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The effect of living plants on root decomposition of four grass species

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We tested whether living plant roots of *Holcus lanatus* and *Festuca ovina* can affect the decomposition rate of dead roots of *Holcus lanatus*, *Festuca rubra*, *Anthoxanthum odoratum* and *Festuca ovina*. Moreover, we investigated whether this effect is dependent on the decomposing root species or the nitrogen supply during the growth of the roots. The selected perennial grass species are typical of grassland habitats in a range from high to low nitrogen availability: *H. lanatus*, *F. rubra*, *A. odoratum* and *F. ovina*. Seedlings of these species were homogeneously labelled with $^{14}CO_2$ for eight weeks. Plants were grown on soil at two nitrogen levels: one without additional nitrogen and one with nitrogen addition (14 g N m^{-2}).

At the start of the decomposition experiment ^{14}C labelled roots were separated from soil and incubated in litterbags (mesh width 1 mm) in fresh soil. These ^{14}C labelled roots were left to decompose for 19 weeks in an open greenhouse in soil planted with *H. lanatus* or *F. ovina* and in unplanted soil. After the incubation period, the decomposition of the ^{14}C labelled roots of the four species was measured. The mass and ^{14}C losses from the dead roots were calculated and the living plant biomass and C, N and P contents of the living plants were measured.

Living plant roots of *F. ovina* had positive effects on the decomposition rate of *F. ovina* root litter, but dead *A. odoratum* roots from the N fertilized treatment decomposed slower in the presence of living *F. ovina* plants. It seems likely that living plants like *F. ovina* exude carbon compounds that stimulate the growth of soil microbes and thereby increase dead root decomposition and mineralization. Root decomposition rates differed among the species. We found no evidence to support our hypothesis that dead roots of high fertility species (i.e. *H. lanatus* and *F. rubra*) decompose faster than dead roots of low fertility species (i.e. *A. odoratum* and *F. ovina*). In unplanted soil, the mass loss and total ^{14}C loss from *A. odoratum* dead roots were higher than those from *H. lanatus*, *F. rubra* and *F. ovina* dead roots. Dead roots of *F. ovina* lost less mass and total ^{14}C than dead roots of *H. lanatus*.

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Dominant plant species can have important effects on carbon and nitrogen flows within ecosystems (Berendse 1990, Wedin and Tilman 1990, Van Vuuren et al. 1993). Such effects can lead to significant positive feedbacks between changes in ecosystem processes and dominant plant species composition resulting in strongly accelerated plant species replacement during succession (Wedin and Tilman 1990, Vinton and Burke 1995, Berendse 1998, Berendse et al. 1998, Wardle et al. 1998).

Much attention has been paid to the effects of plant species on soil processes, such as N mineralization, by the production of different quantities of litter and litters with different decomposabilities (Berendse et al. 1989, Van Vuuren et al. 1993, Brevedan et al. 1996). But in addition to the effects of the dead plant parts that plant

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species produce, they can also affect soil processes by the activity of their living roots (Clarholm 1985, Nicolardot et al. 1995, Brevedan et al. 1996, Cadisch and Giller 1997). Living plants are expected to enhance microbial degradation of dead roots and old soil organic matter and N mineralization by adding easily metabolizable carbon compounds to the soil by rhizodeposition (Clarholm 1985, Robinson et al. 1989, Swinnen et al. 1994a, b). However, the evidence for such effects is contradictory: both negative and positive effects have been observed (Reid and Goss 1982, Sparling et al. 1982, Clarholm 1985, Van Veen et al. 1993, Nicolardot et al. 1995, Bremer and Kuikman 1997). It is possible that part of the variation in these experimental results is explained by the availability of nitrogen in the soil. Soil nitrogen supply may have important effects on rhizodeposition (Liljeroth et al. 1990, Van Veen et al. 1993, Grayston et al. 1996, Bremer and Kuikman 1997).

Earlier studies have shown that compared with species adapted to less fertile conditions, species adapted to fertile soils promote nitrogen mineralization (Janzen and Radder 1989, Van Veen et al. 1993, Berendse et al. 1998). When soil nitrogen availability increases, changes in species composition may lead to important changes in N release, but also phenotypic responses of the litter chemistry and decomposability in plant individuals may alter the release of soil nutrients (Vitousek et al. 1994).

In the study presented here we tested whether living plant roots can affect the decomposition of dead roots and whether these effects are species-dependent. We also studied the effect of the soil nitrogen supply during the growth of the roots on their subsequent decomposability. We focussed on the effect of two grass species (*Festuca ovina*, characteristic of grasslands on nutrient-poor soils; and *Holcus lanatus*, characteristic of haymeadows on relatively fertile soils) on the decomposition of the dead roots of four different grass species. These grass species varied in their preference for the level of soil fertility: *Festuca ovina* (very nutrient-poor), *Anthoxanthum odoratum* (moderately nutrient-poor), *Festuca rubr*a (intermediate) and *Holcus lanatus* (relatively fertile). We hypothesized that: 1) Living plants enhance dead root decomposition. 2) Species of fertile habitats accelerate dead root decomposition more than those from low fertility environments, because they produce more root biomass and consequently more exudates. 3) Increased N availability during root growth increases the decomposability of the roots after their death. 4) Dead roots of species from nutrient-rich habitats decompose more rapidly than those of species from nutrient-poor habitats.

To test these hypotheses we conducted a decomposition experiment with ^{14}C-labelled roots for one growing season. By using the carbon tracer ^{14}C a distinction could be made between respired native-soil carbon (i.e. the carbon present in the soil) and respired carbon from the dead roots. We calculated decomposition rates on the basis of the ^{14}C recovery from ^{14}C-labelled dead root materials in litterbags and the surrounding soil. The litterbags enabled us to easily recover the remaining dead roots after the decomposition period without losing the contact between the dead roots and the soil and allowing the roots of living plants to grow through the decomposing root material.

