Soil Biol. Biochem. Vol. 22, No. 6, pp. 781–787, 1990
Printed in Great Britain.

0038-0717/90 $3.00 + 0.00

EFFECT OF LIVING ROOTS ON SOIL ORGANIC MATTER DECOMPOSITION

WEIXIN CHENG and DAVID C. COLEMAN
Institute of Ecology, University of Georgia, Athens, GA 30602, U.S.A.

(*Accepted* 20 *March* 1990)

Summary—Published information is contradictory about the inhibitory or stimulatory effect of living roots on soil organic matter decomposition. In this study, ^{14}C-labelled rye straw was exposed in fertilized or unfertilized soil with or without plants (winter rye, *Secale cereale*) for 49 days under semi-controlled conditions. Our objective was to study the effect of roots on soil organic matter mineralization under different mineral nutrient conditions. The planted treatment had a higher $^{14}CO_2$ loss and a higher efficiency of ^{14}C-labelled material utilization by microorganisms. Fertilization decreased $^{14}CO_2$ loss. Percent ^{14}C in microbial biomass was positively correlated with percent ^{14}C respired. Total microbial biomass, ^{14}C-labelled microbial biomass and total ^{14}C remaining of the rhizosphere soil were higher compared to bulk soil. Living roots had a stimulatory effect on soil organic matter decomposition due to the higher microbial activity induced by the roots. This stimulatory effect was reduced by application of fertilizer.

INTRODUCTION

Contradictory data exist in the literature about the effects of living roots on soil organic matter decomposition. Decomposition of labelled plant material is markedly lowered in the presence of cultivated plant cover or in natural grasslands, when compared to bare soil controls due to the difference of the physical environment between the plant covered soil and the fallow soil (Fuhr and Sauerbeck, 1968; Shields and Paul, 1973; Jenkinson, 1977). During laboratory experiments under controlled conditions, Reid and Goss (1982, 1983) and Sparling *et al.* (1982) observed that when ^{14}C-labelled plant material was decomposed in soil planted with maize, ryegrass, wheat or barley, $^{14}CO_2$ release from the soil was reduced compared to bare soil controls. They surmised that this negative effect of living roots on soil organic matter decomposition was both due to root uptake of organic C and the competition between the roots and the rhizosphere microflora for substrates. In contrast Helal and Sauerbeck (1984, 1985, 1986, 1987) reported a stimulatory effect of living roots on soil organic matter decomposition based on their laboratory experiments with separate root zone techniques. They suggested that the breakdown of soil aggregates and the stimulation of rhizosphere microflora were the causes of this phenomenon. Sallih and Bottner (1988) demonstrated in a 2 yr study that the presence of plants suppressed the decomposition of newly incorporated ^{14}C-labelled plant material during the first 200 days of decomposition and stimulated the mineralization of the ^{14}C in the soil during the latter stage compared to bare soil.

In our experiment, ^{14}C-labelled plant material was buried in fertilized or unfertilized soil with or without plants for 49 days in a semi-controlled condition. Our objective was to study the effects of living roots on soil organic matter mineralization and microbial biomass under two different mineral nutrient conditions.

MATERIAL AND METHODS

Preparation of ^{14}C-labelled rye straw

Soil was taken from a conventional tillage plot, 0–15 cm layer, in the Horseshoe Bend Research Area of the University of Georgia.

The soil is a Hiwassee series (Typic Kanudult), a well-drained sandy clay loam (66% sand, 13% silt, 21% clay, pH 6) found on a 0–2% slope. Organic C, total Kjeldahl N and available P (dilute HCl and H_2SO_4 extractable) of the soil are 1.13%, 0.11% and 57.3 $\mu g\,g^{-1}$ respectively. A complete site description and management history have been given by Groffman *et al.* (1987). The soil was sieved (<2 mm), homogenized and air-dried before the labelling started.

The labelling procedure was similar to that of Reid and Goss (1982). Briefly, 15 Mason Jars (1 l. jars) were filled with air-dried soil, each planted with a rye (*Secale cereale*) seedling, tap water added to bring the soil water content to *ca* 70% water holding capacity (WHC), and then moved to the Horseshoe Bend field and kept under natural climatic conditions, The soil water content in each jar was maintained by regular watering. The 15 rye plants were pulse-labelled with $^{14}CO_2$ by putting the jars in three closed clear plastic chambers (5 jars each) and acidifying $Na_2{}^{14}CO_3$ solution in the chamber for 24 h. The residual $^{14}CO_2$ in the chamber was absorbed overnight by introducing 200 ml 1 M NaOH solution into a beaker in each chamber. All chambers were opened the next morning after each labelling day. Each chamber had a small electrical fan to circulate the air inside the chamber. A total of 55.6 MBq was supplied on five pulses. The above ground parts of the labelled plants were harvested immediately after flowering, air-dried, then oven-dried and ground (0.4 mm). The specific activity of the ^{14}C-labelled rye straw material was 2.36 MBq g^{-1} of carbon.

