0.1	9	
120 days				3	5	0.2	8	
Cumulative				24	32	2.4	58	
Median		13.5	0.9	14	12.5	2.3	17	
Arithmetic mean		15	2	14	13	2.3	28	

pound translocation have been performed with wheat. Tables 1 and 2 do not include the data on the carbon translocation by plants under hydroponic conditions (for more details, see [115]). Losses of assimilated carbon from different agricultural plants in the course of rhizospheric respiration (root respiration + microbial degradation of exudates) were also reported [91].

An important reason for the differences between the published results is that some authors represent data in percentages of the total tracer in all analyzed components of the system rather than in percentage of the assimilated carbon, e.g., when the dark respiration of plants (which can reach 40% and more of the assimilated carbon [60, 11]) remains ignored, as well as the labeled carbon losses differing for different experimental systems. Therefore, the data in Tables 1 and 2 are evaluated in percentages of the assimilated carbon. These data show that some components of carbon translocation differ significantly depending on the plants and experimental conditions. The most significant differences are associated with the development stage of plants. A decrease in the total translocation of carbon with age is typical for wheat and barley [52], as well as for other crops [65, 99]. Soil and climatic conditions also affect the carbon translocation by plants. No experimental data are available for the climate effect on the tracer partitioning in plants. The results of studies of the effect of soil conditions, particularly of nutrient supply, are presented below.

From the data presented in Tables 1 and 2, we calculated the arithmetic mean of carbon translocation by wheat and barley into the soil. It approximates 30% of the assimilated carbon. The arithmetic mean gives overestimated results, because most experiments have been conducted with young plants, and the expenses of agricultural cereals for the growth of underground organs decrease in the course of plant development. The median gives lower results for the translocation components, as compared to the arithmetic mean. With allowance for the decrease in translocation during growth, plants transfer approximately 20% of assimilated carbon into the soil. About a half of this amount is consumed for the completion of growing roots, and about a third is released as CO_2 due to root respiration and the microbial degradation of exudates. The residual labeled carbon (about 2–4% of assimilated C) is included in soil organic matter and microbial biomass. The weighed mean should be a more adequate parameter for evaluating the carbon translocation. Unfortunately, the weighed mean cannot be calculated from the available published data, because only the percentage distributions of labeled carbon are reported rather than the total plant masses at the time of experiments.

As was shown above, when the pulsed administration of labeled CO_2 is used, the mass of carbon transferred into the soil per time unit, which is necessary for evaluating the carbon fluxes, cannot be correctly calculated from the percentage distribution. Such results derived from the labeled carbon translocation are more rarely presented in the literature (Table 3). From Table 3, it follows that the studied species of herbaceous plants

Table 3. Total content of carbon transferred by different plant species into the soil, as calculated from the ^{14}C distribution

Plant	Soil	Period	kg C/ha	Source
Wheat	Red-brown sandy loam	25 weeks	1300	[52]
	No data	Vegetation period	1000–1500	[69]
	Loam with carbonates	63 days	1765–1790	[70, 71]
	Loamy sand, loam	153 days	2300	[50]
	Different soils	Vegetation period	1200–2900	[115]
	No data	″	1000–1600	[54]
	″	″	941	[66]
Wheat	Sand on clay	167 days	480	[31]
Barley		167 days	580	
	Loam	Vegetation period	1460–2250	[103]
	″	127 days	1650	[45]
Barley	″	4 weeks	210	[88]
Corn		Vegetation period	1135	
Mustard	Loamy sand, loam	73 days	550–2790	[50]
Lolium perenne	Loamy Gleyic Cambisol	95 days	500–650	[59]
	No data	Vegetation period	840–1660	[106]
Festica pratensis	Loamy Mollic Gleysol	49 days	1000–1800	[46]
Meadow plants	Clayey	Vegetation period	2451–4432	[93]
	Clayey red-brown chernozem	5 months	1000	[113]
Median			1300	
Arithmetic mean			1470	

(Vegetation period) no exact data for the time period for which the results are recalculated.

transfer about 1300–1500 kg C/ha, including root residues and excretions, during the vegetation period. For comparison, we present the mean values of carbon translocation into the soil, as obtained by the repeated soil coring generally used to evaluate the root increments: 520–584 [37], 512–640 [38], and 188–272 [39] kg C/ha for barley and 368–420 kg C/ha for wheat [51]. The results obtained by this method are 3–7 times lower than those obtained using the C-tracer method.