Materials and methods

Plant labelling

In 1996 10–20-d-old seedlings of *Holcus lanatus* L., *Festuca rubra* L., *Anthoxanthum odoratum* L. and *Festuca ovina* L. were grown for 8 weeks in an atmosphere containing 350 ppm CO_2 with a specific activity of 0.7 kBq/mg C in the ESPAS (Experimental Soil Plant Atmosphere System). The individual plants were grown in PVC tubes (4.6 cm in diameter and 22 cm length). The bottom of the tubes was closed with 30-μm gauze to prevent roots growing out and to allow water to enter the tubes. A layer of 3 cm silversand was put in the base of the tubes before filling the tubes with a mixture of sandy soil and sand (2:1). Each tube received 15 ml nutrient solution without N (N−) or with N (N+; 24 mg N per tube). The nutrient solution contained: KH_2PO_4 (1.34 mg ml^{-1}); $MgSO_4 \cdot 7H_2O$ (4.73 mg ml^{-1}); K_2SO_4 (1.54 mg ml^{-1}); $MnSO_4 \cdot H_2O$ (20.00 μg ml^{-1}); H_3BO_3 (26.90 μg ml^{-1}); $ZnSO_4 \cdot 7H_2O$ (25.06 μg ml^{-1}); $CuSO_4 \cdot 5H_2O$ (0.78 μg ml^{-1}); $Na_2MoO_4 \cdot 2H_2O$ (1.26 μg ml^{-1}); the pH was 6.5. In addition, the solution for the N+ treatment contained 11.55 mg KNO_3 ml^{-1}. The soil was mulched with plastic granules. The tubes were placed next to each other in a tray lined with felt. Each tube contained a single plant or was plantless. The light and dark periods during the growing period were 14 and 10 h, respectively. During the light period the temperature was 18°C, relative humidity was 70%, CO_2 concentration was 350 ppm and photosynthetic active radiation (PAR) was 350 μmol m^{-2} s^{-1} at plant level. During the dark period the temperature was 14°C, relative humidity was 80% and CO_2 concentration was 350 ppm. Plants were watered by adding water to the tray once or twice per week after weighing individual containers and measuring water loss.

After a growth period of 8 weeks, no water was added, to allow the soil to dry. When soil moisture content dropped below 4%, the shoots were clipped. The intact soil containers were left to dry to a soil moisture content below 1% and then stored in closed containers until the start of the decomposition experiment.

Decomposition experiment

The decomposition experiment started on 22 May and lasted until 2 November 1998. It was carried out in an open greenhouse in a completely randomized design. First, small containers (10 cm diameter and 31 cm height) were filled with 2670 g of a mixture of sandy soil and sand (1:1). Before mixing, the sandy soil was sieved through a 4-mm sieve. The soil mixture had the following characteristics: 5.9 $pH_{(H_2O)}$, 1.17 g total N kg^{-1} soil, 0.43 g total P kg^{-1} soil, C:N ratio of 16.6 and 30 g organic matter kg^{-1} soil. The litterbags (5 cm × 5 cm, mesh width 1 mm) were filled with 0.06–0.37 g labelled roots of *H. lanatus*, *F. rubra*, *A. odoratum* or *F. ovina* and placed on the soil in the containers and than covered with 600 g soil mixture.

In each container, three seedlings of *H. lanatus* or *F. ovina* were planted, aged, respectively, 9 weeks and 11 weeks old. Each species was planted in containers with dead roots of its own species or with dead roots of another species. Roots of the four species were also incubated in containers without living plants. In general, there were eight replicates for labelled roots. Because insufficient labelled root material was available, there were only four or five replicates for N − dead roots of *F. ovina*, three or four replicates for N + dead roots of *F. ovina* and five replicates for N − dead roots of *H. lanatus*. The soil surface was mulched with 50 g (1 cm) of white plastic granules to prevent growth of algae and reduce water loss by evaporation.

Growth of plants in the decomposition period, harvest and analysis

The water content of the containers was kept at 14% w/w by weighing the containers three times a week and then refilled with water to their original weight to compensate for water loss. During the experiment the containers with *H. lanatus* plants lost more water than the containers with *F. ovina* plants or the control containers without growing plants leading to slightly lower soil water contents during the first two months (Fig. 1). The decomposition experiment was harvested at the end of the growing season (2 November). At that time approximately 50% of the shoot biomass of *H. lanatus* was yellow. Shoots were clipped from the soil containers. The soil was carefully pushed out of the containers and separated into four layers: 1) the upper 5 cm above the litterbags (0–5 cm depth), 2) the 5 cm below the litterbags (5–10 cm depth), 3) 10–15 cm depth and 4) 15–27 cm depth. Soil and roots were separated. Shoots, roots and soil were dried at 70°C.

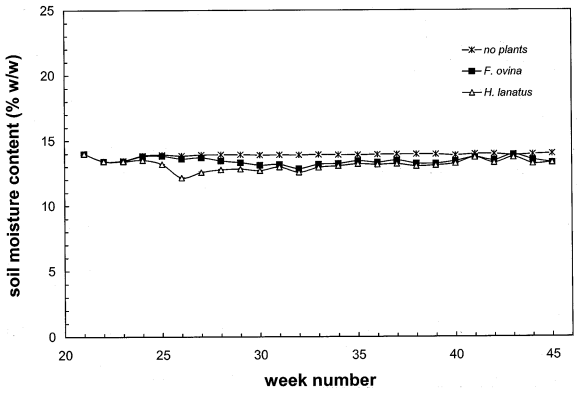

Fig. 1. Water content (percentage w/w) of the soil columns containing the decomposing roots and with either living *H. lanatus* or *F. ovina* plants, or without plants, during the experiment. The experiment started in week 21 (May 1998) and ran until week 45 (end of October 1998).

