Pergamon

Soil Biol. Biochem. Vol. 29, No. 2, pp. 153–162, 1997

Printed in Great Britain
PII: S0038-0717(96)00291-X
0038-0717/97 $17.00 + 0.00

COMPETITION FOR NITROGEN DURING DECOMPOSITION OF PLANT RESIDUES IN SOIL: EFFECT OF SPATIAL PLACEMENT OF N-RICH AND N-POOR PLANT RESIDUES

WANG JINGGUO*† and LARS R. BAKKEN‡

Department of Biotechnological Sciences, Agricultural University of Norway, P.O. Box 5040, N-1432 Aas-NLH, Norway

(Accepted 5 October 1996)

Summary—The distance between "hot spots" for N-mineralization (N-rich clover residues) and for N-immobilization (high C-to-N straw) in soil was experimentally manipulated to investigate its effect on the competition between plant roots and microorganisms for mineralized N. The experiment demonstrated that plant roots were reasonably competitive, resulting in deprivation of the N-supply to the microorganisms growing on the straw material, but this was totally dependent on the distance between the N-rich and the N-poor sites in the soil. The critical distance was somewhere between 3 and 6 mm, above which plant roots outcompeted the microorganisms more or less completely. Our study illustrates an important mechanism by which plant roots can interfere with microbial N-transformations in soil. It may be the mechanism responsible for an often alleged "stimulation" of N-mineralization by plant roots. The mineralization rate of clover- and straw-C was measured in planted as well as unplanted soil. The presence of plant roots retarded the straw-C mineralization significantly, but not clover C. © 1997 Elsevier Science Ltd

INTRODUCTION

The trophic interaction between plant roots and microorganisms in soil is complex. Living plant roots represent an important source of C and energy for the soil microflora (Rovira and Davey, 1974). Microbial assimilation of N is apparently competing with plant roots (Jackson *et al.*, 1989), and hence the root stimulates its own potential competitors for mineral N. Although much of this microbially assimilated N will be remineralized due to rapid turnover rates, a significant part will inevitably remain as relatively stable organic N in soil (Breland and Bakken, 1991). On the other hand, plant roots may apparently compete successfully with microorganisms for mineral N, but their competitiveness seem to be strongly dependent on the spatial heterogeneity of the soil (Wang and Bakken, 1989).

Bakken (1990) has stated that a proper understanding of these mechanisms of interaction may reconcile the apparently conflicting observations that the effect of plant roots on the mineralization of organic C in soil is generally negative (or neutral), whereas the effect on microbial N-mineralization is generally positive.

Wang and Bakken (1989) found circumstantial evidence that plant roots stimulated net N-mineralization not necessarily by an enhancement of microbial activity, but rather by limiting the supply of mineral N to the microflora. This interpretation was strengthened by the fact that the apparent "stimulation" was strongly dependent on the spatial heterogeneity of the soil with respect to "hot spots" for net N-mineralization and N-immobilization. The two types of "hot spots" were created by mixing or layering straw and clover at some distance between each other in the soil.

We have continued and refined these experiments in several ways. The mineralization of C in the two types of organic materials (straw and clover) was monitored throughout the experiment, so as to see if the C-mineralization rates were affected positively or negatively by plant roots. The critical distance between N-rich (clover leaves) and N-poor (barley straw) sites in soil was investigated in more detail. The decomposition of and the microbial growth on the two types of materials have been monitored. Furthermore, the experiments have been taken one step closer to the natural condition by conducting an additional experiment with an agricultural soil as previous experiments were conducted only with a

*Present address: Department of Plant Nutrition, Beijing Agricultural University, Haidian, Beijing 100094, People's Republic of China.
†Author for correspondence.
‡Present address: Department of Soil and Water Sciences, Agricultural University of Norway, PO Box 5028, N-1432 Aas-NLH, Norway.

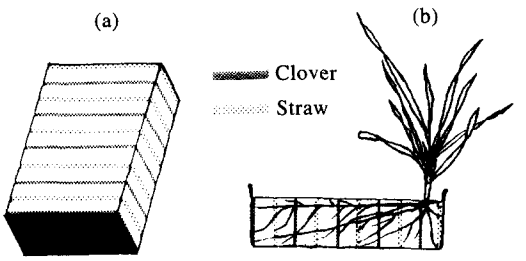

Fig. 1. Arrangement of clover leaves and straw as separate layers in soil (treatment B) (a), and root distribution after transplantation (b).

silty subsoil with extremely low organic matter content.

MATERIALS AND METHODS

Spatial arrangement of plant residues in soil

To experimentally manipulate the physical distance between "hot spots" for immobilization and mineralization of N in soil, we placed two types of plant residues as separate layers in the soil [Fig. 1(a)]. The soil had been air dried, sieved (2 mm) and remoistened to 5% moisture content; the plant residues had been ground (1 mm). The distance between the layers was 3, 6, 9 and 12 mm. In addition, there was also a "0 mm" treatment, in which the finely ground clover and straw material was mixed completely with the soil. The soil and plant residues were layered in a transparent box, then transferred to an open aluminum box and stored at 4°C until the start of the plant experiments (2 d). The use of moderately moist soil was absolutely neccessary to obtain sufficient coherence of the layers for successful transfer to the aluminum trays. The final size of the pot was approximately $100 \times 70 \times 27$ mm.

One-half of the pots were then planted with barley seedlings, and the other half were kept in the same room unplanted. Periodically, a set of pots was taken for measurement of plant N, mineral N and organic C and N in the soil and microbial counts.