TRANSLOCATION OF CARBON INTO THE SOIL BY MEADOW PLANTS

As was noted [35], most publications on the carbon translocation by plants are concerned with three main species of annual cereals: wheat, barley, and corn. It should be kept in mind that the long-lasting selection oriented toward the increase in the aboveground yield has changed the natural ratio between the underground and aboveground organs of crops in favor of the latter. In meadow plants, the portion of underground matter, as well as that of exudates, is higher than in crops [26, 118]: it can reach 80% of the total biomass [115]. Consequently, the estimates of carbon translocation for crops are hardly applicable for the carbon budget of perennial grasses. Experiments with perennial grasses are significantly lower in number than those with crops (Table 4, published data since 1970). Evaluation and differentiation between root respiration and root excretions have been performed in only a few papers [59, 60, 74].

Another problem in comparing agricultural cereals and meadow plants is that cereals under study belong to annual plants, while the portion of perennial grasses in a meadow ecosystem is more than 80%. An intensive but time-limited carbon translocation into the soil is typical for annual plants. For perennial plants, increased translocation is observed during the vegetation period, which allows them to surpass annual plants in the amount of transferred carbon [109]. Hence, the results obtained for cereals cannot be extrapolated to meadow ecosystems; special experiments should be performed.

Meadow plants transfer 30–50% of assimilated carbon into the soil, which is 1.5–2 times higher than cereals (Table 4). The further partitioning of carbon in the soil is similar to that revealed for wheat and barley: about one third is released as CO_2 because of root respiration and microbial degradation of exudates; about half remains in the roots, and the remainder is included into the microbial biomass and humus substances of the soil. A decrease in carbon transfer in the course of plant development was also observed by most authors. Significant differences in the amount of root residues

Table 4. Components of carbon translocation by different species of meadow plants into nonsterile soil (in percentage of assimilated $^{14}C–CO_2$)

Plant species	Plant age, days	Experimental conditions, soil, horizon*	Degraded in soil to CO_2 (1)	Root exudates (2)	Roots (3)	Soil (4)	Total translocation to the soil (1)–(4)	Source
Lolium perenne	36	Laboratory	13.8	8.0	6.8	22.5	36	[59]
	49	p., loamy	10.8	6.7	1.3	27.7	39	
	51	Gleyic	9.8	3.3	1.5	12.7	23	
	55	Cambisol	6.9	4.0	2.4	23.7	31	
	58		7.8	2.0	0.9	8.2	16	
	61		8.8	4.7	3.2	26.5	35	
	68		9.4	7.3	3.4	20	29	
	87		6.5	4.5	1.4	8.6	15	
Lolium perenne	52	Laboratory	2.7		0.8	1.8	5.3	[60]
	55	p., loamy	6.0		1.8	4.2	12.0	
	76	Gleyic	8.0		1.3	2.4	11.7	
	89	Cambisol	10.2		1.8	4.9	16.9	
	103		10.8		2.0	4.6	17.4	
Lolium perenne	28	Laboratory p., loamy sand	1.6		26	0.06	28	[33]
Lolium perenne	79	laboratory p., loamy sand	9		29–40	2.3	39–52	[106]
Lolium perenne	41	Laboratory	16		29	3.0	49	[118]
	62	p., loamy	21		40	2.4	65	
Lolium perenne	14	Loamy sand	17		22	1.8	41	[90]
Lolium perenne	23	Laboratory	22		6		28	[73]
	30	Loamy sand, Ah	24		4		28	
	37		12		8		20	
	51		18		9		27	
	65		4		4		8	
Lolium perenne	28	Field, loamy sand	43		24		67	[73]
	48		16		12		28	
	86		6		9		15	
	102		14		29		44	
	140		14		24		37	
	168		8		6		14	
Lolium perenne	14	Solution Laboratory, p.		1.8	32		33	[74]
Median			10	4.6	6	4.9	28	
Arithmetic mean			13	4.7	14	13	32	
Festuca arundinacea	21	Loam			2.5			[19]
Festuca pratensis	29, ^{14}C	Loamy, Mollic	10		9	3.4	22	[49]
	29 + 15, ^{13}C	Gleysol, c.	11		9		>20	
Festuca pratensis	10	Loamy, Mollic Gleysol, c.	25–31		28	4	44–49	[46, 47]
Bromus madritensis	Early Tillering	Laboratory, p. Cinnamonic					69–75	[109]
	Tillering		24–26				60–64	
	Shooting						30–42	
			5–8				8–12	
Bromus erectus	Early Tillering	Laboratory, p. Cinnamonic					70	[109]
	Tillering	A1, AB	18–24				59–79	
	Shooting						50–66	
			15–23				38–58	
Agropyron/*Koeleria*		Field, chernozem	9–15				35–50	[113]
							80	Sims&
Bouteloua/*Buchloe*		Field						Singh, 1971, [115]
Median			17		9	3.7	50	
Arithmetic mean			17		12	3.7	49	