Chemical analyses

At the start of the decomposition experiment, roots were shaken in 250 ml water to remove soil particles. Then, the roots were dried and the C and N concentrations were measured using an element analyser (Fisons Instruments, EA 1108). The percentage N in the roots grown in soil without and with N addition was 0.8% and 0.9% for *H. lanatus*, 1.1% and 0.9% for *F. rubra*, 0.6% and 0.8% for *A. odoratum* and 0.9% and 1.7% for *F. ovina*, respectively. At the end of the decomposition experiment, the remaining amount of the labelled dead root ^{14}C (kBq) in the litterbags, the soil and the living roots were determined by scintillation counting, using a liquid scintillation counter (Packard, TRI-CARB 2100TR) after chemical destruction with $K_2Cr_2O_7$ (100 g/l). The percentage ^{14}C recovery of initial total root ^{14}C was calculated for the litterbags, for the soils and for the living roots. The amount of ^{14}C recovered in the roots of the living plants was negligible (less than 0.7% of the amount in the dead roots at the start of the experiment).

Shoots and roots of the growing plants were dried at 70°C for 48 h and organic matter content (550°C) and total C and N concentrations (element analyser) were measured. The N and P contents of the shoots and the roots were determined using a continuous flow analyser (Skalar autoanalyser San^{plus} system) after destruction with sulphuric acid, selenium and salicylic acid.

Statistical analyses

Analysis of variance was used to test the effect of living plant species, the effect of the decomposing dead root species and the effect of the N supply during the growth of the decomposing roots on the dead root decomposition rates. Data were analysed using analysis of variance (GLM procedure; SPSS 1995) for a completely randomized design factorial model. The GLM proce-

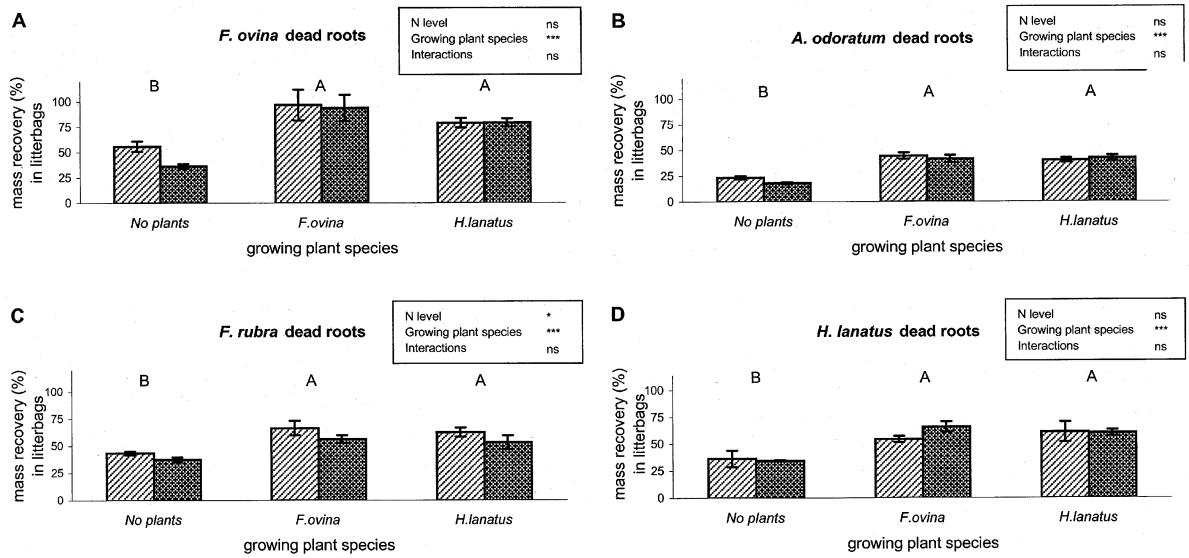

Fig. 2. Remaining mass of *F. ovina* dead roots (A), *A. odoratum* dead roots (B), *F. rubra* dead roots (C) or *H. lanatus* dead roots (D) as the percentage of the initial root mass in the litterbags. The dead roots are from plants grown at low nitrogen availability (hatched bars) or at high nitrogen availability (dark bars). The dead roots decomposed in columns without growing plants, with growing plants of *H. lanatus* or with growing plants of *F. ovina*. Data are means $\pm$ SE. Bars with the same letter are not significantly different (Tukey HSD, $P > 0.05$). * $P < 0.05$, *** $P < 0.001$, ns = not significant.

dure compensates for different numbers of replicates. When variances increased with the means, the data were logarithmically transformed. Where appropriate, a posteriori comparisons were carried out with Tukey's honest significant difference test.

Results

The amount of dead roots remaining in the litterbags

For dead root material of all four species the percentage remaining root mass was significantly higher when the decomposing roots were affected by growing plants (Fig. 2). The effects of the presence of living plant roots on the percentage mass recovery differed between decomposing root material of the four species (Table 1). Without growing plants, the species ranked with respect to remaining mass of decomposing roots in the order *F. ovina* > *F. rubra*, *H. lanatus* > *A. odoratum*. In the pots with living plants the remaining amount of *F. ovina* dead roots was significantly greater than that of the other three species. This difference between *F. ovina* and the other species was greater than in the treatment without living plants.

