Biol Fertil Soils (1994) 17:21–26

ORIGINAL PAPER

S. Bek

Mineralization of ^{14}C-labelled unripe straw in soil with and without rape (*Brassica napus* L.)

Received: 10 August 1992

Abstract Soil was amended with ^{14}C-labelled unripe straw only (C:N ratio ca. 20), with ^{14}C-labelled unripe straw plus unlabelled ripe straw (C:N ratio ca. 100) or with ^{14}C-labelled unripe straw plus glucose. Half the samples with ^{14}C-labelled straw and half the samples with ^{14}C-labelled plus unlabelled straw were cropped with rape plants. A decreased rate of mineralization of the ^{14}C-labelled straw was found in the planted soil compared with the unplanted soil. The reduction was most profound in the soil amended with both labelled and unlabelled straw, indicating that at least part of the reduction was due to competition between plants and microorganisms for mineral N. No other explanations for the decrease in mineralization in the presence of plants were found. The soil amended with glucose which simulated the effect of root exudates showed an increased rate of mineralization. Therefore, the reduction in the presence of plants was probably not due to microbial use of the rhizodeposition in favour of the labelled straw. Only a minor part of the reduction was apparently due to uptake of labelled C by the plant, as only small amounts were found in the roots and shoots at harvest. The difference in ^{14}C mineralization between treatments was not reflected in the number of bacteria in the soil at harvest. The number of bacteria, which was determined by plate counts and direct microscopy, was the same in all the soils, rhizosphere soils as well as bulk soils.

Key words Mineralization · ^{14}C-labelled unripe straw · Plant effect · Bacterial counts · Rhizodeposition

Introduction

To reduce the leaching of NO_3 from agricultural soils it is normal practice to cover the fields with plants for a considerable part of the year. This, combined with an increased incorporation of straw into the soil (burning of straw in the fields has recently been forbidden by law in Denmark), raises the question of whether the mineralization of straw is affected by living roots.

The effect of plants on the transformation of various organic matter has been studied sporadically over the last 25 years, but the published data often appear to be contradictory. In most cases there seems to be less transformation of organic matter in planted soil compared with unplanted soil (Führ and Sauerbeck 1968; Shields and Paul 1973; Reid and Goss 1982; Sparling et al. 1982; Martin 1987), but examples of the opposite tendency have been found as well (Helal and Sauerbeck 1986; Sallih and Bottner 1988).

In field experiments the reduction in organic matter decomposition in the presence of plant cover has been explained in terms of a reduction in microbial activity caused either by insufficient water (Shields and Paul 1973) or by restricted aeration (Führ and Sauerbeck 1968) in the planted soil. In greenhouse/growth chamber experiments with controlled watering and aeration, the reduction in decomposition in the presence of plants has been explained by several mechanisms, e.g., competition between the plants and the microorganisms for organic substrates (Reid and Goss 1982; Sparling et al. 1982) or use of root exudates in preference to the organic matter examined (Reid and Goss 1982). Finally, Martin (1987) argued that the decrease in decomposition of ^{14}C-labelled organic matter in planted soil was possibly more apparent than real, since the lower $^{14}CO_2$ evolution might merely be a result of highly efficient C utilization by the rhizosphere organisms compared with the organisms in the unplanted soil.

The aim of the present experiment was to study the effects of rape plants on the mineralization of ^{14}C-labelled unripe straw. Soil with no further additions was used to create a situation with a low potential for N immobilization and competition between plant roots and microorganisms, and soil with a further addition of unlabelled ripe straw was used to create a situation with a high potential for N immobilization and competition between plant roots and microorganisms.