Two separate experiments were conducted. In experiment 1 a silty subsoil with extremely low content of organic matter was used, so as to allow the decomposition of the plant materials to be monitored by measurement of total organic C and N. In experiment 2 a cultivated clay loam soil was used, in order to control whether the observations in experiment 1 could be reproduced under more "normal" conditions with respect to initial numbers of microorganisms and organic materials.

Soils and plant residues

Experiment 1 The silty subsoil (10–100 μm particle size) was taken at 0.5–1 m depth in a field grown with small grains at Hvam, Norway. This soil contained very little organic matter (Table 1), and a negligible amount of mineral N (below detection limit). To ensure a reasonable pH (the silty subsoil has a very low pH buffering capacity) and an ample supply of all other mineral nutrients than N, the soil was limed (3.2 g of dolomite lime kg^{-1}), fertilized (68 mg P and 133 mg K kg^{-1}), and supplied with a mixture of micronutrients (100 mg "fritt" kg^{-1}, a slow release micronutrient mixture containing Mo, B, Cu, Zn, Mn and Fe), prior to layering. After liming and fertilization, pH (water) was 7.2–7.4, and the values kept constant during the experiment.

To ensure a minimum of active organisms at the onset of the experiment, the pots were inoculated with 5 ml of a 10^{-1} g ml^{-1} of a suspension of freshly sampled clay loam soil (Wang and Bakken, 1989), the soil used in experiment 2.

The amount of soil, straw and clover leaves per pot, and the C and N content of each component is shown in Table 1. The same amount of soil and plant residues was used for each treatment. Five treatments with respect to the distance between clover leaves and straw were used: A, 12 mm; B, 9 mm; C, 6 mm; D, 3 mm; and E, "0 mm" (i.e. complete mixture of soil, straw and clover leaves). A total of 10 replicates of each pot type were prepared, of which five were planted and five were left unplanted.

In addition to the pot types mentioned above, we prepared two extra types of controls. One was a set of five pots in which only clover material was mixed with soil (same proportions as in Table 1). The other was a set of five pots with straw added alone (Table 1) plus 100 mg KNO_3-N per pot. These pots were placed together with the rest, and served as a control for measurements of net N-mineralization and N-immobilization as stimulated by each plant residue alone or in the absence of plant roots.

Experiment 2 The cultivated soil (0–20 cm depth) used was a clay loam soil, classified as Typical Haplaquet, containing 16% clay, 42% silt and 32% sand, with 3% organic C, 0.3% organic N and

Table 1. Nitrogen and C added to soil and plant materials, experiment 1

Materials	Weight (g pot^{-1})	N content (mg g^{-1})	Total N (mg pot^{-1})	Total C (mg pot^{-1})	C-to-N ratio
Silty subsoil	200.0	0.15	29.9	523	17.5
Clover leaves	2.50	30.6	76.5	954	12.6
Straw	5.00	5.04	25.2	2065	81.9
Total	207.50		131.6	3542	26.9

pH 5.7. In contrast to experiment 1, the soil was not allowed to dry out; the moisture content was about 0.15 ml g^{-1} dry weight during pot preparation, to ensure an active microflora at the onset of the experiment. Liming and P, K and micronutrient fertilization was conducted as in experiment 1, but without inoculation.

The amount of soil, clover leaves and straw per pot was the same as in experiment 1, but only two treatments with respect to the distance between clover leaves and straw were used: B, 9 mm; E, "0 mm" (same codes as for experiment 1). For each treatment 16 replicates were prepared, to allow duplicates to be analyzed each time.

Procedure for plant culture for both experiments

One-week-old barley seedlings (germinated on moist paper) were washed with distilled water and transplanted to the pots (three plants per pot). The roots were spread evenly on the soil surface [Fig. 1(b)] and covered with about 20 g of soil, which had been put aside during preparation of the pots. The planted pots were covered by an aluminum lid with a minimum opening for the plants, and placed in a temperature-controlled (15°C) room with constant relative humidity (80–90%) and 18 h of light at an intensity of 225–250 μE m^{-2} s^{-1} (400–700 nm) from a 400 W high-pressure sodium lamp (OSRAM Vialux NAV-T), which was placed 70 cm above the pots. Unplanted pots were partly covered with aluminum foil to minimize evaporation, and placed in the same room.

To avoid or minimize horizonal water movement and splash effects during watering, distilled water was sprayed slowly onto the soil surface. This was done each day while the pot was standing on a balance, so as to carefully adjust the moisture content to a standard value. The soil moisture after watering was 42 g pot^{-1} for the silty subsoil, 67 g pot^{-1} for the clay loam soil. The water losses through evaporation and transpiration were 2–3 and 5–8 g pot^{-1} d^{-1} in unplanted and planted pots, respectively (increasing in planted pots towards the end of experiment). Thus the planted and unplanted pots were not allowed to dry much between each watering. This was considered important so as to minimize possible "drying–rewetting" cycles affecting the mineralization rates in the planted pots.

Sampling and chemical analyses

Sampling Two weeks after planting, samples were taken every week (one pot of each treatment in experiment 1 and two replicates in the second experiment). For treatments A and B (12 and 9 mm distance between layers), the straw and clover layers were separated. The soil was split into thin sections by cutting with a knife through the middle of the soil layer between straw and clover layer. All layers of the same kind (clover or straw) were then combined and a constant amount of soil was separated between clover layers (103.0 ± 4.3 for clover residues and nearby soil) and straw layers (93.0 ± 4.3 for straw residues and nearby soil). The measured variables were related to the total dry weight (including both soil and plant residues). "Clover layer" and "straw layer" refer to corresponding plant residues together with the nearby soils.

