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Soil Biology & Biochemistry 33 (2001) 1067–1075

Soil Biology & Biochemistry

www.elsevier.com/locate/soilbio

Budgets for root-derived C and litter-derived C: comparison between conventional tillage and no tillage soils

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Received 30 August 1999; received in revised form 16 August 2000; accepted 15 November 2000

Abstract

Placement of plant residues in conventional tillage (CT) and no-tillage (NT) soils affects organic matter accumulation and the organization of the associated soil food webs. Root-derived C inputs can be considerable and may also influence soil organic matter dynamics and soil food web organization. In order to differentiate and quantify C contributions from either roots or litter in CT and NT soils, a ^{14}C tracer method was used.

To follow root-derived C, maize plants growing in the field were ^{14}C pulse-labeled, while the plant litter in those plots remained unlabeled. The ^{14}C was measured in NT and CT soils for the different C pools (shoots, roots, soil, soil respiration, microbial biomass). Litter-derived C was followed by applying ^{14}C labeled maize litter to plots which had previously grown unlabeled maize plants. The ^{14}C pools measured for the litter-derived CT and NT plots included organic matter, microbial biomass, soil respiration, and soil organic C.

Of the applied label in the root-derived C plots, 35–55, 6–8, 3, 1.6, and 0.4–2.4% was recovered in the shoots, roots, soil, cumulative soil respiration, and microbial biomass, respectively. The ^{14}C recovered in these pools did not differ between CT and NT treatments, supporting the hypothesis that the rhizosphere microbial biomass in NT and CT may be similar in utilization of root-derived C. Root exudates were estimated to be 8–13% of the applied label. In litter-derived C plots, the percentage of applied label recovered in the particulate organic matter (3.2–82%), microbial biomass (4–6%), or cumulative soil respiration (12.5–14.7%) was the same for CT and NT soils. But the percentage of ^{14}C recovered in CT soil organic C (18–69%) was higher than that in NT (12–43%), suggesting that particulate organic matter (POM) leaching and decomposition occurred at a higher rate in CT than in NT. Results indicate faster turnover of litter-derived C in the CT plots.

Keywords: No tillage; Root exudate; Rhizosphere; Soil organic matter; Microbial biomass; Carbon allocation

1. Introduction

Under conventional tillage (CT) management, plant residues are incorporated into the soil, whereas under no-tillage (NT) management, they are placed on the soil surface. Placement of plant residues, more than tillage itself, may affect decomposition of the residues and the organization of associated soil food webs (Holland and Coleman, 1987; Beare et al., 1992). Studies of soil food webs associated with buried litter and surface litter have indicated that buried litter systems are more bacteria-dominated, while surface litter systems are more fungi-dominated (Hendrix et al., 1986; Holland and Coleman, 1987; Beare et al., 1992, 1995). This is expected to result in faster turnover of inputs in CT with greater stabilization of inputs into organic matter in NT soil. Beare et al. (1997) found that fungi helped increase water-stable aggregates in NT, and that organic matter in macroaggregates was less microbially-processed than organic matter in microaggregates. In a simulated NT lab study, Gale and Cambardella (2000) found that 42% of root-derived C was in the soil, while only 16% of litter-derived C was in the soil after 360 days. They concluded the benefits of NT management are mainly from the increased retention of root-derived C in the soil.

The importance of root-derived C inputs to soil organic matter and soil food webs may be considerable. Campbell et al. (1991) found no differences in soil organic matter

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0038-0717/01/$ - see front matter
PII: S0038-0717(01)00012-8

between treatments with or without litter inputs. They suggested that root inputs may be more important in maintaining soil organic matter. Similarly, Balesdent and Balabane (1996) used stable carbon isotope techniques to demonstrate that maize root-derived C contributed 1.5 times more to soil organic matter than that of above-ground biomass despite a root:shoot biomass ratio less than 0.5. High below-ground production and slow decomposition of root-derived C were cited as the difference.

Recently, the role of root-derived C has been emphasized in contributing to soil organic matter (Balesdent and Balabane, 1992, 1996), maintaining microbial populations (Martens, 1990; Liljeroth et al., 1990; Qian et al., 1997), and aggregate stability (Haynes and Beare, 1997). Previous research suggests the following alternative hypotheses concerning root-derived C in agroecosystems:

1. There is no difference between CT and NT soil in amount of carbon in different pools (soil respiration, microbial biomass, soil organic C). This follows if the C substrate is high quality and would be quickly assimilated by microorganisms. Xu and Juma (1993) showed that root-released water-soluble organic-C was more readily available than soluble organic-C originating from the soil;
2. Alternatively, a greater percentage of root-derived C will be distributed to microbial biomass, soil respiration, and soil in NT since incorporated litter serves as the main source of C in CT plots. This hypothesis was suggested by Holland (1995), who found increased microbial biomass under corn plants grazed by grasshoppers in NT but not in CT plots. The increased rhizodeposition under grazed corn was thought to increase the NT microbial biomass more than in CT due to the litter-derived C available to microorganisms at lower depths in CT soil.