S. Bek
Department of Soil Biology and Chemistry,
The Danish Institute of Plant and Soil Science,
Research Centre Foulum, P.O. Box 23, DK-8830 Tjele, Denmark

Materials and methods

Soil amendments and pots

A coarse sandy soil (Table 1) was collected from the upper 25 cm of an agricultural field and stored at field moisture content (70% of field capacity) until use. The soil was sieved (<2 mm), pre-incubated, and divided into three subsamples. All subsamples were amended with ^{14}C-labelled unripe barley straw cut into 1–2 mm pieces (2 mg g^{-1} soil; specific activity 93 μCi g^{-1} C, 43% C, C:N ratio 19.5). One subsample was amended only with the labelled unripe straw, one subsample was amended in addition with unlabelled ripe barley straw cut into 1–2 mm pieces (5 mg g^{-1} soil; 42% C, C:N ratio 105.0), and one subsample was amended in addition with glucose (10 mg g^{-1} soil). Fertilizer and water were added (100 μg N g^{-1} soil) to a final water content of 10.1% (90% of field capacity). The fertilizer was an NPK nutrient solution (N:P:K, 4:1:3; NO_3-N:NO_4-N, 1.5:1) with Mg, S, Fe, Mn, Mo and B (Hornum nutrient solution, Brøste Industri A/S). The soil was mixed thoroughly and polypropylene tubes (diameter 51 mm, length 155 mm, closed at the bottom with a nylon mesh) were filled with the soil at a final bulk density of 1.49 g cm^{-3}. The tubes were placed in glass pots with moist sand at the bottom. Some of the lids on the pots had a hole (diameter 20 mm) in the centre for plants (see below). The lid of each pot was also provided with two fittings to allow aeration of the pots. Nylon tubes were used for the air inlet and aluminium tubes lined with polyethylene were used for the air outlet. The nylon tubes were extended through the lids and half-way through the soil columns to allow a continuous passage of air.

Plants and incubation procedure

The rape plants (*Brasssica napus* L., summer rape, cultivar Drakkar) were pre-germinated for 3 weeks in small polypropylene tubes (one plant per tube) with loosely packed soil, making it possible to press the whole soil column out without damaging the roots. The plants were planted in the glass pots after their roots had been gently washed in distilled water. Small plastic pipes were placed around the stem bases of the plants, and these were filled with a permanent plastic mass (Terostat IX, A.J. Thurøe) to seal the pots. Half the subsamples with ^{14}C-labelled straw and half the subsamples with ^{14}C-labelled plus unlabelled straw were planted. All the subsamples with ^{14}C-labelled straw plus glucose were left unplanted. So there was a total of five treatments, each with four replicates. Treatment I, soil amended with ^{14}C-labelled unripe straw with plants; II, soil amended with ^{14}C-labelled unripe straw plus unlabelled ripe straw with plants; III, soil amended wit ^{14}C-labelled unripe straw without plants; IV, soil amended with ^{14}C-labelled unripe straw plus unlabelled ripe straw without plants; V, soil amended with ^{14}C-labelled unripe straw plus glucose without plants. A number of control plants, two of which were harvested and weighed once each week during the incubation, were planted as well.

The pots were placed in a room where the daylight was supplemented with three 400-W halogen-mercury lamps (31 500 lumen per lamp) ensuring a day length of 16 h. A minimum temperature of 15 °C was maintained by heating, but the natural daytime temperature in the room typically ranged between 20 ° and 25 °C. Moist atmospheric air, free of CO_2, was continuously led through the soil and subsequently through a CO_2 trap containing 1.5 *N* KOH. The CO_2 traps were changed and their ^{14}C contents measured by liquid scintillation counting at 3-day intervals.

The water content of the soil was adjusted once a day by injecting distilled water through the air-inlet tubes. The pots were weighed, and allowance was made for plant weight based on the control plants.

Analyses

The plants were harvested after 130 days. The shoots were cut off at the soil surface, and the roots were separated from the soil by a combination of dry- and wet-sieving (<0.5 mm). All the soil from the pots containing plants was considered to be rhizosphere soil, as the roots had thoroughly invaded the pots. The ^{14}C content of the dried, ground, and homogenized soil, sand, roots, and shoots was determined by dry combustion with a LECO induction furnace connected to a CO_2 trap containing carbosorb (Packard Institute). The $^{14}CO_2$ content was measured by liquid scintillation counting.