Overall, the N supply during the growth of the decomposing roots had no effect on the percentage mass recovery (Table 1). When data were analysed separately for the four decomposing root species, N availability during growth had a significant stimulating effect on the decomposition rate of the *F. rubra* roots (Fig. 2C), but not on the roots of the three other species (Fig. 2A, B, D).

Table 1. Analyses of variance (GLM) using a complete split-plot design for the percentage of the root mass remaining in litterbags, the percentage of dead root ^{14}C recovered from the litterbags or the soil, and the percentage of total dead root ^{14}C that was lost. The ^{14}C-labelled dead roots are from four species: *H. lanatus*, *F. rubra*, *A. odoratum* and *F. ovina*. Root species, living plant species and nitrogen level were used as main factors.

Effects	df	*F*-values of recovery (%)		*F*-values of loss (%)	
		mass in litterbags	^{14}C in litterbags	^{14}C in soil	total ^{14}C loss
Dead root species (R)	3	55.25***	29.84***	9.37***	19.07***
Living plant species (P)	2	80.78***	16.42***	9.29***	3.20*
Nitrogen level (N)	1	3.66^{NS}	20.80***	19.48***	5.21*
R × N	3	1.91^{NS}	9.16***	2.49^{NS}	7.25***
R × P	6	2.82*	3.42**	2.56*	3.16**
N × P	2	1.24^{NS}	3.11*	0.04^{NS}	0.95^{NS}
R × P × N	6	0.86^{NS}	1.64^{NS}	2.55*	1.70^{NS}

NS = not significant ($P > 0.05$), * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

The quantities of ^{14}C recovered in the litterbags

Both the nitrogen availability when roots were produced, the dead root species and the growing plant species had significant effects on the percentage ^{14}C recovery in the litterbags (Table 1). The percentage ^{14}C recovered from decomposing roots of *F. ovina* was significantly higher in pots with living *H. lanatus* plants than in pots with *F. ovina* plants (Fig. 3A). Living *H. lanatus* plants significantly increased the percentage ^{14}C recovered from decomposing *H. lanatus* roots, and both *H. lanatus* and *F. ovina* living plants increased the ^{14}C recovered from decomposing *F. rubra* roots compared to the treatment without plants (Fig. 3C, D). The amounts of ^{14}C recovered from the high N roots of *A. odoratum* were greater in pots with living *F. ovina* or *H. lanatus* than in pots without plants, but there were no significant differences between percentages recovered 14C from the low N roots (Fig. 3B).

Overall, the amounts of ^{14}C recovered from the dead roots in the litterbags ranked as *F. ovina* > *H. lanatus*, *F. rubra* > *A. odoratum*. N availability during growth had a significant stimulating effect on the decomposition rate of the *F. ovina* and *F. rubra* roots (Fig. 3A, C), but had no effect on the decomposition rate of *H. lanatus* roots (Fig. 3D). The N supply during growth had also no significant effect on the ^{14}C recovery from dead roots of *A. odoratum* in the treatment with living *H. lanatus* plants or without plants, but had a positive effect on the ^{14}C recovery in the treatment with living *F. ovina* plants (Fig. 3B).

The quantities of ^{14}C recovered in the soil

The presence of living plant species, dead root species and the N supply during root growth all had significant effects on the percentage of dead root ^{14}C that was recovered from the soil (Table 1). The presence of growing plants decreased the flux of ^{14}C from decomposing roots of *F. ovina* and *F. rubra* into the soil (Fig. 4A, C). In pots with decomposing root material of *A. odoratum* there were no effects of livings plants (Fig. 4B). In the pots with decomposing *H. lanatus* roots grown at low N availability there were no significant effects of living plants, but in the pots with high N roots of *H. lanatus* there were negative effects of living plants on the quantities of ^{14}C recovered from the soil (Fig. 4D).

Percentage total ^{14}C respiration losses

Total ^{14}C respiration losses can now be calculated by subtracting the amounts of ^{14}C that were recovered in soil and litterbag at the end of the experiment from the initial amounts in the dead roots that were incubated. Again, the presence of living plants, the dead root species and the N availability during the period in which the dead roots were grown had all significant effects on the percentage total dead root ^{14}C loss during the decomposition period (Table 1). There were only significant effects of living plants for decomposing roots of *F. ovina* and *A. odoratum*. The percentage total ^{14}C loss from decomposing roots of *F. ovina* was signifi-

