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SOIL BIOLOGY

The ^{14}C Tracer Study of Carbon Turnover in Soil in a Model Experiment

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Abstract—The translocation of carbon to the soil by lettuce (*Lactuca sativa* L.) was studied by the ^{14}C pulse labeling technique. Carbon dioxide fluxes from the soil were measured over 12 days. Between 20 and 35% of the assimilated labeled carbon was found in the lettuce leaves, 1.5–5% in the roots, and about 5–8% was released as CO_2 from the rhizosphere. The 60-day-old lettuce plants transferred 120–160 kg C/ha to the soil. Lettuce cultivation resulted in an accelerated decomposition of soil organic matter by a factor of 1.5–3.

INTRODUCTION

Much attention has recently been paid to the study of carbon turnover, especially to the emission of carbon dioxide from the soil. This is related to the fact that CO_2 significantly contributes to the greenhouse effect, and an increase in its concentration in the atmosphere can result in global climatic changes [30].

Some links of the carbon cycle are well studied. Abundant data on the carbon influx to the soil with aboveground plant remains are available in the literature [2, 37]. However, much less information has been acquired about the carbon input with underground plant organs. In spite of thorough studies in root morphology [18, 51], only a few, sometimes contradictory, data are available on the amount of carbon transferred by plant roots, especially during plant growth.

The role of root exudates in the so-called priming effect is of special interest. This effect is due to the indirect influence of plants on the turnover of organic matter in the soil, which can accompany their direct contribution to the total CO_2 flux from soil (root respiration and microbial respiration during exudate decomposition). Root exudates represent a readily available carbon source for microorganisms; therefore, the bacterial population and activity in the rhizosphere significantly exceed those in root-free soil [5, 8, 12, 13, 31, 53]. Rhizospheric microorganisms enhance the decomposition of humus when they need additional mobilization of nutrients (particularly, of nitrogen) from soil organic matter, or hamper it upon competition with plants for the limited amount of nutrients. These short-term changes in the turnover rate of soil organic mater are related to priming effects [13, 14, 20]. Similar interactions between plants and microorganisms in the rhizosphere are still poorly understood; they are reliably established only in a few works [6, 12, 13, 19].

Insufficient study of carbon influx to the soil with underground plant organs and its further transformation is largely explained by methodological difficulties: microorganisms rapidly decompose root exudates and dead root remains to CO_2, which is released from the soil together with the CO_2 resulting from the decomposition of soil humus and root respiration.

Separation of these two CO_2 fluxes from the soil and the high rate and complexity of the processes are the main problems in the determination of carbon cycle components in an atmosphere–plant–soil system.

These problems can be solved using the tracer method. This method has long been in use for the quantitative study of carbon translocation by plants to the soil [1, 5, 6, 12, 13, 36, 42–45]. Its advantage is the more complete consideration of all components involved in the carbon turnover in a soil–plant–atmosphere system. The tracer method can determine the origin of the gas evolved from the soil by the separation of the overall CO_2 flux from soil into the CO_2 resulting from the decomposition of soil humus and that from the rhizosphere respiration. Tracer experiments showed that the assimilated carbon is not only used for root construction, but released as CO_2 in the course of root respiration and evolved into the rhizosphere in significant amounts as low- and high-molecular organic compounds (10–14% of assimilated carbon, on the average) [1].

Two methods of plant labeling are commonly used: pulsed (single) and continuous tracer supply. Continuous labeling during plant growth allows for the best separation of the overall CO_2 flux from soil into its components. The separation is based on the decrease in the specific activity of $^{14}CO_{22}$ released from the soil compared to that of assimilated CO_2 [4, 9, 23, 52]. Natural isotopic fractionation can be considered as a ver-

The age of rye-grass plants and the dates of ^{14}C labeling and nitrogen fertilization

Parameter	Plant age, days							
	35	42	43	50	55	59	60	72
Plant growth, days	→							
$^{14}CO_2$ labeling			$^{14}CO_2$		X			
Nitrogen application, kg N/ha	20/40	20/40						
Plant growth, days	→							
$^{14}CO_2$ labeling							$^{14}CO_2$	X
Nitrogen application, kg N/ha	20/40	20/40		20/40		20/40		

Note: (X) the end of experiment.

sion of continuous labeling. This method is based on the difference in isotopic discrimination of $^{13}CO_2$ in the photosynthesis by C3 and C4 plants, which results in a decrease in the ^{13}C: ^{12}C ratio in the C3 and C4 plants by 27 and 12%, respectively, as compared to the atmosphere. The isotopic composition ($\delta^{13}C$) of soil humus formed from plant remains corresponds to the type of vegetation. Thus, when C3 plants are grown on C4 soil, or vice versa, from the values of $\delta^{13}C$ obtained for the CO_2 released, its overall flux can be separated into the components due to (i) humus decomposition and (ii) respiration of roots and microorganisms decomposing root exudates [6, 33]. Natural isotopic fractionation and pulse labeling are suitable for field conditions [33, 41]. In distinction from continuous labeling, the pulse labeling of plants provides more information about the distribution of assimilates at the specific stage of plant development [25]. However, this method allows only approximate evaluation of the portion of biogenic CO_2 because of the continuous dilution of labeled assimilates with recently absorbed unlabeled ones.