Colony-forming units (CFU) of bacteria were counted on a soil-extract agar. Two subsamples of 10 g soil from each sample were mixed with 990 ml diluted Winogradsky salt solution using a blender (Kenwood) for two intervals of 2 1/2 min with intervening cooling. The solutions were further diluted (10-fold), and 0.1-ml samples were spread on an agar plate (five plates per dilution level). The plates were incubated at 20 °C for 1–2 weeks. One sample of each dilution series was afterwards incubated with 2-(*p*-iodophenyl)-3-(*p*-nitrophenyl)-5-phenyl tetrazolium chloride (INT; 0.18 mg ml diluted solution^{-1}. The incubation was carried out in dark glass tubes for 20 min while shaking. Formalin was added (final concentration of formaldehyde 1.8%), and the samples were stored for direct microscopical counts. The total number of bacteria was determined by the acridine orange direct counting method according to Hobbie et al. (1977), and the number of metabolically active bacteria able to reduce INT to visible intracellular deposits of INT formazan (INT-positive bacteria) by a method modified after Tabor and Neihof (1982).

A direct extraction method was used to estimate the contents of C, ^{14}C, and N in the soil microbial biomass. Four subsamples of 30 g soil were taken from each sample and put into 330-ml flasks. The flasks were weighed, and two flasks from each sample were treated in a microwave oven, while the other two were set aside (four flasks in the oven at a time, 780 W, 3 min with rotation). After the microwave treatment the water content of the soil was adjusted by adding distilled water. The samples were shaken for 30 min with 0.5 *M* K_2SO_4 (120 ml flask^{-1}), and after filtration (Whatman no. 5) the organic C, organic ^{14}C, and total N contents of the extracts were determined. The C content was determined by ultraviolet-promoted persulphate oxidation and measurement of the CO_2 product by infrared gas analysis with a TOC Analysator (Dohrmann DC-180). The ^{14}C content was measured by liquid scintillation counting. The N content was determined with a modified Kjeldahl analysis, using a Kjel-Tec instrument. The flushes of organic C, organic ^{14}C, and total N in the extracts after microwave treatment were calculated. A K_c factor of 0.33 (Sparling and West 1988) and a K_n factor of 0.54 (Brookes et al. 1985) were used to convert values for organic C, organic ^{14}C, and total N flush to microbial C, ^{14}C, and N, respectively.

Table 1 Some characteristics of the soil

Clay (%)	Silt (%)	Fine sand (%)	Coarse sand (%)	Total C (%)	$CaCO_3$ (%)	Total N (%)	NH_4-N (ppm)	NO_3-N (ppm)	pH ($CaCl_2$)
4.1	6.1	15.1	71.8	1.95	<0.01	0.13	15.7	12.2	6.4

Soil classification: Orthic Haplohumod, coarse sand, siliceous, mesic

Statistics

Statistical calculations were performed using SAS procedures (GLMP; SAS Institute Inc. 1989).

Results

No differences in the evolution of $^{14}CO_2$ from the different treatments were observed during the first days of incubation (Fig. 1). After 8 days the total quantity of $^{14}CO_2$ evolved from the soil amended with labelled straw plus glucose was significantly larger ($P < 0.05$) than the quantities evolved from all the other soils. At this time there also was a significant difference ($P < 0.05$) between planted and unplanted soil amended with labelled plus unlabelled straw, the largest amount of $^{14}CO_2$ being released from the unplanted soil. After 11 days of incubation the total evolution of $^{14}CO_2$ from the planted and the unplanted soil amended only with labelled straw was significantly different ($P < 0.05$) as well. The largest amount of $^{14}CO_2$ was also in this case released from the unplanted soil. At this time of the incubation there was no significant difference between the two planted treatments (I and II) and the two unplanted treatments without glucose (III and IV). Twenty-three days after the start of incubation there was no difference between the total evolution of $^{14}CO_2$ from two of the treatments without plants (treatments III and IV). All other treatments were different from each other at this time ($P < 0.05$). The observed differences and similarities in the evolution of $^{14}CO_2$ from the different soils determined after 23 days persisted throughout the rest of the incubation period (Fig. 1).

No more than ca. 0.5% of the added ^{14}C was recovered in the plants at harvest, compared with a reduction in the evolution of $^{14}CO_2$ by the plants from 32 to 25 and from 31 to 18%, respectively, in the different treatments (Table 2). The total recovery of ^{14}C from the planted pots was slightly less than the recovery from the unplanted pots, and the differences were significant ($P < 0.05$) in treatments II and IV (Table 2).