In experiment 1, the roots were first separated from soil by dry sieving (2.0 mm mesh). The roots were then washed in two portions of 50 ml distilled water and removed from the wash water by sieving with a special bottle, containing a 1.5 mm steel mesh in the middle. Soil and washes were combined and mixed with a stirrer (detailed description by Breland and Bakken, 1991). Subsamples were taken from the slurry by a syringe during stirring. Sampled slurries used for mineral N determination were mixed 1:1 with 2 M KCl solution (1 M KCl after mixing), shaken for 2 h and filtered. The rest of the soil slurries, except that for biological analysis (Wang and Bakken, 1997), were dried at 105°C, and a small portion was ball-milled for total N and organic C analysis. In experiment 2, roots were not separated from the soil; otherwise the procedures were identical to those for experiment 1.

Soil mineral N NH_4^+-N and NO_3^--N, were determined in the 1 M KCl extracts by flow injection analysis technique (FIA), after extraction with 1 M KCl by shaking on a reciprocal shaker for 2 h.

Total organic C and N Soil samples were dried at 105°C for 24 h, ball-milled, and analyzed for total C and N on a Carlo Erba CHN Elemental Analyzer (Model 1106, Carlo Erba Strumentazione, Italy). Plant materials were dried at 80°C, ball-milled and analyzed with the same equipment.

Statistical analysis

Standard statistical methods (analysis of variance) were used to test the effects of plant roots, distance between clover and straw layers and the interaction between these factors (samplings treated as blocks), and the effects were tested against a residual mean square.

RESULTS

Plant N uptake and root distribution

In experiment 1 [Fig. 2(a)], there was a gradual accumulation of N in the plants in all treatments, but less accumulated in treatment E compared to treatments D and A–C. The latter three treatments were statistically similar. Experiment 2, where a clay loam soil was used [Fig. 2(b)], showed a similar pattern as to the plant N accumulation in treatment B, but treatment E gave much lower values than the same treatment with the silty subsoil in experiment 1. As a whole, the plants grew more slowly in the clay loam soil compared to the silty subsoil,

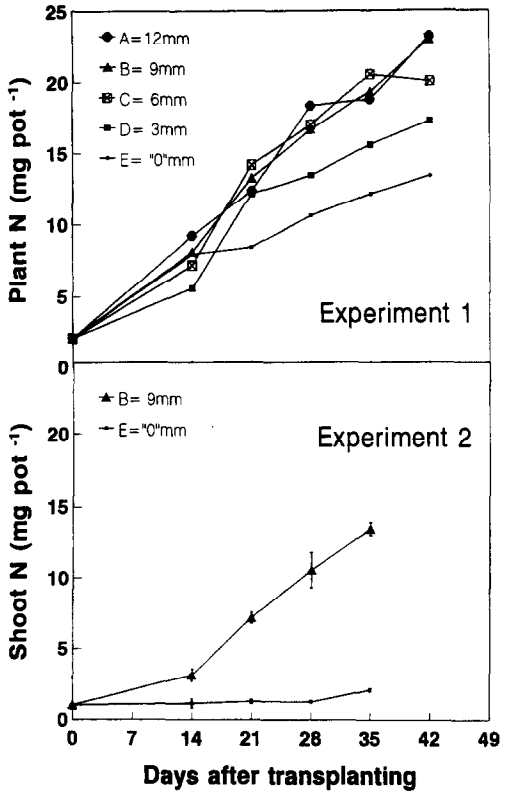

Fig. 2. Total plant N in treatments A–E in experiment 1 (above) and shoot N in treatments B and E in experiment 2 (below). Thickness of soil layers is indicated for each treatment. In experiment 2, standard error is shown as vertical bars (n = 2).

and after 5 wk of growth the plant biomass was 0.77 and 0.27 mg pot^{-1} for treatments B and E, respectively; the corresponding figures were 2.02 and 1.26 mg pot^{-1} in experiment 1. This might be due to the difference in the soil physical conditions. Besides, for treatment E in particular, due to the high clay content of the soil, the very low plant N accumulation may also be attributed to the high soil ammonium-fixing capacity and low mobility of ammonium, which also favors N immobilization.

Root densities in the separate layers from experiment 1 (treatments A and B) are shown in Table 2. It shows a higher root density in the clover layer (statistically significant). As in a previous experiment (Wang and Bakken, 1989), there was little branching of the roots in the straw layers.

Soil mineral N accumulation

The mineral N, mainly consisting of ammonium, was constantly at a low concentration in the planted pots with the maximum values at the first sampling (Fig. 3). In the unplanted pots there was a transient mineral N accumulation. Analysis of variance showed that the mineral N concentrations in treatments A and B were significantly higher than that in treatments C–E, but within each group there were no statistically significant differences (separate ANOVA for the planted and the unplanted pots). The mineral N concentration in the clay loam soil (data not shown) followed a similar pattern as that in experiment 1, but the amounts declined more rapidly to low concentrations (1 mg N pot^{-1} in the planted pots, treatment B).

In experiment 1, soil mineral N mainly consisted of ammonium at the first three samplings. Later, the relative amounts of nitrate increased and reached similar concentrations as ammonium (data not shown). However, in experiment 2 the nitrate concentration was very low throughout the whole experiment.