Few data have been obtained by the tracer method for the transfer of carbon to the soil by plants and subsequent transformation of carbon compounds; they are mainly concerned with cereals and partially with pasture plants [1]. There is practically no information about the translocation of carbon by vegetable plants, although these are intensive row crops and, hence, determine a high mineralization level of soil organic matter. Vegetable crops, in distinction from cereals, can have another distribution of assimilates related to both morphology and intensive selection.

The aim of this work was to quantitatively evaluate the components of carbon translocation to the soil for a legume (lettuce) and the indirect action of its root exudates on the mineralization rate of soil organic matter. The following problems were considered: the relative distribution of assimilated carbon (^{14}C) among the aboveground and underground organs of lettuce, the total carbon translocation to the soil by lettuce as calculated from the relative distribution of assimilated carbon, the effect of lettuce on the amount of microbial biomass in the soil and influx of biogenic carbon, the contribution of the respiration of lettuce roots and microorganisms decomposing the root exudates to the total CO_2 flux from soil, and the effect of lettuce root exudates on the decomposition rate of soil organic matter.

EXPERIMENTAL

Soil. Experiments were conducted on soil samples taken from the plow horizon of a long-term experiment established at the Experimental Station in Grossbeeren (10 km south of Berlin, 52°21′ N and 13°17′ E). The soil was annually fertilized with NPK + 30 t/ha cattle manure. The soil (sandy gleyic Cambisoil, FAO–UNESCO, 1990) has the following parameters: fine earth (<0.0063 mm) content, 6.0%; total carbon (C_{total}), 0.75%; total nitrogen (N_{total}), 0.076%; pH, 6.4; particle density, 2.63 g/cm^3; bulk density, 1.45 g/cm^3; total moisture capacity, 20.0%; and wilting point, 4.5%.

In the model experiment, air-dried soil was sieved through a 2-mm sieve and placed in vegetative vessels (2 kg/vessel).

Plants and growing conditions. Experiments were conducted with the *Libusa RZ* cultivar of lettuce (*Lactuca sativa* L.). One plant was grown in each vessel. The experimental design is given in the table. Plants were cut at an age of 55 or 72 days. Nitrogen was applied as a KNO_3 solution in water at 40 and 80 kg N/ha for plants grown for 55 days and at 80 and 160 kg N/ha for plants grown for 72 days (split into rates of 20 and 40 kg N/ha) (table). Fertilizers were applied at one-week intervals; the last application was done a day before plant labeling. To assess the effect of plants on CO_2 emission, soil without plants was incubated under the same conditions. The experiment was performed at 27 ± 1°C in the daytime and 22 ± 1°C at night. Daylight duration was 14 h; light intensity was 400 μmol m^{-2} s^{-1}. The moisture content in the soil was measured daily by gravimetry and maintained at a level of 60% of the total moisture capacity.

Experimental vessels and labeling procedure. The study of carbon translocation by lettuce plants and the separation of the soil and rhizospheric CO_2 fluxes were performed using the pulse (single) labeling of aboveground lettuce organs with $^{14}CO_2$. Plants were labeled at an age of 43 or 60 days with two levels of nitrogen application.

Plant labeling was performed in special Plexiglass vessels, which consisted of two parts isolated from each other and from the atmosphere (Fig. 1) [26, 50]. The lower vessel chamber (138 mm in diameter, 300 mm in height, soil layer 110 mm thick) with soil and plant roots was covered by a cap with a hole for stems (8 mm in diameter). One day before labeling, the hole was sealed with a soft nontoxic silicone paste, which was impermeable to air and moisture but allowed the normal growth and development of plants.