* (p.) Pulsed labeling; (c.) continuous labeling.

between cereals and meadow plants are associated with the life cycle, rather than with the assimilate partitioning. After maturing, cereals die completely, including their underground organs. The growth and development of the root system of meadow plants continues after cutting, so that a higher general accumulation of root residues in the soil is recorded. In addition, another type of profile distribution is typical for the roots of meadow plants: the major part of the roots occurs in the surface soil layer, sod, or root mat. For example, the upper (0- to 10 cm) layer of prairie soil includes 50–77% of the ^{14}C transferred into the soil [112, 113].

TRANSLOCATION OF CARBON BY WOODY PLANTS

There are little data on the overall translocation of carbon by woody plants. Most estimates refer to the reserves of living (roots) and dead organic matter (litter + humus) in forests, different in productivity, in various zones [1, 5, 96, etc.]. Among numerous papers devoted to the root systems of woody plants, we have found only one study performed with ^{14}C [92]. The translocation of carbon by *Pinus ponderosa* Laws seedlings in a greenhouse under the $^{14}CO_2$ atmosphere was studied. The portion of assimilated carbon that was released with pine exudates was much lower than in the case of herbaceous plants. In spite of the lower relative carbon expenditure by woody plants for root excretions, their overall amount may be higher than that of cereals or grasses because of the higher total carbon assimilation. From the results of an experiment on the separation of the soil CO_2 flux from the oak rhizosphere, it was noted that the root respiration, microbial degradation of root excretions, and the degradation of humus itself compose 32, 20, and 48% of the total CO_2 released from the soil, respectively [53]. The experiment was conducted without labeled carbon; therefore, the distribution of assimilates cannot be derived from the data on the relative distribution of soil CO_2, because the amount of assimilated CO_2, or at least the total increase in biomass during the period under study, is unknown.

The lower relative translocation of carbon by the roots of arboreous plants, as compared to herbaceous plants, is primarily associated with variations in their water and mineral nutrition [4]. Grasses are characterized by the almost complete death of the aboveground phytomass by winter, and the annual return of nutrients into the soil. At the beginning of a new vegetation period, herbaceous plants will supplement their reserves mainly from the soil, which explains the relatively high activity of root excretions. Woody plants do not return deficient nutrients to the soil in winter, but they redeposit them from leaves into the trunk. The annual consumption of elements from the soil composes only a small proportion of their total reserve in the plant. Consequently, the enhanced consumption (per mass unit) of nutrients by roots is absent, as is the expenditure of significant amounts of assimilates for root excretions necessary for the mobilization of deficient nutrients. As the majority of nutrients are stored in the trunk, and no intensive consumption is needed, the ratio of the underground to the aboveground organs is significantly displaced in woody plants.