Mineral N in separate layers

The average across treatments A and B is shown in Fig. 4. For both layers the maximum values were found at the first sampling. The mineral N concentrations in the unplanted pots were much higher than in the planted pots, but the two treatments (planted and unplanted) converged towards similar low concentrations towards the end of the experiment. The nitrate concentration was constantly low ($<$ 1 mg pot^{-1}) in the straw layers (planted and unplanted) as well as in the clover layers of the planted pots. In the clover layers of unplanted pots, however, some nitrate accumulated (1–2 mg NO_3^--N pot^{-1}) towards the end of the experiment (data not shown).

N mineralized from N-rich plant residues

The accumulated microbial N-mineralization in the planted pots was calculated as the sum of measured plant N (root N + shoot N - N in seeds) and mineral N in soil. The results for experiment 1 are shown in Table 3. Similarly calculated values for experiment 2, after subtraction of the initial mineral N in the soil, are shown in Fig. 5. The root N in this case was estimated based on the root-to-

Table 2. Root distribution in separate layers, averaged across treatments A and B, experiment 1 (mg DW pot^{-1})

Days	14	21	28	35	42
Clover layer	105.6 ± 1.2[a]	202.0 ± 5.3	309.7 ± 2.4±	458.2 ± 24.1	445.6 ± 2.8
Straw layer	84.6 ± 4.9	150.0 ± 4.5	170.8 ± 7.7	306.6 ± 7.0	394.9 ± 5.1

[a]Standard error (n = 2).

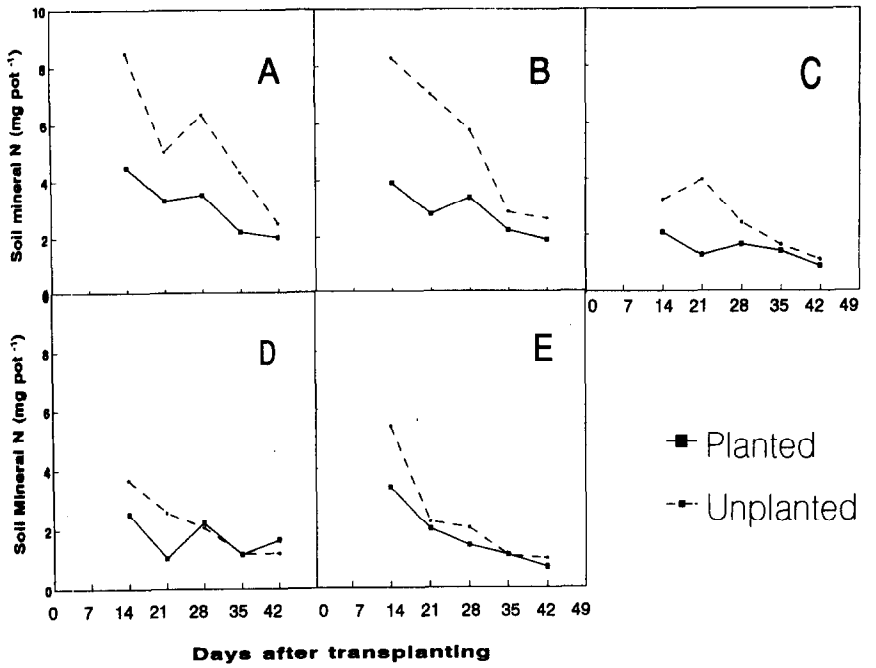

Fig. 3. Soil mineral N (NH_4 and NO_3) in the planted and unplanted pots for each treatment, depending on the distance between the clover and straw layers, in experiment 1 for treatments A–E.

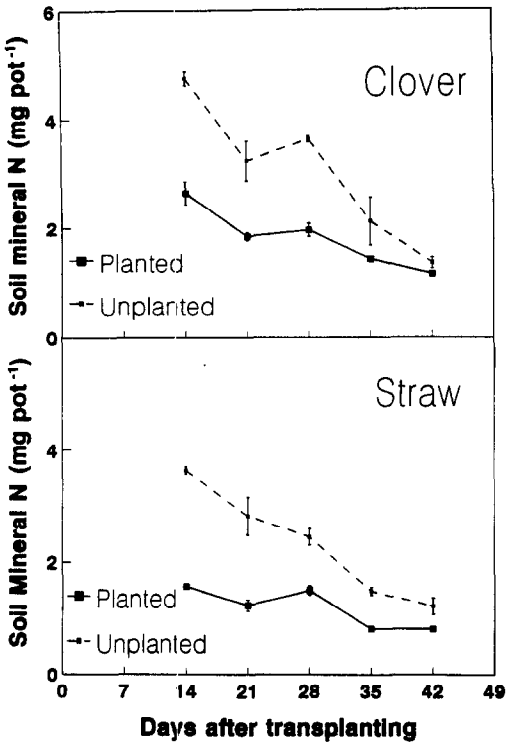

Fig. 4. Soil mineral N in the planted and unplanted clover and straw layers (average across treatments A and B), in experiment 1 with silty subsoil, and also with standard error bars (n = 2).

shoot ratio of the corresponding treatment observed in experiment 1 (data not shown).