Plant labeling was performed as follows. A 2-ml tube with a $Na^{14}CO_3$ solution (580 kBq of ^{14}C) was installed at the top of the lower chamber of the experimental vessel. The upper chamber (138 mm in diameter, 300 mm in height) was then firmly attached. To obtain $^{14}CO_2$, 1 ml of 5 N H_2SO_4 was added to the $Na^{14}CO_3$ solution through a Teflon tube in the upper chamber wall. The plants were exposed to the $^{14}CO_2$ atmosphere for 10 h. During the last 30 min before the end of assimilation (switching off the light), the upper part of the vessel was blown using a membrane pump. The air flow was passed through a NaOH solution to capture the unassimilated CO_2. The next morning, the amount of $^{14}CO_2$ released in the course of leaf dark respiration at night in the upper chamber was also determined. Then, the upper chamber was removed. The lower part of the vessel was continuously blown by means of an air pump for 12 days after the beginning of labeling. The total and labeled CO_2 released in the course of root and microbial respiration was captured in 20 ml of 0.5 N NaOH solution. The NaOH was periodically changed, first at 1.5-h intervals, further increased to twice a day.

Analyses of soil, plants, and CO_2. At the end of the experiment, the aboveground parts of plants were cut and dried at 60°C. Coarse roots were collected, washed, and dried. A part of the soil was used for determining the ^{14}C activity, total carbon, and carbon of microbial biomass (C_{mic}). The rest of soil was washed on a 0.5-mm sieve to remove fine roots.

The amount of CO_2 released from the soil and sorbed by the NaOH solution was determined by titration with 0.2 N HCl in the presence of 0.5 M $BaCl_2$ using phenolphthalein as an indicator [28]. The content of C_{total} in leaves, roots, and soil was determined with a Carlo Erba CN analyzer in two analytical replicates [39].

The content of C_{mic} in the soil was determined by the fumigation–extraction method [48]. The method is based on the comparison of carbon amounts extracted from the soil with 0.5 M K_2SO_4 before and after the treatment of soil with chloroform. The chloroform fumigation of soil destroys microbial cells without affecting the soil organic matter. Hence, the additional amount of carbon in the extract from the chloroform-treated soil is due to the degradation of microbial cells [3, 16]. The value of C_{mic} was obtained after multiplying by a scaling factor of 2.34 [34]. The scaling factor accounted for the incomplete transition of destroyed microbial cells from soil into solution.

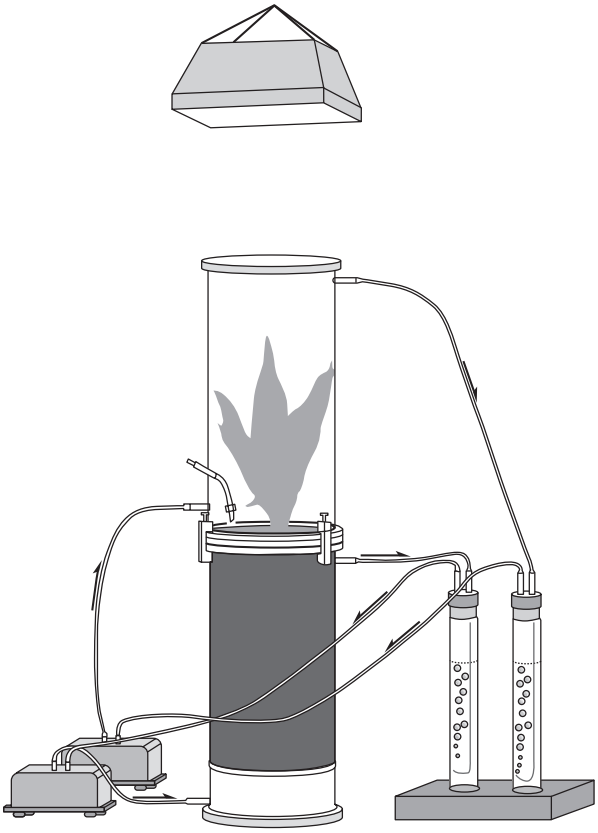

Fig. 1. Two-chamber vessel for plant labeling in the $^{14}CO_2$ atmosphere and studying the translocation and distribution of carbon.

The value of C_{mic} was determined at the soil-to-extractant ratio of 1 : 2 (10 g of soil and 30 ml of 0.5 M K_2SO_4). Soil samples were fumigated with chloroform in a dessicator at a constant temperature of 25°C for 24 h. The determination was performed in four analytical replicates.

The ^{14}C activity in the NaOH solution was measured with a Canberra Packard Tri-Carb 2000CA liquid scintillation analyzer using the Rothiscint 22x scintillation cocktail (Roth Company, Germany) after the end of chemiluminescence. The absolute ^{14}C activity was standardized by the addition of NaOH solution as quencher. The ^{14}C activity in leaves, roots, and soil was

determined after the combustion of samples (1 g for soil and 0.2 g for plant materials) on a Canberra Packard Oxidizer-Unit, Model 307. The released CO_2 was trapped in a solution of scintillation cocktail Permafluor E^+ (Canberra Packard), and the ^{14}C activity was measured with a detection efficiency of 88–90% for ^{14}C.