METHODOLOGICAL PROBLEMS IN THE DISCRIMINATION OF EXUDATES AND ROOT RESPIRATION

Identifying each of these two fluxes is important because of their different roles in the carbon cycle and the energy budget of the soil. At first sight, the simplest methods for the independent determination of exudates and root respiration include the growing of plants on (1) a nutritive solution, or (2) a sterile soil or an artificial substrate without microorganisms. The former method has been previously rejected, because the normal development of plants requires a mechanical stimulus: soil or its analogue. In an aquatic culture, the growth and functioning of roots differ from those under normal soil conditions. Contact with a solid surface and the presence of microorganisms significantly increase the amount of root excretions [8, 10, 34]. Nonetheless, the composition and ratio of some compounds in the root excretions of different plants were determined using the hydroponics method [82; 84, 85 (reviews)]. In most studies, root respiration is calculated from the difference between the $^{14}CO_2$ emission from sterile and nonsterile soils. It is based on the assumption that the sources of $^{14}CO_2$ in the nonsterile soil are the microbiological degradation of exudates, dead roots, and root respiration. In sterile soil, root respiration is a single source of $^{14}CO_2$ [77, 107]. However, some works present evidence that the presence of microorganisms increases both the root respiration and the exudate amount [78]. Root excretions represent the carbon pool of the plant most responsive to the presence of microorganisms [75]. Some bacterial strains increase the root excretions of *Lolium perenne* by 34 times [75] and those of spring wheat by 13 times [76, 79]. However, in most experiments, the amount of exudates in the presence of microorganisms exceeds that recorded under sterile conditions by 1.5–3 times [10, 68]. Similar results were obtained for the stimulation of root excretions by microorganisms in aquatic culture [55, 115]. The larger plant biomass under sterile conditions, as compared to nonsterile ones, is due in part to the additional expenditure for root excretions [9, 77]. It may be suggested that the presence of microorganisms in the rhizosphere displaces the equilibrium between plant and soil because of the enhanced carbon deflux from the plant with exudates [36]. Hence, the subdivision between root and microbial respiration upon the degradation of exudates on the basis of the experiments on soil sterilization, as well as the experiments with hydroponic conditions, is incorrect.

The noted disadvantages of sterilization were partially overcome using the brief inhibition of microbial respiration by mercury *p*-hydroxyphenylsulfonate [41, 42]. It was found that one fifth of the $^{14}CO_2$ emission from the

soil around 21-day-old corn plants is due to root respiration, and four fifths result from the microbial decomposition of root excretions [41, 42]. The degree of inhibition of the respiration of all microorganisms, especially of those inhabiting the endorhizosphere, remains unexplained [25, 35].

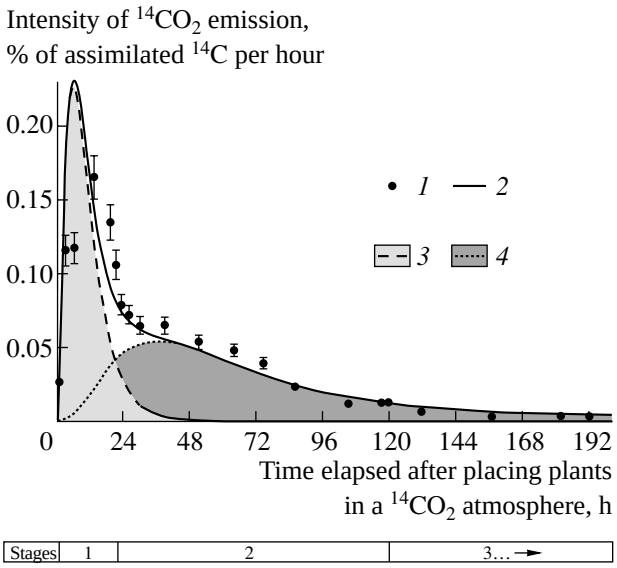
Another, more refined, method of separating root and microbial respiration is based on the isotope dilution technique [18]. Degradable organic substances in the rhizosphere are in excess with respect to other nutrients, especially to nitrogen [18, 21]. Consequently, the increase of microbial population in the rhizosphere is not limited by the easily degradable carbon sources [18, 21, 40]. Therefore, an additional unlabeled, readily degradable, carbon source (^{12}C-glucose) was added to the soil with ^{14}C-labeled plants in order to dilute the labeled exudates released by plant roots [18]. The dilution decreased the specific activity of the $^{14}CO_2$ released from the soil in inverse proportion to the amount of ^{12}C-glucose added. In this method, only the $^{14}CO_2$ resulting from the microbial degradation of root excretions was diluted, and the specific activity of the $^{14}CO_2$ from root respiration did not change. The addition of increasing amounts of unlabeled glucose (in different experimental treatments) accompanied by a decrease in the $^{14}CO_2$ specific activity allowed the calculation of the CO_2 portion released at the exudate degradation. Root respiration was calculated as the difference between the total amount of $^{14}CO_2$ released and the content of CO_2 produced from the microbial degradation of root excretions obtained by the above method. It was shown that the root respiration of three-week old wheat forms was 41%, and the microbial degradation of exudates composes 59% of the total released $^{14}CO_2$ [18]. A disadvantage of the method, in our opinion, is the assumed identity of the whole soil and rhizosphere, although many soil loci are known to be free from roots. In these loci, the degradation of added ^{12}C-glucose is not limited by nitrogen. This forms the basis of the substrate-induced respiration method for determining the total activity of microorganisms in the soil [7]. Another disadvantage of the method is the calculation of the total CO_2 produced from root respiration using the formula:

$$\frac{^{14}CO_2 \text{ with Glucose} - \text{Root Respiration}}{^{14}CO_2 \text{ without Glucose} - \text{Root Respiration}} = \frac{\text{Soluble C}}{\text{Soluble C} + \text{Glucose C}},$$

where the content of readily degradable soluble compounds in the rhizosphere (Soluble C) is also unknown. The equation with two unknowns (Root Respiration and Soluble C) is solved through the system of two equations with different amounts of ^{12}C-glucose added. Both unknowns in this "imperfect mathematical system" are interdependent; therefore, the calculation can result in significant errors.

The second method of separating exudates and root respiration is based on the addition of ^{14}C-labeled model exudates into the soil with unlabeled plants [100]. Organic substances similar to excretions of plant roots were used as model exudates. In the first experimental treatment, the totality of $^{14}CO_2$ released from the soil resulted from the microbial degradation of ^{14}C-labeled model exudates (without root respiration). In the second experimental treatment, plants were labeled "as usual" through the assimilation of $^{14}CO_2$ from the artificial atmosphere. In this case, the labeled CO_2 released from the soil resulted from both root respiration and the microbial degradation of exudates. From the difference between the treatments, root respiration was calculated, which composed 89–95% of the $^{14}CO_2$ released [100]. We consider this value overestimated, because the amount of root excretions appears very low, which does not agree with the results of other authors. The addition of unlabeled model rhizodeposits into the treatment with photosynthetically labeled plants [100] would "equalize" both treatments in terms of the effect on plants and the partitioning of labeled and unlabeled components. This could change the previously calculated ratio between the root and microbial respiration and improve the reliability of conclusions.

The third method for the discrimination of root respiration and the microbial degradation of exudates in the rhizosphere is based on the dynamics of $^{14}CO_2$ emission from the soil after the pulsed labeling of plants [59]. A hypotheses is advanced that the root-respiration $^{14}CO_2$ is first released from the soil after the pulsed tracer administration into the atmosphere with plants. The $^{14}CO_2$ from the root respiration at the utilization of exudates is released with some delay (figure). The delay is explained by the fact that exudates are first released through the wells of root cells; they are absorbed and metabolized by microorganisms and then emitted as CO_2. During root respiration, oxidation proceeds directly in the root without intermediate stages. Thus, the curve of the $^{14}CO_2$ emission from the soil is composed of several sections, each of them being characterized by the corresponding predominant process (figure). The division of the curve into components was performed by optimizing two parameters of the carbon translocation model (the rate of root respiration and the rate of exudate evolving) from experimental data [59]. Other model parameters were taken as constant from the literature [3]. Simulation using these parameters allowed the separate calculation of root respiration and the microbial degradation of exudates. It was found that the root respiration of *Lolium perenne* varies between 17 and 61% (41% on average), and root excretions average 59%, which agrees with the results obtained by the isotopic dilution method [18]. A disadvantage of this approach is that most model parameters are taken from the literature rather than determined for the specific soil and experimental conditions. In addition, the model was not compared with the dynamics of $^{14}CO_2$ emission from sterile soil, where root respiration is the only source of $^{14}CO_2$.