In both experiments, N mineralization was significantly higher in the planted pots than that in the unplanted pots, even for the treatment mixture in the clay loam soil. However, the effect of the spatial placement of N-rich and N-poor plant residues on net mineralized N concentrations was evident. As demonstrated in experiment 1, from treatments C–E the mineralized N gradually decreased with decreasing distance between N-rich and N-poor plant residues (Table 3). In experiment 2 with the clay loam soil there was a significant difference between the two treatments (B and E), corresponding well with the observations with the silty subsoil.

The accumulated mineral N in the unplanted pots with clover added alone was somewhat higher than the estimated microbial N-mineralization in planted pots of treatments A and B (about 26 mg N pot^{-1} after 28 days). The N immobilization in control pots with straw added together with excess nitrate was about 30 mg N per pot (data not shown).

Plant residual C mineralization

Native soil organic matter represented only a small fraction of organic C and N in the pots in experiment 1 (Table 1). The stability of native soil organic matter and its presence as a small fraction of the total organic matter in each pot allows us to assume that C mineralized from native soil organic

Table 3. Mineralized N recovered as plant-N accumulation[a] plus mineral N, experiment 1 (mg N pot^{-1})

Treatment		Days after planting				
		14	21	28	35	42
A	Planted	11.66	13.64	19.82	18.95	21.13
	Unplanted	8.48	5.05	6.38	4.31	2.50
B	Planted	9.97	14.06	18.04	19.53	21.72
	Unplanted	8.30	7.06	5.79	2.89	2.64
C	Planted	7.22	13.43	16.64	19.91	17.89
	Unplanted	3.24	3.96	2.42	1.65	1.12
D	Planted	6.07	12.15	13.65	14.70	16.70
	Unplanted	3.65	2.59	2.06	1.17	1.19
E	Planted	9.28	8.38	10.00	11.18	11.16
	Unplanted	5.42	2.23	2.01	1.08	0.97

[a]N in plants corrected for initial plant N (2.02 mg pot^{-1}).

matter contributed insignificantly to the observed decline in total C. Hence the residual straw- and clover-C were estimated from measured total-C and N minus total-C and N which stems from the soil organic matter (based on the C and N in the original soil materials, Table 1). This calculation has been used throughout the rest of the paper to estimate residual straw- and clover-C in separate layers as well as in the whole pots.

Amounts of residual straw- plus clover-C in treatments C–E are shown in Fig. 6. Initially, the amounts were identical in planted and unplanted pots, but towards the end of the experiment there was a tendency for lower amounts in the unplanted pots compared to the planted pots (significant at $P < 0.05$ for the last two samplings). Amounts of residual C in separate layers is shown in Fig. 7 (average of treatments A and B). The amounts of the residual clover C in the planted pots were identical to that in the unplanted pots throughout the whole experiment. In the straw layers, the planted pots had higher amounts than the unplanted pots towards the end of the experiment (significant difference, $P < 0.05$ for the last three samplings).

The presence of the plants retarded decomposition of plant material, and analyses of the materials in separate layers indicated that it was only straw-mineralization that was affected. Clover leaves mineralized significantly faster than straw throughout the experiment in terms of percentage material decomposed. After 3 wk, 42% of the clover C had been mineralized, whereas only approximately 10% of the straw C had been mineralized. By the end of the experiment the percentage of mineralization was approximately 60% for clover C and 26 and 36% for straw C in the planted and unplanted pots, respectively.

Root material lost during the separation of roots from soil was a possible source of error. It would result in higher residual C values for planted than unplanted, as observed for the straw layers.

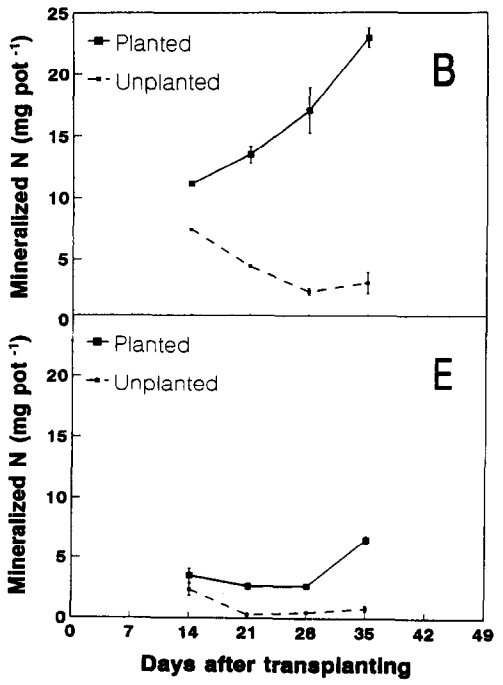

Fig. 5. Total mineralized N estimated as plant N accumulation plus soil mineral N accumulation, the mineral N at the beginning subtracted, for treatment B (B) and E (E) in experiment 2, with standard error bars ($n = 2$).

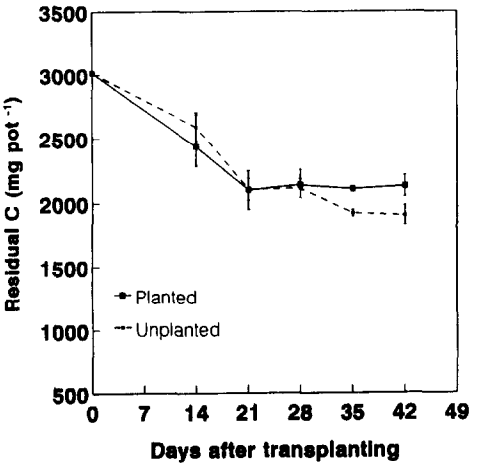

Fig. 6. Changes in plant residual C with standard error bars ($n = 3$) (averaged across treatments C–E), as affected by the plant roots, in the silty subsoil in experiment 1.