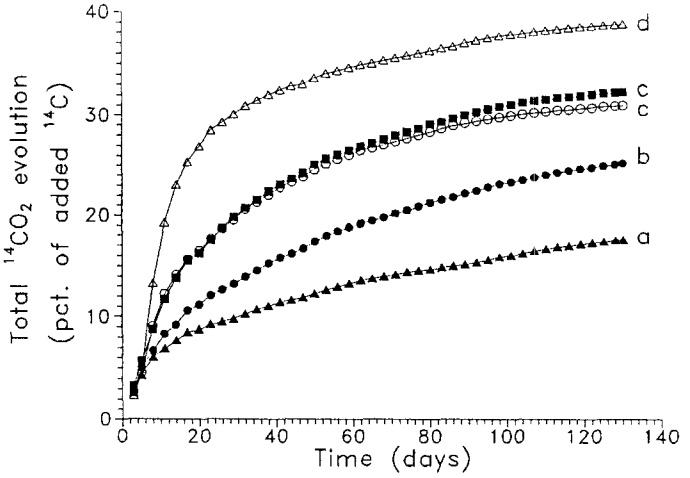

Fig. 1 Accumulated $^{14}CO_2$ evolution from the soil (expressed as percentage of added ^{14}C). ●, Soil amended with ^{14}C-labelled unripe straw, with plants; ▲, soil amended with ^{14}C-labelled unripe straw plus unlabelled ripe straw, with plants; ■, soil amended with ^{14}C-labelled unripe straw, without plants; ○, soil amended with ^{14}C-labelled unripe straw plus unlabelled ripe straw, without plants; △, soil amended with ^{14}C-labelled unripe straw plus glucose, without plants. Means of four replicates. *Curves* not followed by the same *letter* differ significantly ($P < 0.05$)

The size of the labelled biomass was, in most cases, in agreement with the mineralization of the labelled straw in the different treatments. This was seen despite large variations between replicates, and without consistently significant differences between the treatments (Table 3). The soil amended with labelled straw plus glucose thus had both the largest labelled biomass and the largest evolution of $^{14}CO_2$, whereas the planted soil amended with labelled plus unlabelled straw had the smallest labelled biomass and the smallest evolution of $^{14}CO_2$. Nevertheless, the ratios between the total amount of ^{14}C respired and the amount of ^{14}C found in the biomass at harvest were slightly different in some cases (data not shown). The largest ratios were found in the unplanted pots without glucose (treatments III and IV). The differences between planted and unplanted pots in the treatments amended

Table 2 Quantity of ^{14}C respired or left in sand, soil, roots, and shoots at harvest

Treatment	^{14}C respired (% of added ^{14}C)	^{14}C content (% of added ^{14}C)				
		Sand	Soil	Roots	Shoots	Total recovery
I	25.19 (0.48)	0.14 (0.09)	54.38 (3.31)	0.31 (0.07)	0.14 (0.02)	80.2
II	17.87 (0.71)	0.15 (0.12)	59.62 (2.66)	0.38 (0.10)	0.12 (0.01)	78.1
III	32.26 (0.95)	0.12 (0.09)	50.93 (4.42)	–	–	83.3
IV	30.87 (1.23)	0.19 (0.13)	53.35 (4.82)	–	–	84.4
V	38.93 (2.50)	0.04 (0.03)	46.16 (3.81)	–	–	85.1
LSD ($P = 0.05$)						5.8

Means of four replicates (SD). Treatments: I, Soil amended with ^{14}C-labelled unripe straw, with plants; II, soil amended with ^{14}C-labelled unripe straw plus unlabelled ripe straw, with plants; III, soil amended with ^{14}C-labelled unripe straw, without plants; IV, soil amended with ^{14}C-labelled unripe straw plus unlabelled ripe straw, without plants; V, soil amended with ^{14}C-labelled unripe straw plus glucose, without plants. LSD, Least significant difference

Table 3 The Content of microbial biomass C, ^{14}C and N and biomass C:N ratios in the soil at harvest

Treatment	Biomass ($\mu g\ g^{-1}$ soil)			C:N
	C	^{14}C	N	
I	181.7	27.1	15.3	11.7
II	285.6	18.2	12.7	22.8
III	228.8	29.2	18.2	12.6
IV	364.1	25.6	26.4	13.7
V	286.0	46.5	20.5	14.1
LSD ($P = 0.05$)	93.9	10.4	4.1	3.6

For explanations, see footnotes to Table 2

only with labelled straw (treatments I and III) were significant ($P < 0.05$). The ratios found in the pots amended with labelled straw plus glucose (no plants) were similar to the ratios found in the pots with plants and these ratios were significantly different ($P < 0.05$) from those of the other treatments without plants.