Dynamics of CO_2 emission from the soil after the pulsed labeling of plants under a $^{14}CO_2$ atmosphere: (*1*) experimental values (± SD); (*2*) simulated values and separation of $^{14}CO_2$ released from the soil, using model [59], into (*3*) root respiration (predominant in the first stage of $^{14}CO_2$ emission) and (*4*) microbial degradation of root excretions and dead roots (predominant in the second and third stages of $^{14}CO_2$ emission).

Energy released in the course of root respiration is consumed by plants for three main processes: (1) the maintenance of physiological processes (maintenance respiration), (2) the growth processes (growth respiration), and (3) the uptake and transportation of ions (respiration for ion uptake). The energy components of root respiration and methods for their experimental determination are thoroughly examined in the literature on plant physiology, particularly in special reviews [63, 64]. Their separation and determination are not essential for the carbon budget in the soil.

Thus, three methods have now been proposed for the separate evaluation of root respiration and exudates in nonsterile soil. The analysis of root excretions and their role in the carbon and nitrogen cycles in the soil are also noteworthy.

Table 5. Amount of exudates released by sterile roots of different plants [84, 85]

Plant species	Plant age, days	Exudates, mg/g of dry root weight	Source
Wheat	14	515	Prikryl and Vankura, 1980, cited from [85]
Barley	16	62	[9]
	27	50–95	[8]
Different species		6–247	[84]
		30–150	[85]

ROOT EXCRETIONS

Root excretions change the physical, chemical, and biological properties of the soil in the rhizosphere. They affect pH, dissolve nutrients, form chelate compounds with them, and assist in the physicochemical aggregation of soil particles. Exudates not only resupply the pool of available organic matter, but they significantly accelerate the nutrient turnover in the rhizosphere [12, 13, 60, 61]. This acceleration is explained by the fact that root excretions include low-molecular, readily available, rapidly utilizable organic compounds: sugars (50–60%), carbonic acids (25–30%), and amino acids (20–35%) [117]. Thus, the N/C ratio in exudates varies from 1:10 to 1:15. Exudates include 0.1–8.0 mg sugars and 0.04–1.2 mg nitrogen organic compounds per gram of dry root weight released in twenty-four hours [64]. The exudate production rate varies widely depending on species and plant age. Young plants release more exudates than old plants: from 2 to 10 mg C/g of dry root weight daily [34]. Evaluating the results in terms of exudate amount per the root weight increment, 10–100 mg of low-molecular compounds and 20–50 mg of high-molecular substances are released when the root weight increases by 1 g [85]. Some results are summarized in Table 5. The data on the exudate content from the unit root surface vary between 10 and 420 μg/mm^2 daily [87]. In some cases, experimental results are also expressed in terms of concentration in the soil solution. For example, the concentration of readily degradable carbon compounds in the rhizosphere of three-week old wheat was 670 mg C/l of soil moisture [18].

The minute description of the composition of root excretions was reported [16, 84, 85], and it is not the object of our review. We only note that the composition of root excretions depend on the plant species, soil texture [80], moisture content [86], root morphology [34], and the supply of soil or solution with nutrients [48, 55, 81, 93, 104, 109, 119], particularly with phosphorus [15, 29, 95, 117]. The latter is indirect evidence that exudation is an active process [36] rather than the simple loss of dissolved organic matter by plants, since adenosinetriphosphoric acid (ATP) is required for active exudating. Thus, root excretions are affected by all soil factors which change the membrane permeability of root cells [36]: ionic concentration in the soil solution, pH, oxygen content, concentration of plant growth regulators, temperature, moisture content, pathogenic microorganisms, and viruses. The sterilization of soil shows that the presence of microorganisms affects the composition of root excretions only slightly [68]. From the works mentioned, it follows that, under unfavorable soil conditions, plants consume a major part of assimilated compounds for the growth of roots and their functioning (respiration and excretions); i.e., they become less efficient in the production of aboveground biomass. This regularity was revealed for the soil supply with moisture [86] and nutrients [93], particularly with nitrogen

[60]. At a low phosphate level in the soil, the amount of root excretions increases significantly [89].