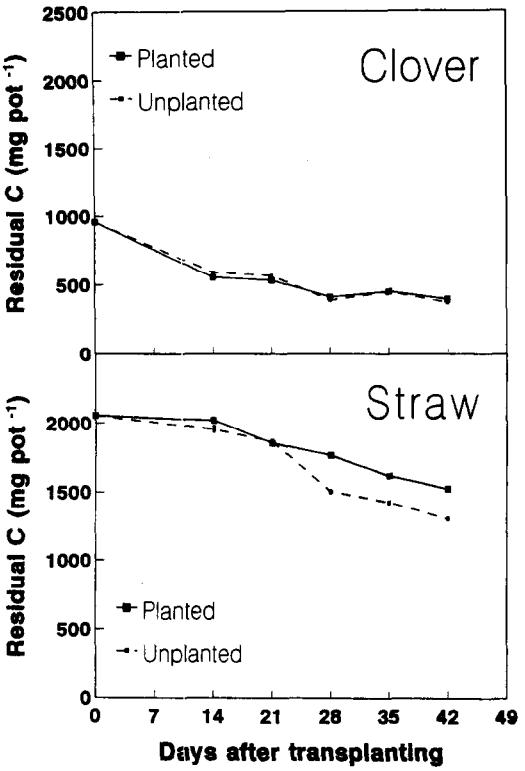

Fig. 7. Changes in plant residual C (averaged across treatments A and B) in the clover (above) and the straw layer (below), as affected by the plant roots in experiment 1, with standard error bars (n = 2).

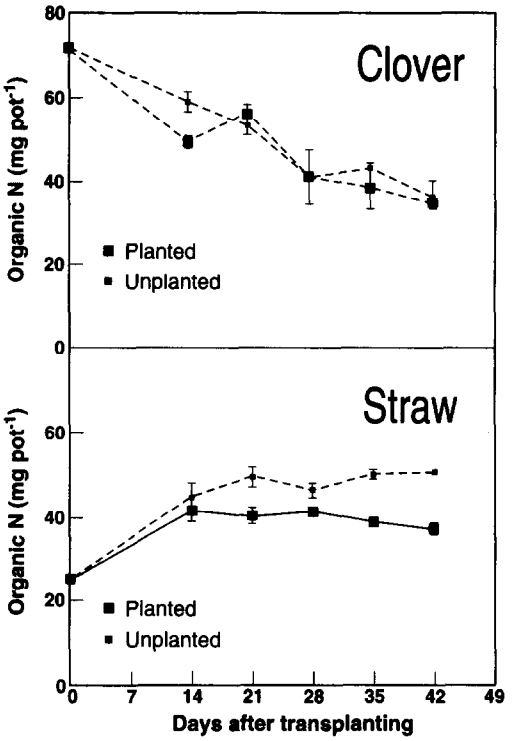

Fig. 8. The effects of plant roots on soil organic N content (original organic N in soil subtracted) in the different layers, clover (above) and straw (below), in experiment 1 with standard error bars (n = 2).

However, the following relationships are essential for evaluating this possible source of error. The difference in residual straw-C (planted vs unplanted) towards the end of the experiment was around 200 mg C per pot. In comparison, the measured amount of roots in the straw layers was 300–400 mg dry weight per pot, which is equivalent to 120–160 mg root-C per pot. Thus, more than 50% of the total root mass would have to be lost in order to meet the observed difference.

Organic N in soil, recovery of immobilized N

The measured organic N (original soil organic C not included) in the separate layers is shown in Fig. 8. In the clover layers, the amounts decreased gradually from 76 to 33 mg N per pot, with no apparent difference between planted and unplanted pots. In the straw layers, the amounts increased initially from 25 to 41 and 44 mg N in planted and unplanted pots, respectively. Thereafter, the amounts continued to increase in the unplanted pots (final value 50 mg N per pot) whereas the amounts in the planted pots gradually declined to 36 mg N per pot. For the unplanted pots of treatments C–E the amounts of organic N were constant throughout the experiment, whereas the amounts in the planted pots gradually declined to amounts which were in good agreement with plant N uptake (data not shown).

N losses and recovery

As judged from the N recovery at the end of experiment 1 (N in plant plus soil), the N-loss (denitrification and ammonia volatilization) was approximately 6 mg N pot^{-1} in the planted pots, and 10 mg N pot^{-1} in the unplanted pots for treatments C–E (data not shown). Somewhat higher (1–2 mg N pot^{-1}) losses (but not statistically significant) were observed for the separate layers of treatments A and B. In experiment 2 with clay loam soil, the N losses were apparently insignificant (98% N recovery).

DISCUSSION

A considerable amount of N was released from the decomposition of clover leaves as indicated by the accumulation of mineral N in unplanted soil without added straw (data not shown), as well as by the remaining clover residual N (Fig. 8). The N immobilization potential of decomposing straw was sufficient to utilize all of the mineralized N from clover leaves, as demonstrated by the mineral N-contents in the unplanted pots, where straw and

clover were mixed completely (treatment E, Table 3 and Fig. 5). Therefore it was obvious that the plant roots and the microorganisms were competing for the same N source. A gradual increase in plant-N from treatments E (mixture) to C (6 mm thickness of soil) in experiment 1, and a large difference in shoot-N between treatments B and E in experiment 2 (Fig. 5), show that the competitiveness of the plants gradually increased with distance between the clover leaves and straw. With further increase in distance from 6 to 12 mm, no extra plant-N was obtained. Net N mineralization in the planted pots in treatments A–C was similar to that in the unplanted clover control in silty subsoil without added straw. This indicated that in the layer treatments with distance ≥6 mm, plants sequestered the majority of mineralized N, and hence they outcompeted the heterotrophic microflora more or less completely. The allocation of more root growth to the clover layer than to the straw layer (Table 2) would help the plant roots to absorb mineralized N more efficiently.