It follows from hypothesis 2 that at lower depths in the NT soil, root-derived C will be a higher percentage of microbial biomass and of soil since this region of soil only receives root-derived C inputs. Hendrix et al. (1987) found that estimates of C inputs based on decay of plant residue in NT plots were less than C outputs (respiration measurements or respiration estimates calculated from standing stocks of microbial biomass). The discrepancy was not found in CT plots. This suggests that root-derived C may play a role in providing more C to the soil food web in NT plots.

In contrast to root-derived C, the following hypotheses are suggested concerning litter-derived C: (1) there is no difference between tillage treatments in amount of litter-derived C in different pools. This could occur if the C-inputs or the organisms using the C are very mobile; (2) in CT soil, litter-derived C will be quickly assimilated by microorganisms which will also increase the litter-derived C in soil respiration and in soil organic C (SOC). In NT soil, the litter-derived C is predicted to remain in the POM pool for a longer time than in CT soil.

Although we have decomposition and respiration comparisons between CT and NT, and can therefore calculate the turnover of litter-derived C, this has not been measured for root-derived C in the field. The distribution of root-derived C to microorganisms, soil respiration, and soil has primarily been measured in growth chamber studies or in tilled soils. The ratio

$$\frac{^{14}CO_2 \text{ respired}}{^{14}C \text{ in roots} + {}^{14}C \text{ in soil}}$$

has been shown to be 1.92 for wheat pulse-labeled in the field, but only 0.29 for wheat pulse-labeled in growth chambers. This suggests that the field-grown wheat roots respire more than those grown in pots or that soil fauna found in the field are contributing to decomposition and CO_2 production (Whipps, 1990). Both of these potential artifacts of growth chamber experiments were avoided with this field study.

We used ^{14}C as a tracer to separate the effects of root-derived C and litter-derived C in CT and NT soil food webs. Pulse-labeled field-grown maize was used to establish root-derived C inputs, while ^{14}C-labeled corn residue was applied to litter-derived C plots. The objective of this study was to quantify root-derived C and litter-derived C flows to soil, microbial biomass, and soil respiration pools in NT and CT soils under field conditions.

2. Methods

2.1. Site description

The Horseshoe Bend Research Area on the University of Georgia campus in Athens, Georgia was used for this study (Hendrix, 1997). The three field plots used have been in no-tillage (NT) or conventional tillage (CT) since 1984. CT plots have been plowed, disked and rotary-tilled in the spring and in the autumn since tillage treatments were established. In autumn of 1995, CT and NT treatments were planted in crimson clover as a winter cover crop which was mowed the following spring prior to planting maize. During the spring of 1996, treatment plots were fertilized (100 kg N ha^{-1}) and the CT plots were plowed, disked, and rotary-tilled prior to planting. Maize was planted for the summer crop using a no-till planter. Acrylic sheeting was inserted into the soil to a depth of 15 cm along the perimeter of the plots (2×1 m) to contain the labeled materials. Differentiation between carbon sources was achieved using ^{14}C as described in the next two sections.

2.2. Root-derived C plots

Root-derived C plots were established by use of a chamber to pulse-label maize plants in the field. Further description of labeling methods is given in Kisselle et al. (1999). Pulse-labeling occurred over 3 consecutive days (10–12 July 1996) for the six plots (three CT, three NT). Each plot contained 28 plants and received 74 MBq of $^{14}CO_2$ (specific activity of 2.1 GBq $mmole^{-1}$). Two shoots were harvested and removed

from the root-derived C plots until maturity (day 69). After last harvest of maize (day 69), all labeled, above-ground plant biomass was removed from the plots, and unlabeled corn residues were added to the plots. A shovel was used to simulate both plowing (inversion) and secondary tillage (chopping of residue and mixing with top 15 cm soil) in the CT plots prior to the winter cover crop of rye being planted in both CT and NT plots. Two soil samples were taken randomly from each root-derived C plot 3, 6, 13, 20, 27, 41, 55, 69, 112, and 316 days after labeling. For all dates, except the last two, these soil samples were directly under a maize plant which was harvested immediately before soil sampling. Soil cores sampled were divided into 0–5 and 5–15 cm depths and stored at 4°C until processed.