EFFICIENCY OF CARBON USE AND EXUDATE-INDUCED PRIMING EFFECTS

When the carbon budget of plants is considered, the problem of the evolutionary and ecological feasibility of exudation arises. In terms of the energy and material balances, plants which lose a major part of assimilates with exudates should fail in evolution as inefficient, as opposed to other plants which lose less carbon. For example, plants accumulate a larger biomass in solution in the absence of microorganisms and, hence, at a low level of exudates, than under nonsterile conditions [9]. Similar results were obtained for soil conditions [77].

Exudation is not a casual process. First, it involves both passive leakage and active secretion, which require energy expenditure [36]. Second, the velocity of the downward movement of organic compounds in plants is significantly higher than that of passive diffusion; it is about 100 cm/h [11] (or 6% of the assimilated amount per hour [90]). The ^{14}C emission to the atmosphere was noted within an hour after exposing the plants to the $^{14}CO_2$ atmosphere [18, 59, 60]. Third, organic compounds are transferred to roots as saccharose, and the main components of exudates are glucose and fructose [111]. Therefore, exudation cannot be considered as the waste of assimilated carbon. The efficiency of carbon use by plants has been considered [77]. The decrease of expenditures for root respiration and root excretions in symbiosis with different strains of microorganisms was studied. The symbiosis of alfalfa with microbial strains, peculiar in their high hydrogenase activity necessary for the fixation of atmospheric N_2, results in a decreased carbon expenditure for root respiration and exudates and, hence, in increased biomass, as compared to symbiosis with less active microorganisms. Thus, the root exudates of legumes are necessary for nodule bacteria as the energy source for atmospheric N_2 fixation. Readily available organic compounds of the rhizosphere also serve as the energy source for the energy-consuming fixation of N_2 from the atmosphere by nonassociative microorganisms [68]. It is calculated that when exudates compose 0.2 mg/g of dry plant weight, the plant meets about 15% of its nitrogen demand by nonassociative rhizospheric fixation of N_2 [9]. Thus, one breeding objective is to select cultivars with decreased losses through root respiration and exudation or with an optimized symbiosis with rhizospheric microorganisms. However, these "yield-optimized" plants are highly productive only under optimal mineral nutrition.

Exudation is also frequently explained by the following hypothesis. Plants release readily available exudates with a relatively high C/N ratio. Rhizospheric microorganisms rapidly consume this available carbon and intensively decompose humus substances because of a nitrogen deficit. Nitrogen from mineralized humus or dead microbial mass is partly consumed by plants. This significant change in the degradation rate of organic matter with a minor action on the soil is named "the priming effect." It can result from the application of mineral or organic fertilizers, plant residues, etc. The priming effect is also referred to as extra nitrogen, additional nitrogen, priming action, and added nitrogen interaction (ANI) [44]. The main reasons and artifacts of priming effects have been reported [43, 44, 57, 61]. Priming effects in the rhizosphere can also be due to exudation and local changes in microbial activity. The degradation rate of organic matter in the soil can also be affected by the activity of microorganisms. Only a few papers on carbon translocation to the soil by plants were concerned with priming effects at exudation. For example, the root excretions of young corn decreased the reserves of organic matter in chernozem and Luvisol by 7% in the root zone and by 5% in the rhizosphere [40, 41]. It is noteworthy that these losses are not replenished by the inclusion of root excretions into humus substances during the same period. An accelerated decomposition of humus substances was also detected by the intensity of CO_2 emission from the soil with plants. An adult *Lolium perenne* is capable of inducing an additional mineralization of humus of up to 60 kg C/ha daily [60, 62], which corresponds to about 6 kg N/ha daily. This high level of priming effect is possible only at a very high content of organic matter in the soil. It is shown that one fourth to one third of the nitrogen consumed by the rhizospheric microorganisms results from humus degradation due to the activation of microorganisms by the root excretions of wheat [12, 13]. In a soil with plants, the mineralization of organic nitrogen is more intensive by 25–30%, as compared to a soil without plants.