As a result of the competitiveness for the same pool of N with the heterotrophic microflora, plant roots had a negative effect on C mineralization. The hypothesis was supported not only as shown by significantly higher residual C, remaining in the planted soil compared to that in the unplanted soil in the later stages of experiment 1 (Figs 3, 6 and 7), but also by measurement of N-mineralization and immobilization potential in soil slurries (Wang and Bakken, 1997). Plant roots had induced a significantly higher N immobilization potential, which indicated that more C substrates were readily available in the planted compared with the unplanted soil.

Knapp *et al.* (1983a) investigated the effect of mineral N-supply on the mineralization rate of straw incubated with soil, and concluded that the mineralization rate of straw was N-limited only during the early phase (0–5 d) of decomposition. A similar conclusion was also made by Smith *et al.* (1989), who stated that N-limitation of microbial decomposition-mineralization of high-C-to-N materials only occurred in the very early stage of decomposition. In contrast to these findings, the measured residual C both in straw layers (Fig. 7) and mixtures of straw and clover (Fig. 6) indicated that the effect of plants on reducing mineralization of straw increased throughout the experiment. This strongly indicates that N-limitation is likely to be more severe and persistent in planted than in unplanted soil. Thus under natural conditions (i.e. in the rhizosphere), N-limitation may have a greater significance than that indicated by the experiments with unplanted soil.

This retardation was associated with a lower bacterial biomass in the planted soil compared with the unplanted soil, as indicated by Wang and Bakken (1989, 1997), and occurred after plant roots had absorbed most of the mineralized N during the experiment. Therefore the negative effect of plant roots on C mineralization was a result of reduction in N availability to straw, which led to a limitation on bacterial growth in planted soil (Wang and Bakken, 1997). Plant roots did not greatly influence N mineralization in the N-rich plant residue, but did affect bacterial growth and N reimmobilization in N-poor (C-rich) plant residue by absorbing mineralized N before it could reach sites of N-poor residues. The same amount of N was mineralized from clover leaves in both the planted and the unplanted soil, and owing to plant uptake of mineralized N, less N moved and was reimmobilized in the planted straw layer so that the organic N content was significantly lower.

It may be argued that plant root deposits and some root losses during sampling might contribute some C to the soil organic C pool in the planted soil. However, this contribution was insignificant since the majority of the root-derived C of barley seedling in the rhizosphere is released as CO_2 and only a small fraction may remain in soil (Barber and Martin, 1976; Whipps, 1984). As discussed earlier, root losses during sampling could not meet the observed difference, simply because the differences in the residual C in the straw layers (planted vs unplanted) exceeded the total amount of intact root C. Furthermore, the evidence that the residual C content in the planted and the unplanted clover layer was practically identical supports the view that root-derived C did not contribute significantly to the measured residual C in the planted straw layers.

When discussing a possible effect of N-limitation on the mineralization of C, several mechanisms must be taken into account. The discussion becomes easier with a scheme (Fig. 9) showing the main mechanisms involved.

Water-soluble fractions of the organic matter are often monomers, which can be absorbed by organisms directly. It seems likely that the uptake rate (2) is less affected by N-limitation compared to its possible effects on fractionation of the absorbed monomers to the three pools indicated (A, B and C). N-deficiency may result in an uncoupling of energy metabolism from biosynthesis (Senez, 1962; Dawes, 1989). N-deficiency also enhances the accumulation of storage materials such as PHB (poly-β-hydroxybutyric acid), but the storage capacity is limited by the biomass of the active cells. The net outcome of these two effects is hard to predict, but it seems likely that there is no severe restriction of the mineralization rate. Thus the decomposition and mineralization of readily available, water-soluble components is unlikely to be severely affected by N-limitation of the microbial growth. On the other hand, severe and persistent N-limitation of

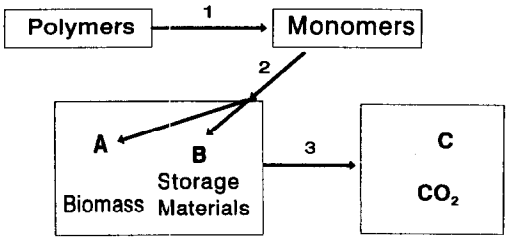

Fig. 9. Scheme to represent decomposition processes of plant residues by soil microorganisms. The monomers and polymer represents the readily available and slowly available C sources for the microbes, respectively, and A, B and C symbolize the possible C pools after microbial transformation. See text for further explanation.

microbial growth is more likely to affect the production of extracellular enzymes for polymer degradation (1 in Fig. 9).