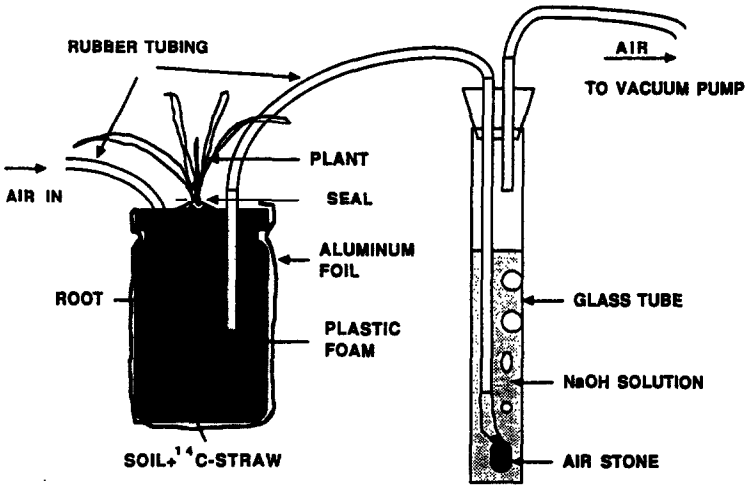

Fig. 1. Apparatus used in the experiment of decomposition of ^{14}C-labelled material (proportions not to scale).

Decomposition of the ^{14}C-labelled material

An apparatus consisting of 20 1 l. Mason jars, 20 CO_2 traps and a vacuum pump was constructed (Fig. 1). All the jars were filled with a mixture of 1230 g of air-dried soil (the same soil used in the labelling step) and 500 mg of the ground ^{14}C-labelled rye straw. Ten of the jars each received a rye (*S. cereale*) seedling and the other 10 were left unplanted. Five of the planted and five of the unplanted jars were watered with distilled water and the other five of each were treated with N–P–K fertilizer solution (20 mg N as NH_4NO_3, 8.7 mg P and 10.9 mg K as KH_2PO_4 per jar) to bring the final soil water content to 70% WHC. All seedlings of the ten planted treatments emerged 4 days after planting. Each jar was capped 5 days after planting with a rubber-sealed lid which had three holes on it. One hole was connected to rubber tubing buried in the soil as an air outlet, another hole connected to a rubber tube as an air inlet, and the hole at the centre of the lid was an opening for the seedling. After the seedling emerged the centre hole was sealed with a non-toxic, non-dryable soft paste (Handi-tak, Super Glue Corp., Hollis, N.Y.). Then all jars were moved to the Horseshoe Bend field. Each air outlet was connected with a CO_2 trap containing 50 ml 1 M NaOH solution, and all the air outlets of the CO_2 traps were connected to the vacuum pump. Atmospheric air was drawn continuously through the soils and the CO_2 traps at an air flow rate *ca* 80 ml min^{-1} controlled by screw clamps. The CO_2 trap consisted of 25 × 2.5 cm dia test tube and an air stone connected at the tip of the air inlet tube. The CO_2 trapping efficiency was >99%. This CO_2 trapping method has been described by Cheng and Coleman (1989). The NaOH solution in the traps was replaced every 1 or 2 days by changing the test tube and the solution together. Radioactivity of the solution was tested by liquid scintillation counting.

The soil water status of each jar was checked by weighing and watering with distilled water every 2–5 days during the early period of growth and each day during the latter part of the experiment when air temperatures and transpiration rates were higher. Calculated soil water contents and air temperatures during the whole experiment period are shown in Table 1.

The experiment ended after 49 days of exposure in the field. Plants were cut at the base, air-dried under a fumehood and then oven-dried. Rhizosphere soil was obtained by collecting the soil adhering to the roots after gently shaking the whole root system of each plant 5 times. Then the soil in each jar was sieved (<2 mm) and homogenized. Roots were hand picked and washed in tap water. All visible particles on the roots were removed by forceps. The washed roots were air-dried and then oven-dried. Rhizosphere and bulk soil samples were put into double plastic bags, sealed tightly and stored in a refrigerator (2°C).

Table 1. Days of incubation (Day), daily $^{14}CO_2$ evolution rate ($^{14}CO_2$-R), average air temperature (T) (data from a weather station two miles away from the field site), and soil water content (SWC) (calculated assuming a linear decrease between any two watering dates) during ^{14}C-labelled rye straw decomposition in fertilized (F) or unfertilized (UF) soil with (P) or without plant (UP)