2.3. Residue-derived C plots

Residue-derived C plots were created by multiple-labeling of maize grown in a separate bed (note: these were not taken from the root-derived C plots) and applying these dried plant residues to the plots (three plots each of CT and NT). Average activity added to each residue-derived C plot was 288 MBq. Residues were added to plots on 26 November 1996. Residues in CT plots were incorporated into the soil to a depth of approximately 15 cm using a shovel to simulate both plowing (inversion) and secondary tillage (chopping of residue and mixing with top 15 cm soil). Two random soil cores were sampled just prior to (0 days) and 5, 8, 14, 21, 36, 49, 65, 97, and 176 days after application of litter. Soil cores sampled were divided into 0–5 and 5–15 cm depths and stored at 4°C until processed.

2.4. Analysis

Soils were hand-picked free of visible organic material which was separated into roots or particulate organic matter (POM). Soils were analyzed for microbial biomass using chloroform fumigation-direct extraction (Vance et al., 1987). Total organic C of extracts was determined on a Shimadzu TOC-500 analyzer (Kyoto, Japan). The ^{14}C activity was measured by adding a 1 ml aliquot from each K_2SO_4 extract to 20 ml of ReadyGel scintillation fluor (Beckman Instruments, Fullerton, CA, USA) and counting for 20 min with a liquid scintillation counter (Beckman LS 3801, Beckman Instruments, Fullerton, CA, USA). Roots picked from soils sampled in root-derived C plots, and POM picked from soils sampled in litter-derived C plots, were oven-dried, weighed, and ground using a Wiley Mill (<2 mm). Soils from both C treatment plots were air-dried, ground with a mortar and pestle, and oven dried (100°C). Roots, POM, and soil were oxidized (Harvey OX500, R. J. Harvey Instrument Co., Hillsdale, NJ, USA) and counted on the liquid scintillation counter. Ash weights of roots, and POM were used to determine ash-free dry weights (AFDW). Mass loss of soil upon combustion (using Harvey oxidizer, 900°C) was used to calculate soil organic C using a conversion factor of 0.58 (Page et al., 1982).

Respiration measurements were made in the field using static base traps (Page et al., 1982) on 0, 1, 2, 9, 12, 19, and 27 days after pulse in the root-derived C plots and 5, 7, 9, 16, 26, 38, 53, 80, 97 days after the addition of residues in the litter-derived C plots. Total CO_2–C was measured by titration of a subsample of NaOH while ^{14}C was measured by adding 0.5 ml of the NaOH to EcoLite scintillation fluor (ICN Biomedicals, Costa Mesa, CA, USA) and counting for 20 min on a liquid scintillation counter.

Using ^{14}C labeled microbial biomass (a measure of the standing stocks of C in that pool) and an assumed production efficiency, the C exuded from plant roots can be estimated (Grayston et al., 1996). Root exudates in root-derived C plots were estimated in two ways for the initial sample date (day 3) using the following equations:

$$\text{root} - \text{derived C exuded} = \frac{\text{microbial} - {}^{14}\text{C}}{\text{microbial production efficiency}}; \quad (1)$$

$$\text{root} - \text{derived C exuded} = \frac{{}^{14}\text{CO}_2}{(1 - \text{microbial production efficiency})}. \quad (2)$$

This estimate assumes immediate availability of exudates to, and complete assimilation by, the microbes. Assumed microbial production efficiencies were derived from two studies. In a clay soil, van Veen et al. (1985) found that the microbial efficiency with which glucose was used was 64% by day 3. Helal and Sauerbeck (1986) (as reported by van Veen et al., 1989) found microbial production efficiency of root exudates to be low (15%) suggesting that nutrients, not carbon, were the limiting factor.

Eq. 2 used for estimating root exudates can be used to calculate the production efficiency of the microbial biomass in the litter-derived C plots. The amount of labeled litter available to the microbial biomass was calculated using the initial amount of label applied and decomposition constants derived from a concurrent litterbag decomposition experiment (Garrett, unpublished data). Decomposition constants were significantly different between CT (0.0059 $days^{-1}$) and NT (0.0041 $days^{-1}$) and lower than those found in a previous study at this site (CT = 0.013 $days^{-1}$; NT = 0.008 $days^{-1}$) (Hendrix et al., 1987). Using the following equation:

$$\text{estimated } {}^{14}\text{CO}_2 = \frac{\text{input of } {}^{14}\text{C from litter}}{(1 - \text{microbial production efficiency})},$$

the production efficiency was adjusted until the estimated $^{14}CO_2$ agreed with the observed $^{14}CO_2$.