Calculations and statistical processing. Data on the ^{14}C radioactivity are expressed in the percentage of the assimilated amount. The assimilated ^{14}C amount was calculated as follows:

$$\text{Assimilated } ^{14}C = \text{applied } ^{14}C - \text{remainder } ^{14}C \text{ in the upper vessel chamber after labeling for 10 h} - \text{remainder } ^{14}C \text{ in the Eppendorf vessel.} \quad (1)$$

Based on the assumption that the distribution of unlabeled assimilates among the components of the soil–plant system was proportional to the labeled carbon flux, we calculated the content of C_{total} transferred to the soil by lettuce plants and included in the microbial biomass during the period between planting and the end of the experiment from the formula:

$$C_{total} = {}^{14}C_a \cdot C_{total,b}/{}^{14}C_b, \quad (2)$$

where C_{total} is the total carbon content of the component studied, mg; $^{14}C_a$ is the percentage of ^{14}C included in the component studied; $C_{total,b}$ is the total carbon content in leaves, mg; and $^{14}C_b$ is the percentage of ^{14}C included in leaves.

The C_{total} : $^{14}C_{total,in}$ leaves ratio was used as the scaling factor, because the carbon mass and the percentage of ^{14}C included in leaves are the most accurately measurable quantities.

The content of C–CO_2, mg, released during the respiration of roots and of microorganisms decomposing the root exudates was also converted according to Eq. (2). To obtain the average daily amount of phytogenic C–CO_2 released from the soil, this value was divided by the number of days from lettuce planting to the end of the experiment. This method of calculation presumes a near-linear dynamics of lettuce growth.

The total C–CO_2 fluxes, mg, from soils with and without plants were calculated from the titration data.

To express the values of carbon amounts and CO_2 fluxes on a per-hectare basis, the density of plants in field conditions was taken equal to 10 plants/m_2 [49].

The priming effect for carbon was measured by the comparison of the CO_2 fluxes due to humus decomposition from the soils with and without plants. The flux of humus CO_2 from the soil with plants was calculated as the difference between the total CO_2 flux and that of $^{14}CO_2$ resulting from the respiration of roots and of microorganisms decomposing the root exudates.

Data on the ^{14}C distribution are given for the moment of labeling, i.e., for the 43- and 60-day-old plants. Data on the total carbon are given for the end of the experiment, i.e., for the 55- and 72-day-old plants.

To assess the effects of nitrogen nutrition and plant age on the emission of CO_2 from soil and the distribution of assimilates, we used the two-factor analysis of variance (MANOVA) with the assessment of the difference significance from the Fisher least significant difference (*t*-test) for the significance level $\alpha \le 5\%$. The lettuce age and the nitrogen rate were taken as independent parameters. The effective parameters were the following: the biomass of roots and aboveground lettuce organs, the distribution of ^{14}C assimilates in the soil–plant system, the amount of C_{mic}, the emission of CO_2 and $^{13}CO_2$ from the soil, and the additional decomposition of soil humus. The experiment was performed in four replicates.

RESULTS AND DISCUSSION

Distribution of ^{14}C assimilates. Lettuce assimilated up to 95% of the labeled CO_2 released after the addition of acid for 10 h. A high transportation rate from leaves to other plant organs was noted for the assimilation products. For example, $^{14}CO_2$ was found in the soil air even 1.5 h after the beginning of labeling. A similarly rapid translocation of assimilates to roots and their emission as CO_2 were previously observed for winter wheat and rye [5], rye-grass (*Lolium perenne*) [19], wheat and barley [10], and corn [29].

A significant portion of assimilated carbon was released in the course of leaf dark respiration. The aboveground lettuce organs released 7–14% of the labeled carbon in the first night after labeling. Up to 40% of plant-assimilated carbon can be released during the dark respiration of rye-grass [19]. About 50% of the assimilated ^{13}C activity was found in all pools at the end of the experiment with lettuce. Similar results were obtained in an experiment with the ^{13}C isotope (30–50%) [40].

Carbon assimilated by plants during photosynthesis (C_{total}) is transferred from the aboveground part of a plant to its roots, where it is included in the root biomass or root exudates, which are released by plants into the rhizosphere. Organic substances released by plants are partially decomposed by microorganisms to CO_2 and partially used for the construction of their biomass or the formation of humus substances in the soil. The transferred organic carbon (C_{org}) comprises root carbon, exudate carbon, and carbon included in microorganisms and humus. Therefore, the C_{org} transfer was calculated as the sum of total root carbon and the carbon of soil and microorganisms, whose amount was calculated from the ^{14}C activity found in the soil and microorganisms.