	T (°C)	SWC (% w/w)		$^{14}CO_2$-R (Bq·jar^{-1}·day^{-1})			
Day	All	P	UP	P–F	P–UF	UP–F	UP–UF
1	17.5	15.5	16.2	480	527	453	470
2	15.8	15.0	16.1	459	447	386	476
3	13.6	14.5	16.0	344	388	324	345
10	18.9	14.0	15.0	358	364	313	370
12	20.8	13.5	14.7	378	390	380	426
14	20.8	13.0	14.4	195	203	223	240
16	21.4	12.2	14.1	233	218	299	359
18	22.8	11.5	13.8	166	141	259	294
20	23.6	10.6	13.5	132	110	243	270
22	18.9	16.2	13.2	293	335	208	232
23	20.3	15.3	13.1	265	327	183	217
25	23.6	13.5	12.8	231	262	192	224
27	23.1	11.9	12.7	214	236	209	230
29	20.0	9.6	12.4	98	106	120	136
31	19.7	8.7	12.1	78	70	122	140
33	24.4	7.9	16.2	96	85	184	199
35	25.6	16.2	15.8	278	308	159	172
37	25.3	13.8	15.5	280	274	166	176
39	19.2	11.3	14.9	221	203	110	117
41	23.9	16.2	14.2	190	223	123	128
43	27.5	12.9	13.5	218	231	144	156
45	21.4	12.5	12.8	153	177	90	95
47	21.9	12.1	12.2	152	176	87	102
49	24.4	12.0	11.5	135	182	101	107

Table 2. A budget of ^{14}C-labelled rye straw after 49 days of decomposition in fertilized or unfertilized soil with or without plants

	Plant[1]			Fertilizer[2]		
Components	P	NP	SF[3]	F	NF	SF
Respired	38.88 (2.08)	31.82 (2.76)	**	35.51 (4.57)	35.19 (4.33)	
In soil MB[4]	16.65 (1.26)	12.58 (1.25)	**	14.90 (2.50)	14.33 (2.43)	
In soil	112.46 (10.1)	109.9 (18.3)		118.4 (11.5)	104.0 (13.9)	*
Total remaining in soil	129.11 (9.41)	122.5 (18.6)		133.3 (11.1)	118.3 (14.5)	*
In plant	0.16 (0.07)	0		0.09 (0.11)	0.07 (0.08)	
Total recovered	168.2 (9.08)	154.3 (19.6)	*	168.9 (12.5)	153.6 (16.9)	*

Numbers are means of 10 replicates with 1 SD in parentheses (mg C jar^{-1}).
[1]P = planted; NP = not planted.
[2]F = fertilized; NF = not fertilized.
[3]SF = significance by ANOVA; * = $P < 0.05$; ** = $P < 0.01$.
[4]Microbial biomass-C in the soil.

Determination of microbial biomass-C

Total and ^{14}C microbial biomass-C were measured using the fumigation–incubation method (Jenkinson and Powlson, 1976). The soil sample size for the microbial biomass testing was 50 g fresh weight for the bulk soils and 8 g fresh weight for the rhizosphere soils. Each soil sample was put into a 100 ml glass beaker and fumigated with alcohol-free $CHCl_3$ for 48 h, and subsequently degassed under vacuum and room air 6 times to remove the $CHCl_3$ residue, and reinoculated with 0.5 g fresh soil from the same source. The water content of both fumigated and unfumigated soils was adjusted to 60% WHC. Each beaker with either fumigated or unfumigated soil was put into a Mason jar with 10 ml of water at the bottom and a 50 ml beaker with 25 ml of either 0.5 M or 0.1 M NaOH solution, for bulk soil and rhizosphere soil respectively. Then the jars were closed tightly, and kept in a dark cabinet for 10 days. Then the NaOH solution in each jar was tested for radioactivity by liquid scintillation counting and titrated with either 0.2 M or 50 mM HCl for bulk soil and rhizosphere soil respectively. Total and ^{14}C biomass-C were calculated from the amount of CO_2 released during the 10 day period from fumigated soil minus that from unfumigated soil, taking $K_c = 0.41$ (Anderson and Domsch, 1978).

Plant and soil analyses

Remaining ^{14}C in the soil was determined by the dry combustion method using an OX-300 Biological Oxidizer (R. J. Harvey Instrument Co., Hillsdale, N.J.). Before combustion, 5 g of bulk and rhizosphere soil were dried on a slide dryer (85°C) under a fumehood for 24 h and then oven-dried (60°C) for at least 48 h. Three replicates of *ca* 1 g dry soil sample from each field replicate were combusted (900°C). CO_2 from the combustion chamber was trapped in a 10 ml ethanolamine scintillation fluid and counted by liquid scintillation. An average of three laboratory replicates was used to represent the value of a field replicate. All results were corrected for trapping errors and counting efficiency determined by internal standards.