3. Results

3.1. Root-derived C plots

For the dates sampled in the root-derived C plots, 33–55% of the applied label was incorporated into the above-ground biomass (mean of all dates was 38.2% in CT and

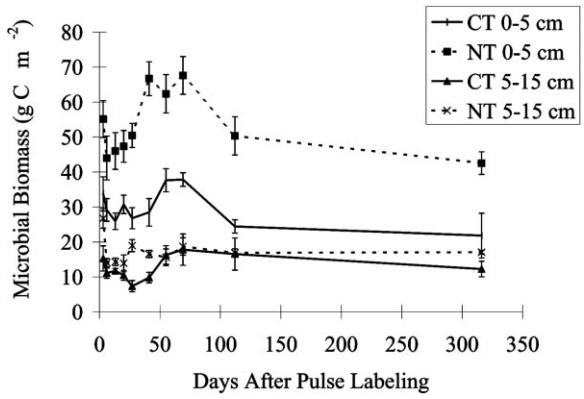

Fig. 1. Total microbial biomass in root-derived C plots. CT, conventional tillage; NT, no tillage; 0–5 and 5–15 cm refer to soil depth increment. Vertical lines represent standard errors.

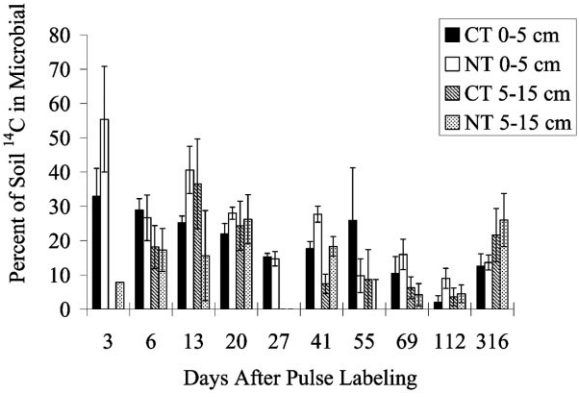

Fig. 2. Percent of soil ^{14}C in microbial biomass in root-derived C plots. Legend as in Fig. 1. Vertical lines represent standard errors.

45.5% in NT) and 5–11% into the roots (mean of all dates was 7.0% in CT and 5.6% in NT). There was no significant tillage or temporal trend on above-ground incorporation or on allocation of label to the roots. A higher percentage of labeled roots was found in the 0–5 cm depth than in the 5–15 cm depth for both tillages (total root biomass followed the same trend) (Kisselle et al., 1999).

Total microbial biomass C was higher in NT than in CT soil during the growing season (Fig. 1). Between 0.2 and 2.4% of the label applied was found in the microbial biomass on any sampling date (mean for all dates was 0.8% for CT and 1.0% for NT). There was no effect of tillage on labeled microbial biomass hence there was a higher specific activity of the CT microbial biomass.

Total soil organic C (SOC) did not change significantly over the course of the study. SOC was higher in NT than in CT for the 0–5 cm depth (44.4 vs 34.9 g C kg soil^{-1} over all dates), but there was not a tillage difference for the lower depth. Three percent of the applied label was recovered in the SOC, and of this, more was in the 0–5 cm depth than in the 5–15 cm depth. SOC-^{14}C at either depth interval or for the combined depths was not significantly different between tillage treatments. The proportion of soil ^{14}C in microbial biomass was highest in the NT 0–5 cm samples (9–55%) (Fig. 2). The microbial component of the soil ^{14}C decreased until the spring sampling on day 316.

Soil respiration followed the same pattern as microbial biomass, with a tillage effect on total, but not labeled, soil respiration. Total soil respiration was significantly higher in NT than in CT plots (96.0 vs 73.5 mg CO_2–C m^{-2} h^{-1} over all dates), but there was not a tillage effect on the cumulative percentage of $^{14}CO_2$ respired. Only 1.7% of the applied label could be accounted for by cumulative labeled respiration after 55 days (Table 1).

Root exudates estimated from microbial biomass ^{14}C did not significantly differ between tillage treatments (Table 2). CT and NT root exudates were ca. 2–3% of the applied label, using an assumed 64% production efficiency, and ca. 8–13% of the applied label using an assumed 15% efficiency. Estimates based on the $^{14}CO_2$ measurements were one to two orders of magnitude smaller than those based on microbial biomass ^{14}C.

Root:shoot ratios of dry weight and of specific activities did not differ due to tillage (Table 3).