Contradictory results reported in the literature concerning the effect of plant cover on the decomposition of plant residues indicate the complexity of the process. Many factors, abiotic and biotic, including properties of plant residues, are involved. Among them, C and N availability in plant residues are major rate-controlling factors in decomposition (Knapp *et al.*, 1983a,b; Reinertsen *et al.*, 1984; Jawson and Elliot, 1986; Broder and Wagner, 1988; Müller *et al.*, 1988; Kirchmann and Bergqvist, 1989). In our investigation, differences in the effects of plant roots on the decomposition of the two plant residues existed: a negative effect on the decomposition of straw and apparently no clear effect on the decomposition of clover leaves.

However, plant roots might have had a "real" stimulating effect on the decomposition of the clover material. This conclusion is apparently contradicted by the observation that the measured residual C in clover layers was identical in planted and unplanted pots. Considering that the measured residual C included remains of lost root materials (sloughed cells and exudates), a possible stimulation of decomposition and C-mineralization by plant roots may have been "hidden" by a similar amount of root-derived C in the planted clover layers. Since the amounts of root C (as measured in the intact roots) is fairly large compared to the remaining C in the clover layers (170 and 350 mg pot^{-1}, respectively, at the end of the experiment), this source of error in the residual clover C measurement may be significant.

In conclusion, considering competition for N between plant roots and heterotrophic microorganisms, it is apparent that plant roots play a central role by two opposite effects. Root deposits supply microbial cells with substrates to sustain a substantial microbial population in rhizosphere soil (Newman, 1985). In return, a considerable amount of N is immobilized (Breland and Bakken, 1991). On the other hand, plant roots compete for the same available N with microorganisms in soil by reducing N reimmobilization, as demonstrated by Wang and Bakken (1989) and in the present investigation. Retardation of plant roots on C decomposition varied with residues and decomposition stages. Moreover, microbial growth in soil could be limited by N deficiency.

REFERENCES

Bakken L. R. (1990) Microbial growth and immobilization/mineralization of N in the rhizosphere. *Symbiosis* **9,** 37–41.

Barber D. A. and Martin J. K. (1976) The release of organic substances by cereal roots into soil. *New Phytologist* **76,** 69–80.

Breland T. A. and Bakken L. R. (1991) Microbial growth and nitrogen immobilization in the root zone of barley (*Hordeum vulgare* L), Italian ryegrass (*Lolium multiflorum* Lam) and white clover (*Trifolium repens* L). *Biology and Fertility of Soils* **12,** 154–160.

Broder M. W. and Wagner G. H. (1988) Microbial colonization and decomposition of corn, wheat, and soybean residue. *Soil Science Society of America Journal* **52,** 112–117.

Dawes D. E. (1989) Growth and survival of bacteria. In *Bacteria in Nature, Vol 3: Structure, Physiology, and Genetic Adaptability* (J. S. Poindexter and E. R. Leadbetter, Eds), pp. 67–188. Plenum, New York.

Jackson L. E., Schimel J. P. and Firestone M. K. (1989) Short-term partitioning of ammonium and nitrate between plants and microbes in an annual grassland. *Soil Biology and Biochemistry* **21,** 409–415.

Jawson M. D. and Elliott L. F. (1986) Carbon and nitrogen transformations during wheat straw and root decomposition. *Soil Biology and Biochemistry* **18,** 15–22.

Kirchmann H. and Bergqvist R. (1989) Carbon and nitrogen mineralization of white clover plants (*Trifolium repens* L) of different age during aerobic incubation with soil. *Zeitschrift fur Pflanzenernährung Bodenkunde* **152,** 283–288.

Knapp F. E., Elliott L. and Campbell G. S. (1983a) Microbial respiration and growth during the decomposition of wheat straw. *Soil Biology and Biochemistry* **15,** 319–323.

Knapp F. E., Elliott L. and Campbell G. S. (1983b) Carbon, nitrogen and biomass inter-relationships during the decomposition of wheat straw: a mechanistic simulation model. *Soil Biology and Biochemistry* **15,** 455–461.

Müller M. M., Sundman V., Soininvaara O. and Meriläinen A. (1988) Effect of chemical composition on the release of nitrogen from agricultural plant materials decomposing in soil under field conditions. *Biology and Fertility of Soils* **6,** 78–83.

Newman E. A. (1985) The rhizosphere: Carbon source and microbial population. In *Ecological Interactions in Soil* (A. H. Fitter, Ed.), pp. 107–122. Blackwell Scientific, Oxford.

Reinertsen S. A., Elliott L. F., Cochran V. L. and Campbell G. S. (1984) Role of available carbon and nitrogen in determining the rate of wheat straw decomposition. *Soil Biology and Biochemistry* **16,** 459–464.

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

Senez J. C. (1962) Some considerations on the energetics of bacterial growth. *Bacteriological Reviews* **26,** 95–107.

Smith M. S., Rice C. W. and Paul E. A. (1989) Metabolism of labelled organic nitrogen in soil: regulation by inorganic nitrogen. *Soil Science Society of America Journal* **53,** 768–773.

Wang J. G. and Bakken L. R. (1989) Nitrogen mineralization in rhizosphere and non-rhizosphere soil, effect of the spatial distribution of N-rich and N-poor plant residues. In *Nitrogen in Organic Wastes Applied to Soils* (J. A. Hansen and K. Henriksen, Eds), pp. 81–97. Academic, London.

Wang J. G. and Bakken L. R. (1997) Competition for nitrogen during mineralization of plant residues in soil: microbial response to C and N availability. *Soil Biology and Biochemistry.* **29,** 163–170.

Whipps J. M. (1984) Environmental factors affecting the loss of carbon from the roots of wheat and barley seedlings. *Journal of Experimental Botany* **36,** 644–651.