RESULTS

We calculated a budget of ^{14}C-labelled material applied to the soil (Table 2). The presence of plants induced a significant net increase of ^{14}C loss in the form of $^{14}CO_2$ and ^{14}C-labelled microbial biomass compared to the unplanted treatment. Fertilized treatments had significantly higher total ^{14}C remaining in the soil compared to the unfertilized treatments. The planted treatment and the fertilized treatment both had significantly higher total ^{14}C recovered by the end of the experiment compared to the unplanted and the unfertilized. The relative distribution of the total ^{14}C recovered in all components was calculated and expressed as a proportion of total ^{14}C-labelled material recovered at the end of the experiment (Table 3), i.e. the sum of amount respired, soil residue and amount in the plants. All significant treatment effects presented in Table 2 were also found in Table 3. The ^{14}C remaining in the soil represented 76.7 and 79.2% of the total ^{14}C added with or without plants, respectively. Application of fertilizer reduced ^{14}C loss. The differences between the two treatments were 2.1%, significant at the $P < 0.05$ level. Analysis of variance indicated no significant plant by fertilizer interactions in terms of ^{14}C loss as $^{14}CO_2$, total remaining in soil and in soil microbial biomass.

Table 3. Distribution of ^{14}C-labelled rye straw after 49 days of decomposition in fertilized or unfertilized soil with or without plants

	Plant[1]			Fertilizer[2]		
Components	P	NP	SF[3]	F	NF	SF
% Respired	23.19 (1.80)	20.84 (2.50)	*	21.04 (2.40)	22.98 (2.17)	*
% In soil MB[4]	9.94 (1.08)	8.24 (1.03)	**	8.84 (1.44)	9.34 (1.28)	
% In soil	66.77 (2.62)	70.93 (3.47)	*	70.07 (3.71)	67.63 (3.39)	
% Total remaining in soil	76.71 (1.77)	79.16 (2.50)	*	78.90 (2.41)	76.97 (2.20)	*
% In plant	0.097 (0.04)	0		0.055 (0.07)	0.042 (0.05)	

Numbers are means of 10 replicates with 1 SD in parentheses (% of recovered).
[1]P = planted; NP = not planted.
[2]F = fertilized; NF = not fertilized.
[3]SF = significance by ANOVA; * = $P < 0.05$; ** = $P < 0.01$.
[4]Microbial biomass-C in the soil.

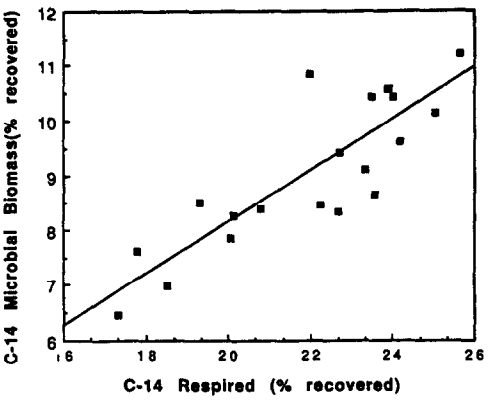

Fig. 2. Linear correlation between percent ^{14}C respired and percent ^{14}C in the soil microbial biomass after 49 days of decomposition of ^{14}C-labelled material in fertilized or unfertilized soil with or without plants. The regression equation is: Y (MB%) = 1.2707 + 0.4706 X (R%) ($r = 0.85$, $n = 20$, $P < 0.001$).

The amount of ^{14}C taken up by the plants was small, only about 0.1% of the total ^{14}C added or 0.4% of ^{14}C respired. Of the ^{14}C taken up by plants 64% was found in roots and 36% in shoots. The proportion of ^{14}C in soil microbial biomass in planted treatments was significantly higher than in unplanted treatments ($P < 0.01$).

Efficiency of ^{14}C utilization by the soil microorganisms was calculated based on percent microbial biomass produced per unit of ^{14}C-labelled material used. This is equal to ^{14}C microbial biomass divided by the sum of ^{14}C respired and the ^{14}C microbial biomass, multiplied by 100%. The efficiency of ^{14}C utilization by microorganisms was 29.98% for the planted treatment and 28.33% for the unplanted (difference significant at $P < 0.05$).

Percent ^{14}C respired was significantly correlated with percent ^{14}C in the soil microbial biomass, $r = 0.85$, $n = 20$, $P < 0.001$ (Fig. 2). The slope was equal to 0.47, which represents a growth efficiency, or amount of growth per unit of substrate respired (Payne and Wiebe, 1978).

A linear regression analysis was adopted to analyse daily $^{14}CO_2$ evolution data using days of incubation (X_1), average air temperature (X_2) (°C), soil water content (X_3) (% w/w) and fertilization (X_4) and plant (X_5) factors as independent variables (Table 4). For linearization, the dependent variable, daily $^{14}CO_2$ evolution rate (Y) (Bq jar^{-1} day^{-1}), was corrected for the total ^{14}C added and then natural log-transformed in the regression analysis, and percent water content was arc-sine–square–root transformed too. The qualitative variables, plant and fertilizer, were given the values of either (1) or (0) corresponding the planted (1) or unplanted (0) and fertilized (1) or unfertilized (0). The regression function:

$$Y = 1.986 - 0.025\,X_1 + 0.032\,X_2 + 0.151\,X_3 - 0.118\,X_4 + 0.255\,X_5$$

was significant, $r = 0.93$, $n = 92$, $P < 0.001$. The coefficients of the five independent variables were all significant ($P < 0.05$). The presence of plants increased the intercept of the regression function, or increased the rate of ^{14}C loss. Fertilization of the soil reduced the intercept of the function, which translated to a decreased ^{14}C loss. These results confirm the findings of the analysis of variance.