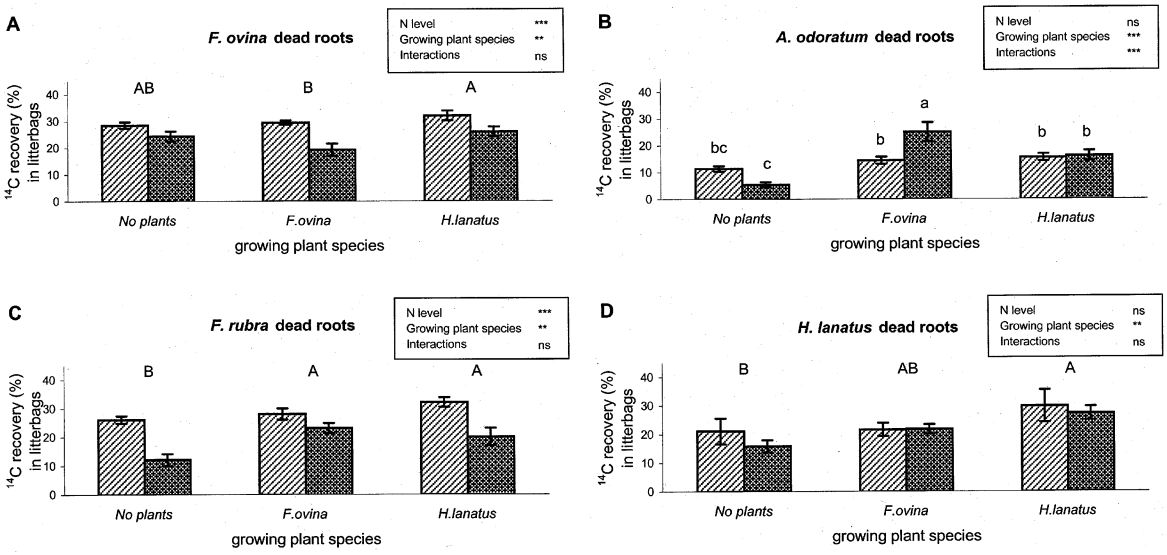

Fig. 3. Recovered quantities of ^{14}C from dead *F. ovina* roots (A), dead *A. odoratum* roots (B), dead *F. rubra* roots (C) or dead *H. lanatus* roots (D) in the litterbags as percentage of the initial amount of dead root ^{14}C in the litterbags. The dead roots are from plants grown at low nitrogen availability (hatched bars) or at high nitrogen availability (dark bars). The dead roots decomposed in columns without growing plants, or with growing plants of *H. lanatus* or with growing plants of *F. ovina*. Data are means ± SE. Bars with the same letter are not significantly different (Tukey HSD, $P > 0.05$). ** $P < 0.01$, *** $P < 0.001$, ns = not significant.

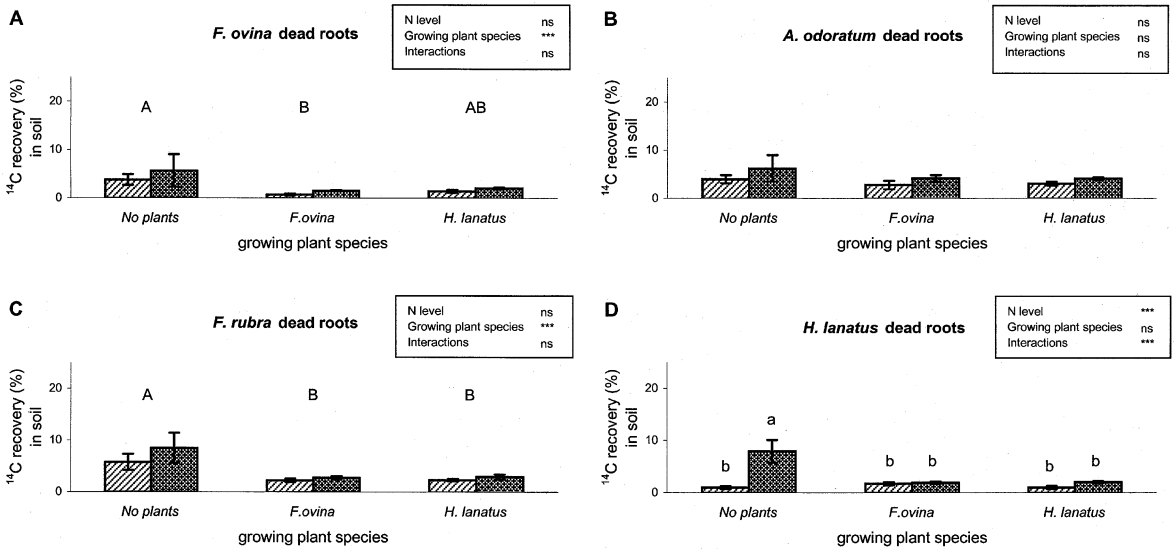

Fig. 4. Recovered quantities of ^{14}C in the soil from dead roots of *F. ovina* (A), dead roots of *A. odoratum* (B), dead roots of *F. rubra* (C) or dead roots of *H. lanatus* (D), as percentage of the initial amount of dead root ^{14}C in the litterbags. The dead roots are from plants grown at low nitrogen availability (hatched bars) or at high nitrogen availability (dark bars). The dead roots decomposed in columns without growing plants, with growing plants of *H. lanatus* or with growing plants of *F. ovina*. Data are means $\pm$ SE. Bars with the same letter are not significantly different (Tukey HSD, $P > 0.05$). *** $P < 0.001$, ns = not significant.

cantly higher in pots with living *F. ovina* plants (Fig. 5A). But the total ^{14}C loss from *A. odoratum* roots that were grown at high N supply was found to be inhibited by living *F. ovina* plants (Fig. 5B). N availability during growth had a significant positive effect on the total ^{14}C loss from *F. ovina* and *F. rubra* roots (Fig. 5A, C), but not on that from decomposing roots of *H. lanatus* (Fig. 5B).

In the pots without growing plants, the total ^{14}C loss from the four dead root species ranked in the order *F. ovina* < *H. lanatus*, *Festuca rubra* < *A. odoratum* roots. The ^{14}C loss of low N roots in pots with *Holcus lanatus*