The relative content of ^{14}C in the leaves 12 days after labeling was 4–20 times higher than that in the roots (Fig. 2). This indicated both the lower inclusion of ^{14}C

in roots compared to leaves and the high rate of root renewal. When the plant age increased from 43 to 60 days, the rate of relative carbon inclusion in leaves decreased from 35 to 20%; an inverse tendency (an increase from 1.5 to 3.6–5.1%) was observed for roots.

For most other cultivated plants, the rate of ^{14}C inclusion in roots decreases and that in leaves increases with the growth of the plants [10, 17, 24, 42–44]. This is explained by the fact that an intensive growth of aboveground organs is observed for cereal crops when going from the tillering to shooting stage, while the growth of roots is decelerated and less carbon is used for the construction of root mass [17, 24]. Most new assimilates arrive to the growing organs [35]. In lettuce, on the contrary, the growth of vegetative organs was still not completed by the end of the experiment, because lettuce was harvested at the stage of intensive growth, unlike cereals. Therefore, the relative root increment was higher in the second period, and the inclusion of assimilated labeled carbon in the root mass increased respectively.

The application of nitrogen fertilizers exerted no significant effect on the inclusion of ^{14}C in lettuce leaves (Fig. 2). A 1.3-fold difference was observed between the leaf C_{total} masses in the treatments with high and low fertilizer rates (5.33 and 4.07 g, respectively, at an age of 72 days). Similar results attesting to the equal inclusion of ^{14}C in the aboveground organs of differently fertilized plants were obtained for winter wheat [44]. However, an increase in the relative inclusion of ^{14}C in lettuce roots was noted for the lower nitrogen rate compared to the plants grown at the higher level of nitrogen nutrition. The difference was statistically significant only for more adult (60-day-old) plants. The enhanced nitrogen nutrition also decreased the transfer of ^{14}C to the roots of cereal plants and perennial grasses [15, 24, 32, 46]. This effect is typical not only for nitrogen fertilizers but also for phosphorus ones [40]. This is explained by the fact that roots consume 20–60% of the energy obtained during respiration for the uptake and transfer of nutrients [22, 47]. With deficient nutrition, the rate of unproductive losses is higher. The release of $^{14}CO_2$ from soil upon the application of the lower fertilizer rate was equal to 8% of the assimilated ^{14}C activity compared to 6% in the more fertilized treatment. However, it should be noted that an opposite tendency was reported in some works; e.g., an increase in the ^{14}C inclusion in barley roots was observed for the improved nitrogen nutrition [44].

Total carbon transfer by lettuce plants to the soil. When the root mass is determined by conventional methods (e.g., by washing), root exudates and dead fine roots remain unmeasured. In addition, the washing procedure involves high losses of fine roots and root filaments, which can reach 50–60% [36] and even 85% for fine roots [21]. The tracer method (in particular, the ^{14}C labeling of plants) allows a more objective estimation

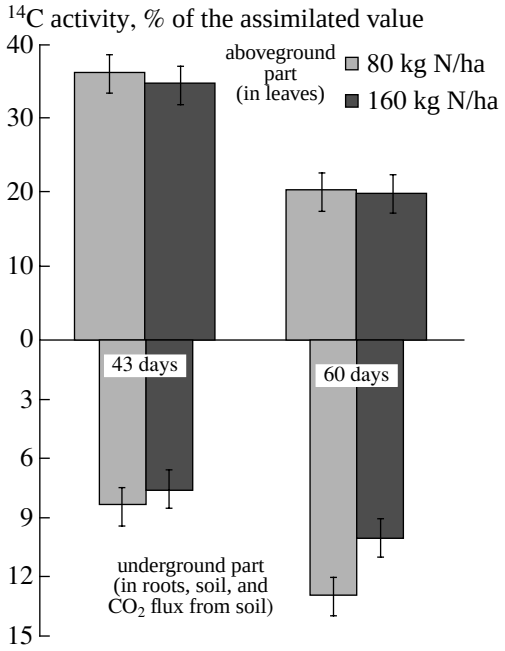

Fig. 2. Inclusion of ^{14}C in lettuce leaves and translocation to the soil (sum of the ^{14}C found in roots and soil and the CO_2 flux from the soil) as depending on the plant development stage and nitrogen supply, % of assimilated ^{14}C ($x \pm 0.5$ LSD; $p = 0.05$).

of the total carbon transferred by a plant to the soil. It was found that the translocation of total assimilated labeled carbon to the soil increased in the course of plant development from 7.6–8.4% of assimilated ^{14}C activity (43 days) to 10.4–13.3% (60 days) for the fertilizer rates of 160 and 80 kg N/ha, respectively (Fig. 2). In this case, the translocation of total carbon is determined as the total percentage of ^{14}C found in roots, soil CO_2 flux, soil, and microorganisms.