The content of C in the soil microbial biomass at harvest was larger in the bulk soil compared with the rhizosphere soil within corresponding treatments (I and III, II and IV). The variations between the replicates were, however, large, and the differences were not significant (Table 3). The lowest levels of biomass N were found in the planted pots, and the differences between the planted and unplanted soil amended with the labelled plus unlabelled straw (treatments II and IV) were significant. The highest C:N ratios in the microbial biomass were found in the planted soil amended with labelled plus unlabelled straw (Table 3).

The number of bacteria in the soil was the same in all the pots at harvest (Table 4). This result was obtained by viable counts (plate dilution) as well as by total direct counts (acridine orange) and active counts (INT-positive bacteria).

Table 4 Number of bacteria in the soil at harvest, determined by plate counts and direct microscopy

Treatment	Bacteria		
	CFU ($\times 10^7\ g^{-1}$ soil)	AODC ($\times 10^9\ g^{-1}$ soil)	INT-positive ($\times 10^8\ g^{-1}$ soil)
I	2.9	1.6	2.6
II	2.7	1.3	2.5
III	2.4	1.6	2.5
IV	2.7	1.4	2.8
V	2.5	1.4	2.2
LSD ($P = 0.05$)	0.8	0.5	0.7

CFU, Number of colony-forming units of bacteria; AODC, total number of bacteria (acridine orange direct counting); INT-positive, number of metabolically active bacteria able to reduce 2-(*p*-iodophenyl)-3-(*p*-nitrophenyl)-5-phenyl tetrazolium chloride. For explanation of treatments, see footnotes to Table 2

Discussion

The addition of unlabelled straw with a C:N ratio of ca. 100 to the soil created a situation with a large potential for a net microbial N immobilization and competition between plants and microorganisms for mineral N. In the soil amended only with the labelled straw which had a relatively small C:N ratio of ca. 20, the potential for net microbial N immobilization was much smaller. The decreased rate of mineralization of labelled straw in the planted soil was most profound in the soil amended with both labelled plus unlabelled straw (Fig. 1). This can be explained in terms of strong competition for mineral N by the plants, leaving insufficient amounts for the microorganisms. Successful competition for mineral N by the plants would have a more profound effect on mineralization of labelled straw in the soil with a high potential for N immobilization, i.e., in the soil amended with both labelled plus unlabelled straw. The ability of plants to compete successfully with microorganisms in the soil for mineral N has been demonstrated by Wang and Bakken (1989). The plants may also have lowered the mineral N level in the soil indirectly by the release of organic materials from the roots, resulting in microbial N immobilization when these materials were used by microorganisms.

As the soil was continuously aerated, and the water content of the soil was adjusted once a day, the argument used in some field experiments (Führ and Sauerbeck 1968; Shields and Paul 1973), that a reduction in microbial activity was caused by restricted water availability and aeration in the planted soil, cannot be applied in this experiment.

Living plant roots continuously provide the soil with small amounts of a wide variety of typically easily accessible organic compounds termed rhizodeposition (Newman 1985). Microbial utilization of the rhizodeposition in preference to the material examined, as suggested by Reid and Goss (1982), did not seem to explain the effect of the plants either. The addition of glucose, which simulated the effect of the rhizodeposited material, stimulated mineralization of the labelled straw (Fig. 1). Although the rhizodeposited material may have had a very complex composition it seemed most likely that its net effect on the mineralization of the labelled straw would have been similar to the effect of glucose. Although the mineralization of glucose must have caused some N immobilization, this apparently did not lead to N limitation in the glucose-amended soil.