Root excretions are composed of high- and low-molecular compounds. High-molecular root excretions accelerate the degradation of organic matter only slightly [67]. The degradation is mainly enhanced by low-molecular compounds, particularly, by glucose. By the intensity of induced priming effects, exudates can be arranged in a row: glucose > high-molecular root excretions > roots themselves. The degree of additional carbon mineralization is found to be directly proportional to the content of compounds added; it varied from 1 to 5% of the soil C during six months, which agreed with the published data [41]. The data on the additional mineralization of humus carbon were not confirmed in the same experiment [67]. Other authors also did not observe the additional mineralization of humus substances due to the activation of rhizospheric microorganisms by root excretions [58, 104].

A decrease in the rate of humus degradation by 37%, as compared to the soil without plants, was observed in the experiment on the separation of soil and rhizosphere respiration based on the natural discrimination of C isotopes [17]. The decreased degradation rate of humus substances can be attributed to the competition of microorganisms and plant roots for nutrients. The rhizospheric microorganisms themselves do not lose nitrogen upon

dying, but they are intensively consumed by protozoa and nematodes (for bacteria) or microarthtopods (for fungi) [22, 32]. This results in an intensive emission of mineral nitrogen [61]. However, this succession of carbon transformation in the rhizosphere involving protozoa has not yet been verified using a C tracer.

The availability of nutrients in the rhizosphere increases due to both the increased activity of microorganisms and the direct "chemical" action of exudates. In the case of phosphorus deficiency, the portion of carbonic acids in root excretions increases, and that of sugars decreases [117]. Carbonic acids acidify the soil and thus increase the solubility of phosphoric compounds. Thus, plants can choose a process (chemical or microbiological) for the modification of nutrients by changing the exudate composition.

MAIN TRENDS OF RESEARCH AND CONCLUSION

Recent publications make it possible to specify ways for studying the translocation of carbon by plants from the atmosphere into the soil. The doubling of CO_2 content in the atmosphere is predicted for the next century. This will result in changing the amounts of plant-assimilated carbon and the partition of assimilates among the plant organs, which in turn will affect the carbon cycle in the atmosphere–plant–soil system. From the results of most experiments, the total over-ground biomass of C3-plants increases with the CO_2 content in the atmosphere. The partition of assimilates is most affected. The increase in root growth, intensity of root respiration, and root excretions (by 110 [106] or 60% [20]) was observed in almost all studies. Thus, when the CO_2 concentration in the atmosphere increases, the total fixation of CO_2 is enhanced, and the partition of assimilates is displaced: the portion of carbon translocated by plants into the soil increases. The increase in CO_2 concentration does not affect the composition of rhizospheric microorganisms [33]. An additional enhancement of carbon translocation is noted in some works, when the mineral fertilizer nitrogen is used [20]. Reviews of studies of carbon translocation by plants into the soil and its utilization by microorganisms at an increased content of CO_2 in the atmosphere have been published previously [24, 30].

From this review, it follows that, in spite of a number of publications concerning the translocation of carbon by plants into the soil, many problems remain unsolved. No models of the carbon cycle in the rhizosphere were developed, because of poor knowledge about the transformation of organic compounds in the rhizosphere. The existing models of carbon translocation give a simplified description of organic matter transformation in the rhizosphere and cannot be used for comparison with experimental data.

For further study, the following topics have potential:

—the refinement of existing techniques and the development of new laboratory and field methods for the separation of root respiration and microbial degradation of exudates;

—the evaluation of carbon translocation by perennial meadow grasses and woody plants;

—the determination of additional humus mineralization and fixation of atmospheric nitrogen due to the activation of free-living and symbiotic rhizospheric microorganisms by root excretions. Of importance is the study of processes resulting in the replenishment of humus mineralized due to priming effects, as well as the determination of time periods when this resupply takes place;

—the development of models taking into account different forms of carbon translocation by plants into the soil, particularly root excretions and root respiration, as well as the transformation of exudates by rhizospheric microorganisms.

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