According to the calculations based on the ^{14}C distribution (Eq. (2)), the 72-day-old lettuce transferred 120–160 kg C_{org}/ha to the soil (Fig. 3). The lower relative translocation of carbon to the soil at the higher rate of nitrogen fertilizer (Fig. 2) was balanced by the more intensive growth of the plant. Therefore, in spite of the lower relative ^{14}C inclusion, plants with a higher nitrogen level transferred a higher ^{14}C amount to the soil than plants with a lower level of nitrogen nutrition (Fig. 3). A similar effect of nitrogen application on the ratio of ^{14}C inclusion in plant organs to the total biomass accumulation was also observed for winter wheat and barley [44]. It should be noted that the amount of carbon transferred by lettuce to the soil was 5–8 times lower than that transferred by cereals [10, 17, 44, 52] and grasses [19, 21]. This is related to the different ratios between aboveground and underground organs in lettuce and cereals. As the growth of lettuce was not completed in our experiment, it can be supposed that a

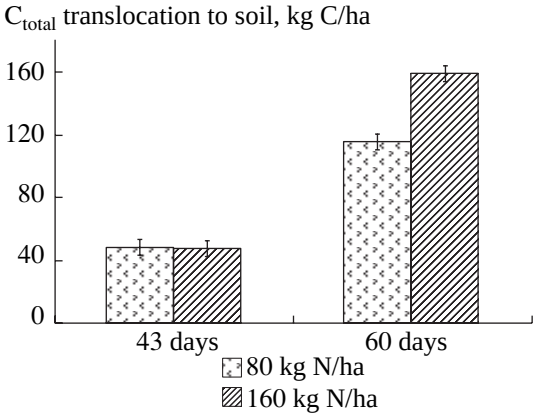

Fig. 3. Translocation of total carbon by 43- and 60-day-old lettuce plants to soil at two levels of nitrogen supply ($x \pm$ LSD; $p = 0.05$).

1.3–1.5-fold greater amount of carbon would be transferred to the soil by the end of the vegetation period.

Inclusion of ^{14}C in the microbial biomass of soil. The total microbial biomass increased during the growth of plants. No distinctions among the differently fertilized treatments were found for the 55-day-old lettuce plants; for the 72-day-old plants, a reliable increase in biomass (from 44 to 73 mg C/kg soil) was observed at the higher rate of nitrogen fertilizer (Fig. 4, top). This was due to the fact that the loamy sandy soil used in the experiment had a low nitrogen content and that fertilizer created more favorable conditions for root growth and the total emission of organic substances into the rhizosphere, and, hence, an increase in microbial biomass. Similar results were obtained in an experiment with corn [27], but no reliable difference in biomass was found for wheat plants grown at two levels of nitrogen nutrition [24].

A tendency for an increase in relative ^{14}C inclusion in microbial biomass at the lower level of nitrogen nutrition in the experiment with lettuce plants (Fig. 4, bottom) was revealed. This was related to a higher ^{14}C inclusion in roots and the enhanced exudation at a deficient or smaller total amount of microorganisms. An increase in the ^{14}C inclusion in biomass at the higher nitrogen rate was revealed using the continuous $^{14}CO_2$ labeling [24, 27]. Differences in the results obtained are due to the methods of study, because continuous labeling ensures similar specific activities of ^{14}C in all exudates for a long time period. This increases the ^{14}C content in microorganisms until the specific activity of microbial ^{14}C becomes equal to that of exudates multiplied by their contribution to microbial nutrition.

CO_2 emission from soil. The total CO_2 flux from soil results from (1) root respiration, (2) respiration of microorganisms decomposing exudates from plant roots (basal respiration), and (3) additional microbial decomposition of humus due to the increased microbial