3.2. Litter-derived C plots

There was more total POM in the NT plots than in the CT plots before (day 0), and after labeled-litter additions (Fig. 3). POM in both tillage treatments increased after litter addition and slowly decreased over time. There was a depth effect in NT but not in CT. There was not a tillage effect on total amount

Table 1
Percentage of applied label recovered in root-derived C plots 3, 6, and 55 days after pulse labeling. Means of three replicates with standard errors in parentheses. CT, conventional tillage; NT, no tillage; ND, not determined

	3 days		13 days		55 days	
	CT	NT	CT	NT	CT	NT
Above-ground biomass	ND	ND	41.0 (8.4)	44.8 (8.1)	39.4 (5.9)	38.9 (9.6)
Roots	6.4 (3.2)	5.7 (1.2)	6.2 (0.8)	7.0 (1.7)	6.6 (2.6)	5.4 (2.5)
Microbial biomass	1.2 (0.4)	2.4 (0.9)	1.1 (0.03)	1.3 (0.09)	1.0 (0.2)	0.4 (0.1)
Non-microbial SOC	3.9 (0.4)	2.6 (0.7)	3.7 (0.3)	3.5 (0.4)	1.9 (0.7)	3.8 (0.5)
Cumulative soil respiration	0.8 (0.04)	0.9 (0.01)	1.3 (0.2)	1.3 (0.05)	1.7 (0.3)	1.7 (0.1)
Total % recovered	ND	ND	53.3	57.9	50.6	50.2

Table 2
Estimates of percent applied label recovered in root exudates based on Eqs. 1 and 2 (see text). Production efficiencies were taken from van Veen et al. (1985, 1989) when C is limiting (64%) and when nutrients are limiting (15%). CT, conventional tillage; NT, no tillage

Production efficiency	Based on 0–5 cm microbial biomass ^{14}C at day 3		Based on CO_2-^{14}C at day 3	
	CT	NT	CT	NT
64%	1.83 (0.59)	3.02 (1.17)	0.065 (0.006)	0.066 (0.009)
15%	7.81 (2.50)	12.88 (4.99)	0.027 (0.003)	0.028 (0.004)

Table 3
Root:shoot ratios of dry weight and C-14 of maize in root-derived C plots. Means reported with standard errors. CT, conventional tillage; NT, no tillage; ND, not determined

Days after pulse labeling	Root dry weight: shoot dry weight		Root C-14 specific activity: shoot C-14 specific activity	
	CT	NT	CT	NT
6	ND	ND	1.03 (0.08)	1.17 (0.16)
13	0.118 (0.006)	0.147 (0.040)	2.88 (0.85)	2.13 (0.44)
20	0.122 (0.016)	0.257 (0.050)	3.17 (0.46)	2.88 (0.58)
27	0.191 (0.031)	0.202 (0.034)	ND	ND
41	0.182 (0.020)	0.198 (0.058)	ND	ND
55	0.444 (0.198)	0.187 (0.075)	ND	ND
69	0.363 (0.202)	0.316 (0.057)	ND	ND

of labeled POM over the 0–15 cm interval (data not shown), but there was a trend for more labeled POM in the 0–5 cm depth than the 5–15 cm depth, especially in the NT plots (18.1 vs 3.5 μg ^{14}C m^{-2} over all dates).

Total microbial biomass C showed tillage effects, with higher standing stocks in NT than in CT in upper depths but similar standing stocks at lower depths (Fig. 4). Plowing and the addition of litter increased total microbial biomass in CT. The percentage of litter-applied ^{14}C recovered in microbial biomass averaged 4.8% in CT plots and 3.5% in NT plots over all sample dates. The amount of ^{14}C in microbial biomass did not show consistent tillage or depth effects, but microbial biomass ^{14}C specific activity was greater in CT than in NT due to higher total microbial biomass C in NT (Fig. 5). The efficiency for the microbial utilization of labeled litter over 97 days was 0.26 for CT and 0.03 for NT.

There was a trend toward higher total soil respiration in NT than in CT (32.9 vs 23.2 mg CO_2–C m^{-2} h^{-1} over all dates) and higher cumulative respired $^{14}CO_2$ in NT (Table 4). Specific activity of ^{14}C in soil respiration was higher in CT than in NT for the first 53 days after litter addition (Fig. 6) but was higher in NT after this date.

A tillage effect on total SOC was present only in the 0–5 cm depth (47.5 vs 36.0 g C kg soil^{-1} in NT vs CT). There was a tillage effect (CT > NT) and a depth effect (0–5 > 5–15 cm) on the percent label recovered in SOC. Of the applied label measured in SOC for both depths, the mean for all dates in CT was 41.6% while NT was only 20.8%. CT

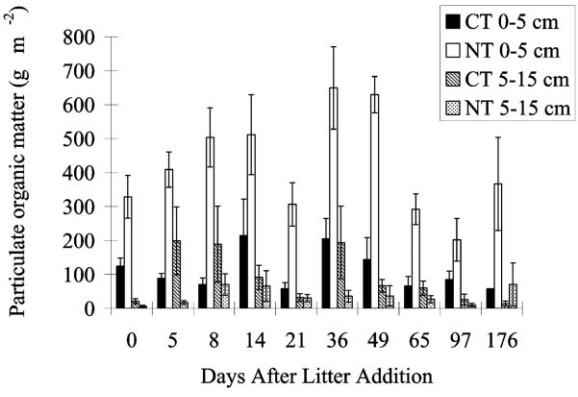

Fig. 3. Ash-free dry weight of particulate organic matter in litter-derived C plots. Legend as in Fig. 1. Vertical lines represent standard errors.