Rhizosphere soil had more ^{14}C-remaining, more ^{14}C-labelled microbial biomass and more total microbial biomass then the bulk soil in the planted treatment (Table 4). The proportion of the microbial biomass that was ^{14}C-labelled in rhizosphere soil was less than in bulk soil. The rhizosphere soil in the fertilized treatments had a higher percent labelled microbial biomass and less total microbial biomass than that of unfertilized treatments.

DISCUSSION

The amount of ^{14}C-labelled microbial biomass was linearly correlated with the amount of ^{14}C respired (Fig. 2). The presence of plants induced a higher $^{14}CO_2$ evolution rate and a higher ^{14}C-labelled microbial biomass than the unplanted treatments. This suggests a causal relationship between the stimulation of microbial growth or activity and the enhancement of soil organic matter decomposition by living roots. Helal and Sauerbeck (1986, 1987) have shown a higher microbial biomass and a higher soil organic matter decomposition in the rooted zone compared to the root-free zones. Bottner *et al.* (1988) and Sallih and Bottner (1988) have reported a lower microbial biomass and reduced soil organic matter loss during the initial 150 days of decomposition and a higher

Table 4. Comparisons of total carbon and ^{14}C-labelled carbon distribution in rhizosphere and bulk soil in the planted treatment after 49 days of decomposition with or without fertilizer

Treatment	^{14}C-remaining[1] in soil ($\mu g\,g^{-1}$)	Total MB[2] ($^{12}C + ^{14}C$) ($\mu g\,C\,g^{-1}$)	^{14}C-MB ($\mu g\,C\,g^{-1}$)	% ^{14}C-MB[3] (%)
Rhizosphere fertilized	152.4[a]* (11.33)	679.2[a] (62.75)	18.62[a] (4.46)	2.71[a] (0.43)
Rhizosphere unfertilized	148.7[a] (11.44)	847.7[c] (119.6)	18.01[a] (3.83)	2.12[c] (0.33)
Bulk fertilized	108.6[b] (5.61)	447.4[b] (62.85)	13.59[b] (1.32)	3.08[b] (0.43)
Bulk unfertilized	100.8[b] (7.76)	454.9[b] (43.15)	13.41[b] (0.76)	2.96[b] (0.21)

Numbers are means of five replicates with one standard deviation in parentheses.
[1]Total C from ^{14}C-labelled rye straw after plant roots were removed from the soil.
[2]MB = microbial biomass.
[3](^{14}C-MB/total MB) × 100.
*Numbers with the same letter are not significantly different by Duncans multiple range test ($P < 0.05$).

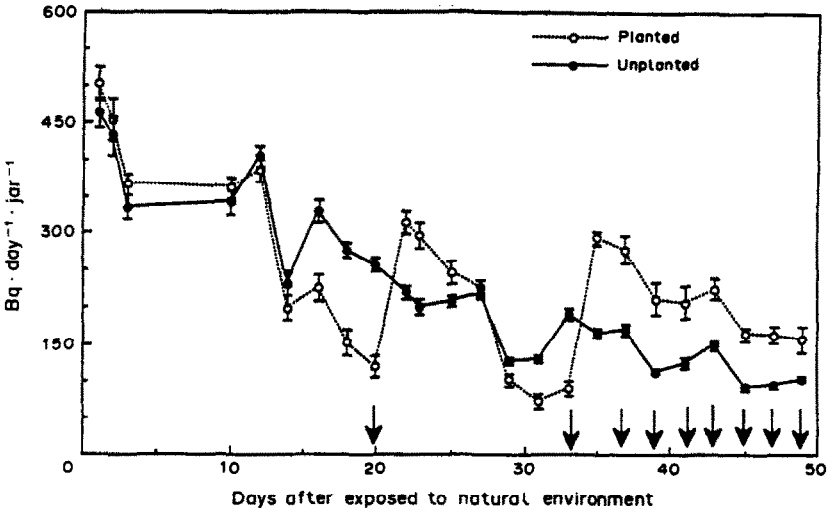

Fig. 3. Daily $^{14}CO_2$ evolution rates of planted and unplanted treatments. Arrows indicate dates of watering. Bars are 2 SE.

microbial biomass and a higher soil organic matter loss during the latter period of the experiment for the planted treatments compared to the unplanted soil. Based on the above evidence, we surmise that the response of total microbial metabolism is what determines the effect of roots on soil organic matter decomposition. If the presence of roots induces greater microbial growth, it will stimulate loss of soil organic matter. If the presence of plants reduces microbial growth, it will also reduce the loss of soil organic matter.