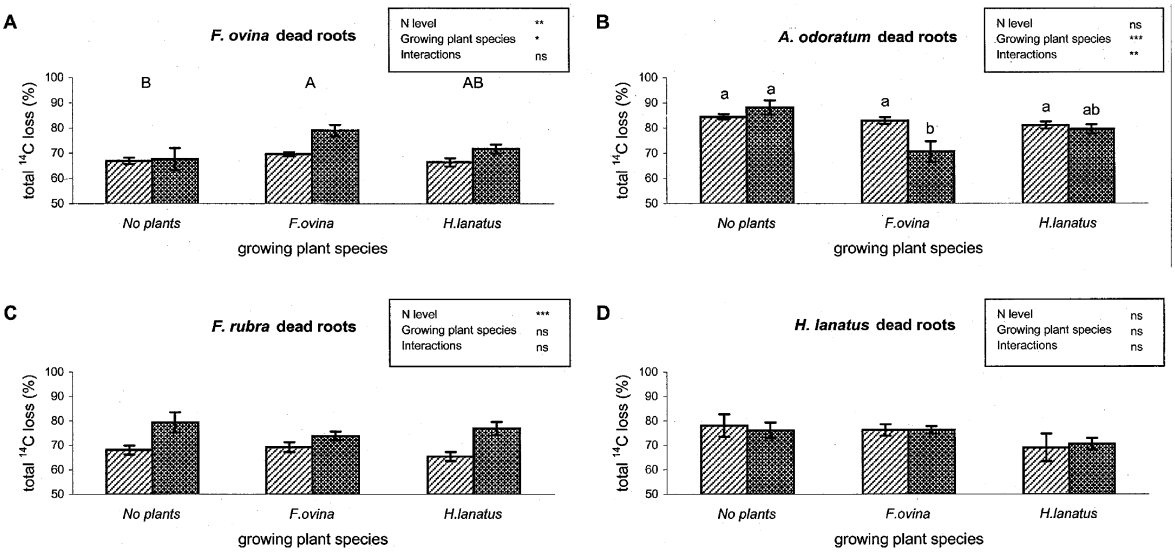

Fig. 5. Total quantities of ^{14}C from dead roots of *F. ovina* dead roots (A), *A. odoratum* (B), *F. rubra* (C) or *H. lanatus* (D) that were lost, expressed as percentage of the initial amount of dead root ^{14}C in the litterbags. The dead roots are from plants grown at low nitrogen availability (hatched bars) or at high nitrogen availability (dark bars). The dead roots decomposed in columns without growing plants, with growing plants of *H. lanatus* or with growing plants of *F. ovina*. Data are means $\pm$ SE. Bars with the same letter are not significantly different (Tukey HSD, $P > 0.05$). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant.

showed the same differences. In the treatments with growing *F. ovina* plants, however, the differences between the amounts of ^{14}C lost from the low N roots were smaller. There were no significant differences between ^{14}C losses from the high N roots of the four species in the treatments with living plants of *H. lanatus* and *F. ovina*.

Plant growth in the decomposition experiment

At the end of the experiment, the total plant biomass production did not differ between *F. ovina* and *H. lanatus* plants and was affected neither by the decomposing root species nor by the N level at which the roots were grown (Fig. 6A, Table 2). In the living *F.*