The quantity of ^{14}C recovered in the plants at harvest did not indicate that plant uptake of labelled material was an explanation for the reduction in the evolution of $^{14}CO_2$ from the planted soil (Table 2). However, the amount of ^{14}C taken up by the plants may have been larger earlier in the incubation period. This may have led to competition for substrate at that time. In a similar way, Sparling et al. (1982) found that the amount of ^{14}C taken up by plants reached a maximum at 28 days and then declined. Decreasing quantities of ^{14}C in the plants may be

due, for example, to liberation of $^{14}CO_2$ from the roots and shoots ($^{14}CO_2$ from the shoots was not trapped in this experiment) or to root death. Evolution of $^{14}CO_2$ from the shoots would result in a lower recovery of ^{14}C. The total recovery of ^{14}C from the planted pots was, as mentioned before, slightly less than the recovery from the unplanted pots. However, the quantity of ^{14}C in the plants might not have been larger at all earlier in the incubation period, and even if this had been the case, at least part of the decline was probably due to root death, which delivered labelled organic material back to the soil.

The suggestion by Martin (1987) concerning an enrichment in the rhizosphere of organisms with a high efficiency of C utilization may be valid in the present experiment. Some of the decrease in the rate of decomposition of the labelled straw in the planted soil would then be more apparent than real in accordance with the hypothesis of Martin (1987). The actual finding of an apparently high efficiency of C utilization by the rhizosphere organisms compared with the organisms in the unplanted soil, as suggested by Martin (1987), was quite surprising. A high efficiency of C utilization by microorganisms living in an environment relatively rich in substrates compared with microorganisms living in a typically more oligotrophic environment did by no means stand to reason. However, differences in the ratio of respired ^{14}C to biomass ^{14}C may also have been caused by differences in the turnover of labelled biomass in the soils.

The quantity of biomass C in the soil at harvest was higher in the pots amended with unlabelled straw or glucose in addition to the labelled straw (Table 3). Since the different amendments were not reflected in the number of bacterial cells in the soil, the differences in biomass C may have been due, for example, to differences in the size of the bacterial cells or to different ratios between bacteria and fungi (or other microorganisms) in the different treatments.

The flushes of N, determined by extraction after microwave irradiation, seemed to be relatively low, giving unrealistically high C:N ratios in the microbial biomass (Table 3). Microbial C values estimated by microwave treatment-extraction have previously been compared with those estimated by fumigation-incubation (data not shown) and the estimates were in agreement. Estimates of microbial N by microwave treatment-extraction have not yet been compared with other estimates. However, the results of the present experiment indicated that the K_n factor of 0.54 proposed by Brookes et al. (1985) to convert the N flush to microbial N after fumigation-extraction should be decreased in order to take account of a seemingly lower extraction of microbial N after microwave treatment. Although the absolute N figures were not correct, it seemed reasonable to examine the relative proportions of biomass N in the different treatments. Likewise, the highest C:N ratios in the microbial biomass as mentioned previously were found in the planted soil amended with labelled plus unlabelled straw. This was a further indication of successful competition by the plants for mineral N, which had the most profound effect in the soil with a large potential for N immobilization.

The difference in ^{14}C mineralization between treatments was in most cases reflected in the size of the labelled biomass but not in the number of bacteria in the soil at harvest. The presence of plants was not reflected in the number of bacteria, either. The number of bacteria is most often larger in rhizosphere soil compared with bulk soil, because rhizodeposited materials typically sustain microbial growth. The equal numbers of bacteria found in the planted and unplanted pots in the present experiment may have been the result of limited rhizodeposition at the time of harvest. The plants were harvested after 130 days, and so the roots were probably not very active during the final period of incubation. Another possible explanation is that the positive effect of the rhizodeposition in the present experiment was counterbalanced by N limitation in the planted pots.

The presence of living plant roots in soil influence microorganisms as well as physical and chemical parameters, which again influence each other. The presence of living roots therefore creates a very complex situation, which was illustrated in the present experiment. The decreased rate of mineralization of labelled straw in the planted soil was, as mentioned previously, probably to some extent a result of competition between plants and microorganisms for mineral N. Since the plants also decreased the rate of mineralization of labelled straw in the pots with a low potential for N immobilization and competition between plant roots and microorganisms, there must, however, have been other explantations as well, but these have not so far been found.

Acknowledgements ^{14}C-labelled straw was supplied by the National Research Centre Risø. The work was financed by the Danish Agricultural and Veterinary Research Council.

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