The effect of plants on ^{14}C loss was partially confounded with the effect of soil water condition since the presence of a plant inevitably induced greater drying of the soil between watering, especially during the latter period of the experiment when air temperature and transpiration were higher. Possibly the higher $^{14}CO_2$ evolved in the planted treatments was solely due to the repeated wet and dry cycles, so called 'Birch Effect', which have been demonstrated to enhance soil organic matter decomposition (Birch, 1958; Jager and Bruins, 1975). However, this is unlikely since more $^{14}CO_2$ evolved from the planted soil even during the early period of the experiment when the soil water conditions were almost the same for both the planted and the unplanted treatment (Fig. 3). The regression analysis also indicated that the presence of plants had a significant positive effect on decomposition of the ^{14}C-labelled material after the effect of soil moisture was included.

The presence of plants increased the efficiency of ^{14}C-substrate utilization by the soil microbes (Table 2). This result tends to support the hypothesis of Martin (1987) that the rhizosphere microbial population has a higher efficiency of C utilization than the bulk soil population. However, in our experiment, the higher efficiency of the microbes in the rhizosphere did not result in a decreased ^{14}C loss as Martin (1987) implied. On the contrary, it increased ^{14}C loss because the total metabolism of the microbial population in the presence of plants was high enough to outweigh this effect.

The regression analysis indicated that all of the five independent variables are controlling factors of soil organic matter decomposition. The relative importance of each variable may change when the set of conditions is changed. This analysis is preliminary due to the narrow range of soil water content and air temperature employed in our study.

Reid and Goss (1982) and Sparling *et al.* (1982) suggested that plant uptake of organic C was one of the primary reasons for the suppressive effect of living roots on soil organic matter decomposition. Our experiment showed little of the ^{14}C was taken up by plants (0.1% of the total ^{14}C added, 0.4% of ^{14}C respired). This result is in conflict with theirs, but in accordance with Sallih and Bottner (1988).

The higher total microbial biomass in the rhizosphere soil than in bulk soil shown in Table 4 is widely known (Hiltner, 1904; Rovira and Davey, 1974). However, the higher ^{14}C-remaining and higher ^{14}C-labelled microbial biomass in the rhizosphere are in some degree unexpected and difficult to explain. The ^{14}C budget shows a higher ^{14}C loss in the presence of plants. If the effect of the plant on ^{14}C loss was mostly due to the presence of roots and the rhizosphere effects, ^{14}C remaining in the rhizosphere should be lower assuming that there is no movement of ^{14}C-labelled material in the soil. The linear correlation between the amount of ^{14}C-microbial biomass and the amount of $^{14}CO_2$ evolved shown above should also mean that the ^{14}C remaining in the rhizosphere should be lower if the ^{14}C-labelled microbial biomass is higher. Some possible causes of these results are:

(1) the way in which the rhizosphere soil was sampled introduced some possibilities of incorrect measurements of microbial biomass due to the presence of small rootlets and root debris;
(2) there was physical, chemical or biological transportation of ^{14}C-labelled materials between the rhizosphere and the bulk soil;

(3) enhanced decomposition of ^{14}C-labelled material outside the immediate rhizosphere by plant and roots overcame the suppression effect of roots on ^{14}C decomposition in the immediate rhizosphere, resulting in a greater overall $^{14}CO_2$ evolution in the planted treatments;
(4) other unknown experimental errors.

The lowered ^{14}C specific activity of the rhizosphere microbial biomass obtained in this experiment can be explained by the dilution effect of root exudation and deposition. This dilution effect was reduced in the fertilized treatment since the specific activity of the rhizosphere biomass in the fertilized treatment was not significantly lower than the bulk soil. If the dilution was simply due to root exudation, the fertilization might have caused a lower degree of root exudation. This mechanism has been demonstrated by Turner and Newman (1984) and Turner *et al.* (1985). Presumably, as a result of lowered exudation in the fertilized treatment, the total microbial biomass of the rhizosphere soil was also lowered (Table 4).

There is a conflict between results from $^{14}CO_2$ evolution measurements and those from ^{14}C remaining in the soil. If the addition of ^{14}C had been fairly uniform and all treatments had received the same amount of ^{14}C at the beginning of the experiment, more $^{14}CO_2$ evolution should have resulted in less ^{14}C remaining in the soil for one treatment or vice versa. The results in Table 2 indicate more $^{14}CO_2$ evolved and also more ^{14}C remained in the soil for the planted treatments and the amount of total ^{14}C-labelled C recovered among different treatments is significantly different (Table 2). The exact causes of these conflicting results are unknown and need further investigation in later studies. However, there is a possibility that the amount of ^{14}C introduced at the beginning is the main cause of this recovery discrepancy due to the heterogeneity of the pulse-labelled rye straw used in this experiment. If this is correct, the relative distribution of ^{14}C in all components in terms of percent recovered is a legitimate measure of the treatment effects. This may also suggest that using more than one type of measurement is a safer approach than using one type of measurement in similar kinds of experiments.