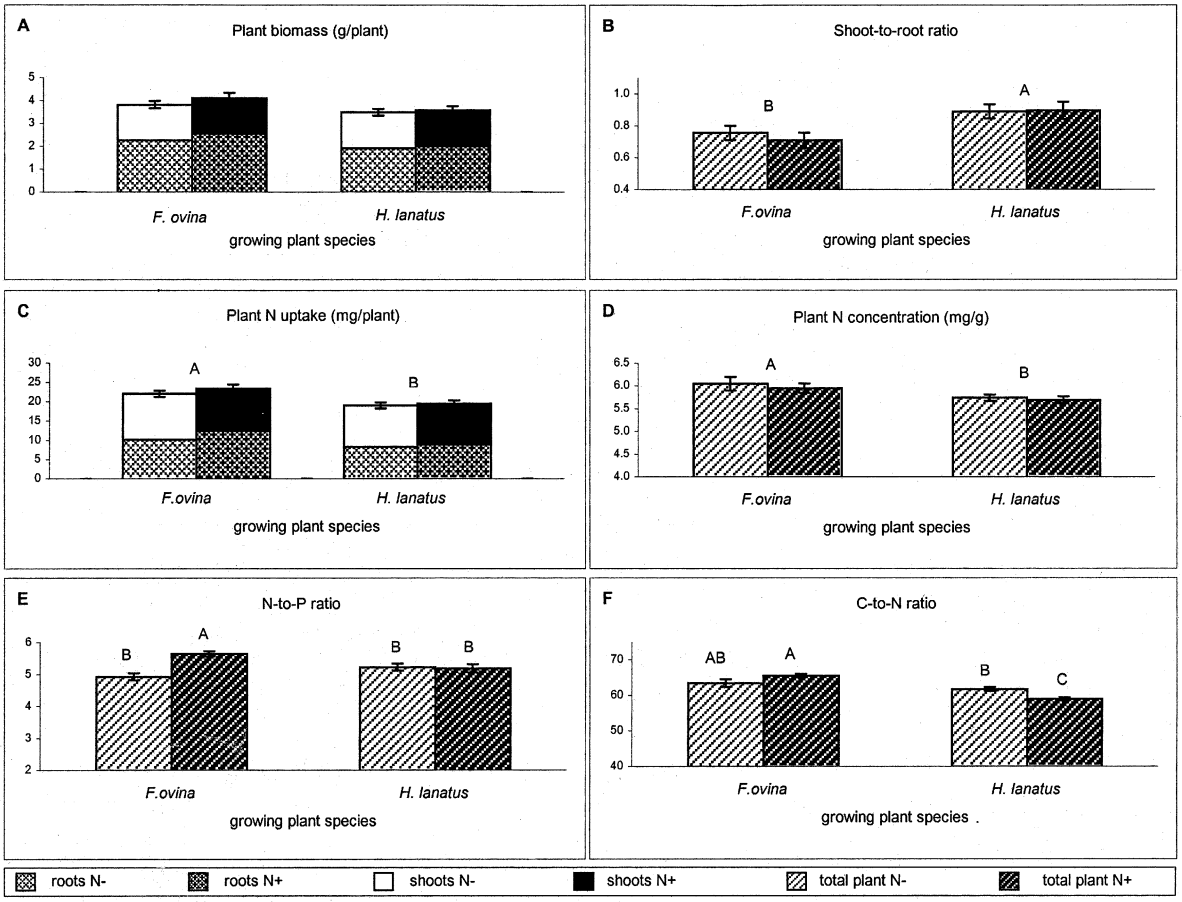

Fig. 6. The total biomass production (A), the shoot-to-root ratio of the plant (B), the total N uptake by the plant (C), the N concentration in the total plant (D), the N:P ratio (E) and the C:N ratio (F) of total living plants of *H. lanatus* and *F. ovina* grown on soil with decomposing roots of the four species *H. lanatus*, *F. rubra*, *A. odoratum* and *F. ovina* after a growing period of 22 weeks. The decomposing roots are from plants grown at a low nitrogen availability (light bars) or at high nitrogen availability (dark bars). Data are means $\pm$ SE. Bars with the same letter are not significantly different (Tukey HSD, $P > 0.05$).

Table 2. *F*-values of the ANOVA using a complete split-plot design for the total plant biomass production, the shoot:root ratio of the plant, the total N uptake by the plant, the N concentration in the total plant, the N:P ratio and the C:N ratio in whole plants of *H. lanatus* and *F. ovina* grown on soil with decomposing roots of the four species *H. lanatus*, *F. rubra*, *A. odoratum* and *F. ovina* after a growing period of 22 weeks. Root species, living plant species and nitrogen level were used as main factors.

Effects	df	biomass (g)	S:R ratio	N uptake (mg)	N concentration (mg/g)	N:P ratio	C:N ratio
Root species (R)	3	0.55^{NS}	0.11^{NS}	1.67^{NS}	0.76^{NS}	1.43^{NS}	1.18^{NS}
Living plant species (P)	1	3.82^{NS}	6.07*	12.37***	8.53**	0.33^{NS}	38.74***
Nitrogen level (N)	1	1.06^{NS}	0.97^{NS}	0.94^{NS}	0.67^{NS}	9.84**	0.49^{NS}
R × N	3	0.29^{NS}	0.89^{NS}	0.22^{NS}	1.52^{NS}	0.72^{NS}	0.24^{NS}
R × P	3	1.89^{NS}	1.63^{NS}	1.59^{NS}	0.62^{NS}	1.39^{NS}	1.09^{NS}
N × P	1	0.10^{NS}	0.15^{NS}	0.23^{NS}	0.01^{NS}	14.32***	12.71***
R × P × N	3	0.29^{NS}	0.16^{NS}	0.29^{NS}	0.41^{NS}	1.32^{NS}	2.97*

NS = not significant ($P > 0.05$), * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

ovina plants the total amount of N and the N concentration were higher than in the living *H. lanatus* plants (Fig. 6C, D). The total amount of N and the N concentration in the living plants were not affected by the kind of decomposing root material (Table 2). The shoot-to-root ratio of *H. lanatus* plants was higher than that of *F. ovina* plants (Fig. 6B), because *H. lanatus* had a smaller root biomass compared to *F. ovina*. Living plants of *F. ovina* grown on soil with decomposing roots that had been grown at high N supply had a significantly higher N-to-P ratio than *F. ovina* plants grown on decomposing roots grown at low N supply or living *H. lanatus* plants (Fig. 6E). The C:N ratio of living *H. lanatus* plants grown on soil with decomposing roots that had been grown in N+ soil was significantly lower than the C:N ratio of the other living plants (Fig. 6F, Table 2). The C:N ratio of living *F. ovina* plants grown on soil with decomposing roots that had been grown in N+ soil was significantly higher than the C:N ratio of the living *H. lanatus* plants, but did not differ from that of living *F. ovina* plants grown on decomposing roots that had been grown on N− soil (Fig. 6F).

Discussion

In this study we tested whether living plant roots affect the decomposition of dead roots and whether this effect differs between plant species. The ^{14}C labelling approach enabled us to measure the remaining quantities of carbon in the labelled material precisely, including the carbon that had moved to the soil through leaching or fungal growth. We found that living plants of *F. ovina* stimulated significantly the decomposition of dead root material of *F. ovina*. On the other hand, we measured clear negative effects of *F. ovina* plants on the decomposition of dead roots of *A. odoratum* that were grown at high N supply. There were no effects of living plants on the amounts of ^{14}C that were lost from the root litter of *F. rubra* or *H. lanatus*. It seems that the living *F. ovina* plants are able to accelerate the decomposition of dead roots of *F. ovina* by activating the microbial biomass with their rhizodeposits. It is striking that this positive effect was only found for *F. ovina* root litter that was produced at high N supply. The initial N concentrations in all root materials varied between 0.6 and 1.1%, but in high N root litter of *F. ovina* the N concentration was much higher (1.7%) due to the low maximum growth rate of this species. In the roots of this slow-growing species also the concentrations of phenolic compounds may be high (Eissenstat and Yanai 1997). This combination of chemical characteristics may have resulted in a reduced availability of carbon to the decomposing microorganisms, while N did not limit microbial activity. Under such circumstances the addition of easily available carbon compounds in rhizodeposits by living plant roots can be expected to have positive effects on the decomposition process.

We measured both the remaining dead root mass in the litterbags and the remaining quantities of dead root ^{14}C in the litterbags and in the soil. The results for the remaining root mass and the ^{14}C recovery in litterbags ran counter to the results for total ^{14}C losses. In contrast to the total ^{14}C losses, the data on mass recovery and ^{14}C recovery in the litterbags strongly suggested that living plant species inhibit dead root decomposition. The data on total ^{14}C loss clearly show that this is not true. The contrast is to be explained by the amount of ^{14}C recovered from the soil. The more dead root ^{14}C was lost from the litterbags, the more ^{14}C was recovered from the soil. These observations show once again that conclusions about decomposition from litterbag experiments have to be considered carefully. Our results suggest that decomposition measurements with ^{14}C-labelled roots are far more accurate than simple mass loss measurements.