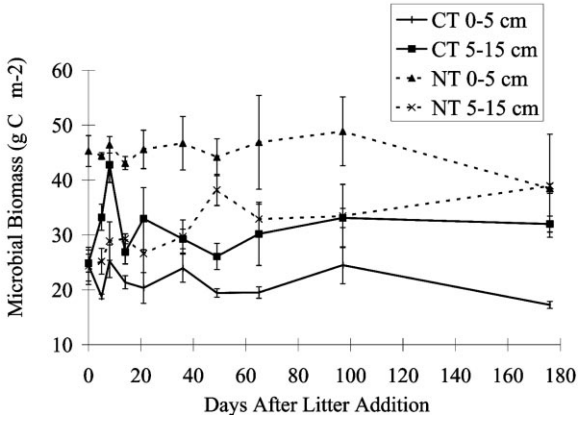

Fig. 4. Total microbial biomass in litter-derived C plots. Legend as in Fig. 1. Vertical lines represent standard errors.

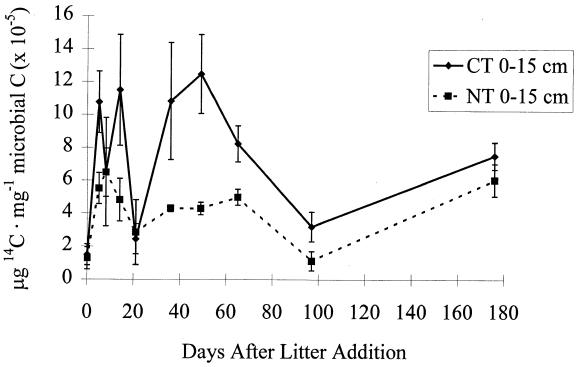

Fig. 5. Specific activity of microbial biomass over both depths in litter-derived C plots. Legend as in Fig. 1. Vertical lines represent standard errors.

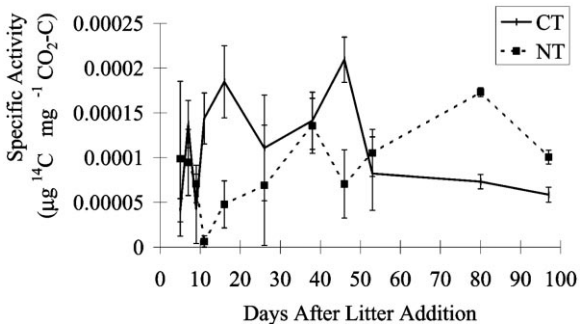

Fig. 6. Soil respiration specific activity in litter-derived C plots. Legend as in Fig. 1. Vertical lines represent standard errors.

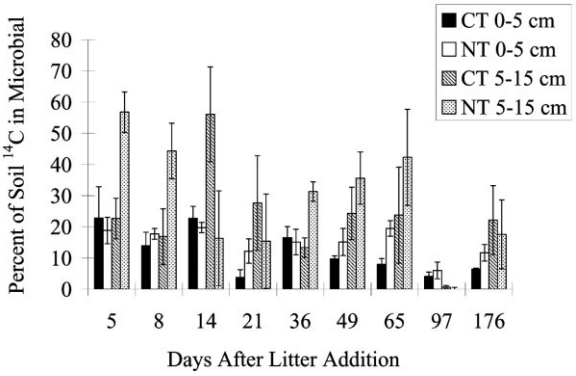

Fig. 7. Microbial percentage of soil ^{14}C in litter-derived C plots. Legend as in Fig. 1. Vertical lines represent standard errors.

plots at both depths had an initial increase of labeled SOC shortly after incorporation of the labeled litter. The upper depth of NT, however, had a relatively slower increase over the study. By spring the amount of labeled SOC in the 0–5 cm depth of both tillages was not significantly different. The percentage of SOC ^{14}C that was recovered in microbial biomass was often highest in the lower soil depth, frequently NT 5–15 cm (Fig. 7).

4. Discussion

4.1. Root-derived C plots

Higher levels of available C and enhanced physical environmental conditions found in NT have been linked with higher total microbial biomass and soil respiration compared to CT (Doran, 1980; Phillips and Phillips, 1984; Hendrix et al., 1988). This study agreed with these findings and values were in the same range for soil C, microbial C, and respiration rates for both tillage treatments. There is an apparent contradiction with the NT soil having higher soil respiration than CT soil and yet accumulating more C than CT soil. The peak of soil respiration associated with plowing the CT soil accounts for higher losses of C from the CT soil despite CT soil respiration being lower than that of NT soil the rest of the year (Hendrix et al., 1988).