Our study did not solve the controversy about the effect of living roots on soil organic matter decomposition, but shed more light on it. This contradiction may signal that the effects of roots on soil organic matter decomposition is two-sided (Chao *et al.*, 1988) and condition-dependent. It has been demonstrated that living roots not only exude certain amounts and types of organic substances (Rovira and Davey, 1974; Barber and Martin, 1976; Johnen and Sauerbeck, 1977; Whipps and Lynch, 1983; Merckx *et al.*, 1985, 1986), but also take up mineral nutrients, water and other substances (Krassilnikov, 1961; Fuhr and Sauerbeck, 1966; Vaughan and Ord, 1981; Okada and Kumura, 1986), and induce various changes in the rhizosphere, such as pH, nutrient availability and soil structure (Helal and Sauerbeck, 1986, 1987; Hemming, 1986; Marschner *et al.*, 1987). As is widely known, soil organic matter decomposition is controlled by many factors, including all the factors that living roots can alter. At present, studies on root effects on soil organic matter decomposition have mainly been conducted with different experimental designs under different sets of experimental conditions, For example, Helal and Sauerbeck (1984, 1986, 1987) grew maize (*Zea mays*) in pots with separate zones with homogeneously labelled maize straws mixed in the fertilized soil, whereas Reid and Goss (1982) planted maize or ryegrass (*Lolium perenne*) in smaller pots filled with soil which had been incubated with ^{14}C pulse-labelled barley (*Hordeum vulgare*) roots for 67 days and not fertilized. The amount of soil per plant was 210 g in Helal and Sauerbeck's experiments, whereas it was 344 g for Reid and Goss (1982), 8 g for Sparling *et al.* (1982), 133 g for Sallih and Bottner (1988), and 1230 g for ours. The duration of plant growth also varied from 30 days (Helal and Sauerbeck, 1986) to 2 yr (Sallih and Bottner, 1988). The types and fertilities of the soils used in these experiments were also different. All these differences in experimental conditions might have contributed to the contradictory results and make general interpretation impossible at this stage. In order to fully understand the effect of the rhizosphere on soil organic matter decomposition, further research should focus on the mechanisms of both biotic and abiotic interactions both in the rhizosphere and in the bulk soil.

Acknowledgements—We thank James Barber and Kim Hill for their laboratory assistance. We appreciate the comments of Drs D. A. Crossley Jr, Frank B. Golley, Bruce L. Haines, Peter G. Hartel, Paul F. Hendrix, David H. Wright, Joan G. Ehrenfeld and Robert W. Parmelee on the manuscript. This work was supported by a National Science Foundation grant awarded to the University of Georgia.

REFERENCES

Anderson J. P. E. and Domsch K. H. (1978) Mineralization of bacteria and fungi in chloroform-fumigated soils. *Soil Biology & Biochemistry* **10**, 207–213.

Barber D. A. and Martin J. K. (1976) The release of organic substances by cereal roots in to soil. *New Phytologist* **76**, 69–81.

Birch H. F. (1958) The effect of soil drying on humus decomposition and nitrogen availability. *Plant and Soil* **10**, 9–32.

Bottner P., Sallih Z. and Billes G. (1988) Root activity and carbon metabolism in soils. *Biology and Fertility of Soils* **7**, 71–81.

Chao W., Li R. and Chang W. (1988) Effect of root agglutinin on microbial activities in the rhizosphere. *Applied Environmental Microbiology* **54**, 1838–1841.

Cheng W. and Coleman D. C. (1989) A simple method for measuring CO_2 in a continuous air flow system: modifications to the substrate-induced respiration technique. *Soil Biology & Biochemistry* **21**, 385–388.

Fuhr F. and Sauerbeck D. R. (1966) The uptake of straw decomposition products by plant roots. In *The Use of Isotopes in Soil Organic Matter Studies*, pp. 73–83. FAO/IAEA, Brunswick-Volkenrode.

Fuhr F. and Sauerbeck D. R. (1968) Decomposition of wheat straw in the field as influenced by cropping and rotation. In *Isotopes and Radiation in Soil Organic Matter Studies*, pp. 241–250. IAEA, Vienna.

Groffman P. M., Hendrix P. F. and Crossley D. A. (1987) Nitrogen dynamics in conventional and no-tillage agroecosystems with inorganic fertilizer or legume nitrogen input. *Plant and Soil* **97**, 315–332.

Helal H. M. and Sauerbeck D. R. (1984) Influence of plant roots on C and P metabolism in soil. *Plant and Soil* **76**, 175–182.

Helal H. M. and Sauerbeck D. R. (1985) Transformation of ^{14}C labelled plant residues and development of microbial biomass in soil as affected by maize roots. *Landwirtschaftliche Forschung* **38**, 104–109.

Helal H. M. and Sauerbeck D. R. (1986) Effect of plant roots on carbon metabolism of soil microbial biomass. *Zeitschrift für Pflanzenernährung Bodenkunde* **149**, 181–188.

Helal H. M. and Sauerbeck D. R. (1987) Direct and indirect influences of plant roots on organic matter and phosphorus turnover in soil. *INTECOL Bulletin* **15**, 49–58.