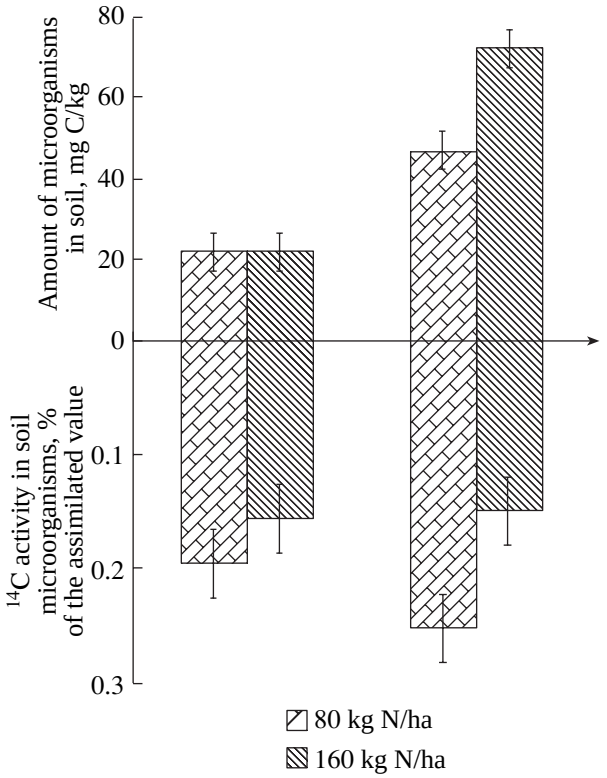

Fig. 4. Microbial biomass in the soil with lettuce plants and ^{14}C inclusion ($x \pm 0.5$ LSD; $p = 0.05$).

population (priming effect, see below) (Fig. 5). The quantitative evaluation of separate components of the total CO_2 flux from soil with plants can be performed using the tracer method in combination with a comparison of CO_2 fluxes from the soil with plants and from clean fallow.

The ^{14}C activity in the CO_2 flux from the soil with lettuce plants under experimental conditions was due to the activity of plants. Part of the labeled assimilates were rapidly transferred from leaves to roots, where they were oxidized to carbon dioxide during root respiration or released into the soil as root exudates. In the soil, exudates were rapidly decomposed by microorganisms to CO_2: 5–8% of assimilated ^{14}C was released from the lettuce rhizosphere within 12 days after $^{14}CO_2$ assimilation. This amount corresponded to the release of 0.44 and 2.204 kg C–CO_2 ha^{-1} day^{-1} by the 43- and 60-day-old plants, respectively (Fig. 6). The obtained values were lower than those found for other plant types. The root and microbial respiration from the rhizosphere of cereals included 16–30% of assimilated carbon [5, 10, 42]. The emission of $^{14}CO_2$ from the soil with rye-grass decreased when the age of plants increased [25]; an opposite tendency was observed for lettuce. This difference was due to the fact that lettuce was harvested at the stage of intensive growth.

From the portion of $^{14}CO_2$ released from the soil, the contribution of plants to the total CO_2 flux from the soil was calculated. According to our data, from 15 to 60% of the total CO_2 flux from the soil with lettuce plants was of root origin: respiration of roots and microorganisms decomposing the root exudates and dead root remains (Fig. 6). The direct contribution of lettuce to the total CO_2 flux from the soil was comparable to that of other agricultural crops [19, 36]. However, it should be kept in mind that the C_{total} content in the experimental soil was low (0.75%). Therefore, the CO_2 flux due to humus decomposition was relatively low. In a humus-enriched soil, the portion of CO_2 due to root respiration and exudate decomposition would be lower.

Priming effect due to root exudations. The fluxes of humus CO_2 from the soils with and without plants were compared, and the additional decomposition of soil humus in the presence of plants was calculated. Lettuce accelerated the decomposition of soil humus by a factor of 1.5–3 (a positive priming effect) in the experimental conditions (Fig. 6). The additional CO_2 emission was 0.5–1.8 kg C–CO_2 ha^{-1} day^{-1}. Taking the C : N ratio similar for different fractions of soil organic matter, this corresponded to an additional mineralization of 0.05 to 0.18 kg N ha^{-1} day^{-1}. This amount of nitrogen could not cover the needs of plants growing on the soil studied, which was relatively poor in nitrogen. An additional mineralization of nitrogen up to 6 kg N ha^{-1} day^{-1} was found for other soils with better developed root systems and on soils richer in organic matter [19]. A 4–5-fold acceleration in soil humus decomposition was also observed in experiments with the continuous labeling of plants [12, 13]. However, the decomposition of organic matter in a soil with wheat plants, as measured using the natural ^{13}C fractionation, was slower by a factor of 1.5 compared to a fallow soil (a negative priming effect) [6]. These differences in the decomposition rate of soil organic matter during plant growth could be due to the differences in soils and plants under study, as well as in studying methods. Therefore, it is important to check the presence and direction of the priming effect using two different methods in the same experiment.