Soil respiration ^{14}C in the root-derived C plots was probably underestimated. Label distribution to shoots, roots, microbial biomass, and soil was similar to that found by Liljeroth et al. (1990) with two varieties of wheat. Yet, while they had measured a cumulative 17.5–25.9% of the label from soil respiration after 55 days, we can account for only 1.6% by day 55. In our study soil respiration was measured adjacent to, not directly above, the rhizosphere. Contributions to labeled respiration would thus come primarily from rhizo-microbial respiration of lateral maize roots in the soil near the respiration chambers. Respiration estimates made from standing stock of labeled microbial biomass using production/biomass and production/respiration ratios (Hendrix et al., 1987) and converting this labeled microbial respiration estimate to labeled rhizo-microbial respiration (Cheng et al., 1993) gave instantaneous estimates

Table 4
Percentage of applied labeled recovered in litter-derived C plots 5 and 97 days after litter addition. Means of three replicates with standard errors in parentheses. CT, conventional tillage; NT, no tillage

	5 days		97 days	
	CT	NT	CT	NT
POM	37.9% (11.6%)	49.7% (17.0%)	29.8% (15.6%)	3.2% (1.5%)
Microbial biomass	6.8% (1.4%)	3.9% (1.0%)	1.7% (0.6%)	1.0% (0.5%)
Non-microbial SOC	37.9% (8.7%)	9.9% (4.0%)	67.5% (14.6%)	28.9% (8.5%)
Cumulative soil respiration	0.7% (0.4%)	2.7% (2.4%)	12.5% (2.8%)	16.3% (1.6%)
Total % recovered	83.4%	66.2%	111.4%	49.3%

from 1–10% of applied label, strengthening the argument that labeled soil respiration was underestimated. Further evidence is the discrepancy between the estimate of root exudates based on the microbial biomass ^{14}C and those based on the $^{14}CO_2$ (Table 2).

Minirhizotron observations by Cheng et al. (1990) found that sorghum (*Sorghum bicolor*) root distribution differed due to tillage: NT had higher root densities closer to the soil surface (0–5 cm) and at very deep depths (>60 cm), while CT had higher root densities in the 5–60 cm depth. Although this trend was not shown with either the ash-free dried weight (AFDW) of roots or the amount of labeled root in the present study, there was no correlation between the minirhizotron data and soil core estimates of root density in the previous research. Haynes and Beare (1997) found a linear relationship between root-length, root mass and rhizodeposition, and microbial C for non-leguminous crops. If tillage differences in root distribution (and subsequent rhizodeposition) had occurred in our study, they were not detected by differences in labeled soil or microbial biomass at the depths sampled.

Root exudation calculations based on $^{14}CO_2$ were much lower than estimates based on microbial biomass ^{14}C (Table 2). This is attributed to the underestimation of soil respiration, as described above. Estimates of root exudation based on microbial biomass ^{14}C agree with previous studies when a production efficiency of 15%, but not 64%, is used (Helal and Sauerbeck, 1984; Haller and Stold, 1985; Johansson, 1992). This suggests that other factors, such as nutrient availability, may be limiting microbial assimilation of root exudates. Limiting nutrients, specifically nitrogen, have been shown to lower the microbial utilization of root-derived C in the soil (van Veen et al., 1989).

Although the percentage of applied label distributed to the microbial biomass was similar to that of other studies (Liljeroth et al., 1990; Martens, 1990), the proportion of microbial biomass using root-derived C (3.4×10^{-6}% for CT; 2.6×10^{-6}% for NT) was much less (Qian et al., 1997). Rapid utilization and turnover of root-derived C by microorganisms after labeling but before the first sampling may account for the disparity. Xu and Juma (1993) found that ^{14}C in the soil was highest 3.5 h after labeling and declined after 5 days to a level which remained constant for the next 62 days of the study. A subsequent field study at our site with earlier sampling (26 h after pulse) still found only $1.02–1.69 \times 10^{-5}$% of total microbial biomass being labeled (unpublished data). Microbial biomass associated with the bulk soil may have become mixed with rhizospheric microbial biomass, decreasing overall microbial specific activity. This assumes that non-rhizospheric microorganisms were not labeled because they were either not active or were using different C sources (i.e. litter, soil organic matter). The small proportion of microbial biomass found to be labeled could also have been an artifact of the sample preparation for fumigation extraction. Roots and particulate organic matter were removed from the soil sample before exposure to chloroform to reduce the contribution of C and ^{14}C from lysed plant cells. Although this prevented an overestimate of microbial C and ^{14}C, it may have also underestimated the microbial contribution since these are sites of high microbial activity (Beare et al., 1995). This same caveat applies to measurements of labeled microbial biomass in litter-derived C plots (discussed below). If the labeled microbial biomass was underestimated, the estimates for root exudates and soil respiration based on the biomass will also be low.