Hemming B. C. (1986) Microbial–iron interactions in the plant rhizosphere: an overview. *Journal of Plant Nutrition* **9**, 505–521.

Hiltner L. (1904) Ueber neuere erfahrungen und probleme auf dem gebiet der boden-bakteriologie und unter besonderer Berucksichtigung der Grundungung und Brache. *Arbeiten der Deutschen Landwirtschafts-Gesellschaft* **98**, 59–78 (from Rovira and Davey, 1971).

Jager G. and Bruins E. H. (1975) Effect of repeated drying at different temperatures on soil organic matter decomposition and characteristics, and on the soil microflora. *Soil Biology & Biochemistry* **7**, 153–159.

Jenkinson D. S. (1977) Studies on decomposition of plant material in soil: V. The effect of plant cover and soil type on the loss of carbon from ^{14}C labelled ryegrass decomposing under field conditions. *Journal of Soil Science* **28**, 424–434.

Jenkinson D. S. and Powlson D. S. (1976) The effects of biological treatments on metabolism in soil: V. A method for measuring soil biomass. *Soil Biology & Biochemistry* **8**, 209–213.

Johnen B. G. and Sauerbeck D. R. (1977) A tracer technique for measuring growth, mass and microbial breakdown of plant roots during vegetation. *Soil Organisms as Components of Ecosystems, Ecological Bulletin (Stockholm)* **25**, 366–373.

Krassilnikov N. A. (1961) Biological factors of soil fertility. In *Soil Microorganism and Higher Plants* (English translation), pp. 204–264. Israel Program for Scientific Translation, Jerusalem.

Lynch J. M. (1982) The rhizosphere. In *Experimental Microbial Ecology* (R. G. Burns and J. H. Slater, Eds), pp. 395–411. Blackwell Scientific, Oxford.

Marschner H., Romheld V. and Cakmak I. (1987) Root-induced changes of nutrient availability in the rhizosphere. *Journal of Plant Nutrition* **10**, 1175–1184.

Martin J. K. (1987) Effect of plants on the decomposition of ^{14}C-labelled soil organic matter. *Soil Biology & Biochemistry* **19**, 473–474.

Merckx R. A., Hartog D. and van Veen J. A. (1985) Turnover of root-derived material and related microbial biomass formation in soil of different texture. *Soil Biology & Biochemistry* **17**, 565–569.

Merckx R. A., Van Ginkel J. H., Sinnaeve J. and Cemers A. (1986) Plant-induced changes in the rhizosphere of maize and wheat: I. Production and turnover of root-derived material in the rhizosphere of maize and wheat. *Plant and Soil* **96**, 85–93.

Okada K. and Kumura A. (1986) Uptake of organic matter by the roots of sweet potato: analysis of δ-^{14}C value of plants. *Plant and Soil* **91**, 209–219.

Payne W. J. and Wiebe W. J. (1978) Growth yield and efficiency in chemosynthetic microorganisms. *Annual Review of Microbiology* **32**, 155–183.

Reid J. B. and Goss M. J. (1982) Suppression of decomposition of ^{14}C-labelled plant roots in the presence of living roots of maize and perennial ryegrass. *Journal of Soil Science* **33**, 387–395.

Reid J. B. and Goss M. J. (1983) Growing crops and transformations of ^{14}C-labelled soil organic matter. *Soil Biology & Biochemistry* **15**, 687–691.

Rovira A. D. and Davey C. B. (1974) Biology of the rhizosphere. In *The Plant Root and Its Environment* (E. D. Carson, Ed.), pp. 153–204. University Press of Virginia, Virginia.

Sallih Z. and Bottner P. (1988) Effect of wheat (*Triticum aestivum*) roots on mineralization rates of soil organic matter. *Biology & Fertility of Soils* **7**, 67–70.

Shields J. A. and Paul E. A. (1973) Decomposition of ^{14}C-labelled plant material under field conditions. *Canadian Journal of Soil Science* **53**, 297–306.

Sparling G. S., Cheshire M. V. and Mundie C. M. (1982) Effect of barley plants on the decomposition of ^{14}C-labelled soil organic matter. *Journal of Soil Science* **33**, 89–100.

Turner S. M. and Newman E. I. (1984) Fungal abundance on *Lolium perenne* roots: the influence of nitrogen and phosphorus. *Transactions of the British Mycological Society* **82**, 315–322.

Turner S. M., Newman E. I. and Campbell R. (1985) Microbial population of ryegrass root surfaces: influence of nitrogen and phosphorus supply. *Soil Biology & Biochemistry* **17**, 711–715.

Vaughan D. and Ord B. G. (1981) Uptake and incorporation of ^{14}C-labelled soil organic matter by roots of *Pisum sativum* L. *Journal of Experimental Botany* **32**, 679–687.

Whipps J. M. and Lynch J. M. (1983) Substrate flow and utilization in the rhizosphere of cereals. *New Phytologist* **95**, 605–623.