The results of studies show that the exudation of organic substances from roots is an efficient mechanism for the ecological adaptation of plants. When the activity and population of microorganisms in the rhizosphere increase, the mineralization of humus is accelerated [12, 13, 38]. This covers the enhanced need of the increased soil biomass for nutrients, primarily for nitrogen. Part of the nitrogen mineralized by microorganisms is absorbed by plants. Thus, plants acquire additional nutrients from soil or dead microbial biomass due to the exudation of readily decomposable organic substances to the soil. In summarizing, the following scheme can be proposed for the processes inducing an additional decomposition of soil organic matter (the positive priming effect):

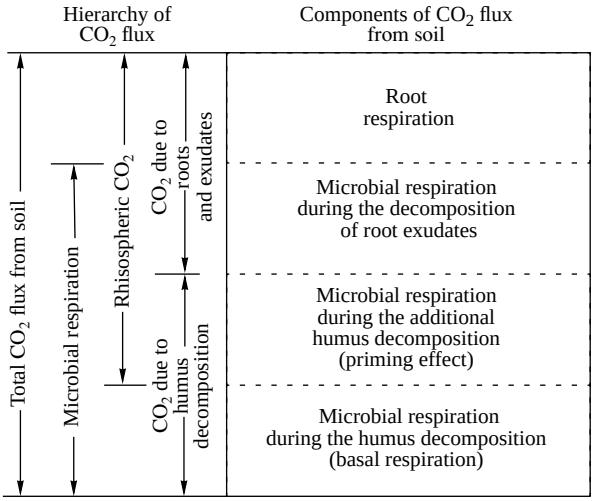

Fig. 5. Components of a CO_2 flux from soil and their hierarchy.

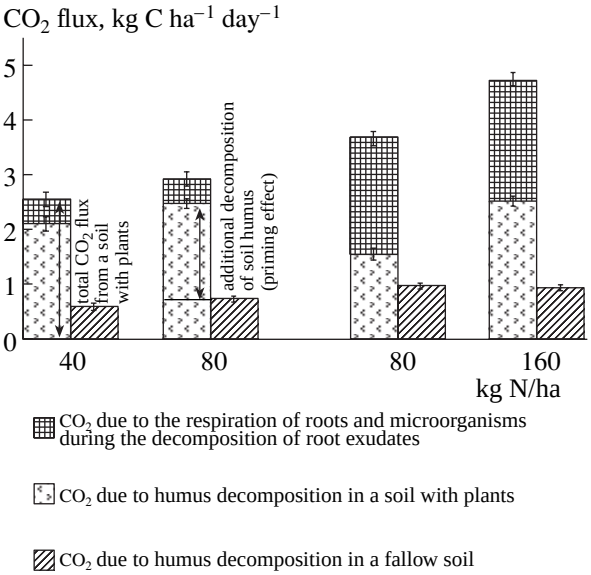

Fig. 6. Components of the total CO_2 flux from a soil with 43- and 60-day-old lettuce plants (respiration of roots and microorganisms during the decomposition of root exudates and soil humus) at two levels of nitrogen supply, CO_2 resulting from the decomposition of humus substances in clean fallow ($x \pm 0.5$ LSD; $p = 0.05$), and priming effect due to additional decomposition of soil humus.

(1) exudation of organic substances with a wide C : N ratio readily available to microorganisms by plants into the rhizosphere;

(2) accelerated growth of soil microbial biomass in the presence of this carbon source;

(3) limitation of further microbial growth due to the deficiency of mineral nitrogen in the rhizosphere;

(4) intensive decomposition of soil organic matter to yield nitrogen; and

(5) partial absorption of mineralized nitrogen by plants.

The consideration of soil fauna activity significantly complicates the proposed scheme [20]. Increased emission of CO_2 and acceleration of mineralization were noted upon the consumption of microorganisms by nematodes and Protozoa [7, 11].

CONCLUSION

The relative inclusion of ^{14}C in the aboveground organs of lettuce decreased from 35 to 20% of the assimilated carbon during the development of plants. The amount of ^{14}C found in roots 12 days after the assimilation, on the contrary, increased from 1.5 to 5.1% during the growth of lettuce. The increase in the nitrogen content in soil reliably reduced the ^{14}C inclusion in the roots of 60-day-old lettuce plants (5.1 and 3.6% for nitrogen rates of 80 and 160 kg N/ha). The transfer of organic carbon to soil by 72-day-old lettuce plants was 120 and 160 kg C_{org}/ha for the low and high nitrogen rate, respectively.

Five to eight percent of the assimilated ^{14}C was released from the lettuce rhizosphere over 12 days; the increase in the nitrogen fertilizer rate decreased the carbon losses from the rhizosphere. The contribution of lettuce to the total CO_2 flux from the soil increased from 15 to 60% during the development of plants.

The amount of microorganisms in the soil with a high nitrogen rate was 1.5 times higher than that in the soil with a low nitrogen rate; however, the portion of assimilated carbon included in microorganisms was lower. Growing lettuce accelerated the decomposition of soil organic matter by a factor of 1.5–3. The additional emission of CO_2 was 0.5–1.8 kg $C–CO_2$ ha^{-1} day^{-1}.

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