The microbial component of total SOC-^{14}C tended to be greater in the NT 0–5 cm soil samples even though SOC in CT 0–5 was more highly labeled overall. This indicates that C turned over faster through the CT microbial biomass with microbially-processed ^{14}C remaining in the soil.

The lack of difference between CT and NT in the label found in microbial biomass, soil respiration, and soil, indicates that the root-derived C was quickly and similarly utilized by microorganisms in both tillage treatments. Similarly, van Gestel et al. (1996) found maize plant extract was readily and equally available to microorganisms associated with different particle-size fractions and that the net utilization efficiencies of these microorganisms were similar. This contradicts the hypothesis that microorganisms in CT will use less of the root-derived C in the presence of litter-derived C in the plow layer during the growing season (Holland, 1995). It is likely that a labile C source would be preferentially used by microorganisms in either tillage treatment. Although different plant species have been found to influence rhizospheric microbial C utilization (Grayston et al., 1998), the same plant species under different management regimes had similar rhizospheric microorganisms (Buyer and Kaufman, 1996); no differences were found in total counts, diversity, or evenness of corn rhizosphere bacteria or fungi when comparing a conventional corn-soybean rotation with low-input systems. Although previous research indicates different microbial communities associated with litter-derived C inputs in NT and CT (Doran, 1980; Beare et al., 1992), the rhizosphere microorganisms in NT and CT may be more similar in composition or, at least, in function with regard to utilization of root-derived C.

4.2. Litter-derived C Plots

Although POM did not show a clear difference between tillage treatments with respect to C dynamics, the higher percentage of label recovered in the soil and microbial biomass, and the higher initial specific activity of soil respiration in the CT plots suggest faster turnover of the litter in the tilled plots. SOC was more highly labeled in the CT plots, where residues were incorporated, than in the NT plots. Holland and Coleman (1987) found similar results for the microbial biomass, which they attributed to a larger microbial pool or one which turned over more quickly in CT soil. In our study, total microbial biomass was smaller in CT than in NT,

but the more highly labeled SOC in CT plots was due to more highly labeled microbial biomass-C and non-microbial biomass-C, indicating higher turnover of litter-derived C through the microbial biomass in CT.

van Veen et al. (1989) found that low nutrient availability may limit microbial utilization of organic substrates. The difference in the efficiencies of the microbial utilization in the litter-derived C plots may be attributed to a lower nutrient availability in NT than in CT soils. Soil nutrient content was not explicitly measured in this experiment. Although soil structure and texture have been cited to affect microbial efficiency (van Veen et al., 1989) this was controlled for by having both CT and NT treatments on the same soil.

The specific activity of soil respiration from CT plots was initially higher, but, by late winter, fell below that of NT plots. This is consistent with faster decomposition of the incorporated plant residues in CT and slower decomposition of litter on the surface of NT.

The proportion of soil organic ^{14}C in microbial biomass was significantly higher for the NT 5–15 cm soil samples for several sample dates. Fungal translocation has been suggested to move C from surface litter to underlying soil (Holland and Coleman, 1987; Zhang and Hendrix, 1995). Soluble carbon may also be carried from the litter by mass flow through macropores (worm burrows or old root channels) which are more prevalent in NT soils. Earthworms actively pulling residues into burrows would also allow microorganisms in the lower depth to access labeled residues and casts.

A total of 45–65% of the applied label was recovered in the pools measured in the root-derived C plots (Table 1). This does not include estimates of the above-ground plant respiration (i.e. directly from plant leaves). Ryle and Powell (1974) found that 25% of assimilated ^{14}C was respired directly from photosynthesizing maize leaves in the first 24 h and that this contributed more than 90% of the $^{14}CO_2$ respired from the plant. By including a similar respiratory loss in our budget, our total ^{14}C recovery increase to 60–90% for the root-derived C treatments. There was no difference in recovery of the label between tillage treatments. Over all dates sampled, the recovered label summed for all measured pools in the litter-derived C plots was 28–134% for CT and 36–110% for NT (Table 4 shows these for days 5 and 97). Much of this variability was due to the spatial heterogeneity of the applied labeled litter.

Acknowledgements

This research was completed with support from the National Science Foundation. Appreciation is expressed to Betty Weise for technical, field, and lab assistance. Thanks to Natalie Hyslop and Mark Witcher for sample processing.

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