Our second hypothesis was that species of fertile habitats accelerate dead root decomposition more than those from low-fertility environments, because they produce more root biomass and consequently more exudates. *H. lanatus* has a higher maximum relative growth rate than *F. ovina* (225 mg g^{-1} d^{-1} versus 140 mg g^{-1} d^{-1}), but the expected higher root decomposition in the presence of *H. lanatus* than in the presence of *F. ovina* did not occur. In the present experiment, however, the root biomass of living *H. lanatus* plants was even lower than that of *F. ovina* plants. This could account for the greater stimulating effect on *F. ovina* dead root decomposition of *F. ovina* plants compared to living *H. lanatus* plants.

The observed positive effects of living plant roots on dead root decomposition contradict those of other experimental studies where root growth suppressed the decomposition and transformation of dead roots or soil organic matter (Reid and Goss 1982, Sparling et al. 1982, Nicolardot et al. 1995), but agree with another study where the presence of living roots increased decomposition rates (Clarholm 1985). In addition to our rhizodeposition hypothesis, there are several other mechanisms that could explain how plants affect the decomposition of labelled roots and the N mineralization from plant remains.

One important process affecting the decomposition process is the drying and rewetting cycle of soils as a result of water uptake by plants. Such cycles may lead both to activation of the microbial biomass (Van Schreven 1967) or to a retarded decomposition of plant material (Magid et al. 1999). Earlier studies have shown that in field experiments, decomposition rates were reduced in the presence of plant cover (Jenkinson 1977, Sparling et al. 1982). These authors suggested that the living plants could inhibit the microbial activity by the

desiccation of the soil as a result of water uptake and transpiration (Jenkinson 1977, Sparling et al. 1982). In our study we eliminated the water effect as much as possible by keeping the pots at equal soil water contents by weighing them with time intervals of 2–3 d. The mean water content of the containers fluctuated between 12% and 14%. We cannot exclude that such small variations in water content have had significant effects on microbial activity.

A second possible mechanism whereby living plants can affect the microbial activity is when soil microorganisms prefer to use materials released from the living roots instead of the compounds from dead roots (Reid and Goss 1982, Nicolardot et al. 1995). This mechanism accounts for living plants having an inhibiting effect on dead root decomposition. In their "preferential substrate utilization concept" Van Veen et al. (1993) stated that rhizodeposits provide an energy-rich basis for energy and biosynthesis processes for microbes and that microbes might prefer these root-released carbon compounds over native soil organic matter.

Finally, another possible mechanism is competition for N between plants and soil microbes. In an earlier study with the same species, we also found that living plants activated root decomposition (Van der Krift et al. unpubl.). However, the stimulating effect of the living plants in that study was much stronger than in the present experiment. A possible reason for this difference is given by the characteristics of the decomposing plant material in the two experiments: the C:N ratio in the present study was almost double the C:N ratio in the earlier study. It is possible that in the present experiment the C:N ratio of the decomposing roots was above the critical C:N ratio for the decomposer organisms (Cadisch and Giller 1997, Seneviratne 2000), so that the decomposing dead roots immobilized inorganic nitrogen. This would have led to competition for nitrogen between growing plants and microbes, which may have reduced the positive effects of living plants on ^{14}C loss in this study compared to the earlier study (Van der Krift et al. unpubl.). The only material that showed increased decomposition in pots with living plants was the high N *F. ovina* root litter that had apparently a sufficiently low C:N ratio.

Our third hypothesis was that higher N availability during growth could increase the decomposability of dead roots and thereby the N mineralization. The addition of N during the period in which the roots had been growing increased total ^{14}C losses and ^{14}C losses from the litterbags in the case of decomposing *F. ovina* and *F. rubra* roots but did not increase the ^{14}C loss of dead *H. lanatus* roots. *F. ovina* roots grown at high N supply had higher N concentrations, but the N content in the dead roots of *F. rubra* did not change if they had been grown with N addition. In contrast, N addition during the growth of *A. odoratum* roots decreased the decomposition rate of these roots in the treatment with *F. ovina* plants.

Finally, we hypothesized that dead roots of species from fertile habitats decompose more rapidly than dead roots of species from nutrient-poor habitats. In the present study, plant species differed in dead root decomposition rates but there was no evidence for the hypothesis that dead roots of high fertility species decompose faster than dead roots of low fertility species. In bare soil, the decomposability of *A. odoratum* dead roots was higher than that of *H. lanatus*, *F. rubra* and *F. ovina* dead roots. This confirms the results of earlier studies on the same grass species (Van der Krift et al. unpubl.).

An intriguing question is whether the decomposing roots had an effect on the growth and the N uptake of the living plant species. In the present study, added amounts of N in the dead roots were very small (1.54 mg N) compared to the total amount of N in the soil organic matter (3.29 g N per container). Nevertheless, in the presence of decomposing roots, *F. ovina* plants took up more N. It is striking that the overall N uptake by the *F. ovina* plants exceeded the N uptake by *H. lanatus* plants. It is possible that living plants of *F. ovina* not only stimulated the dead root decomposition, but that they could also take advantage of this effect. However, the differences in N uptake of *F. ovina* and *H. lanatus* plants is not solely attributable to the N release from litterbags (max. 1 mg N/litterbag = 0.3 mg N/plant). So, possibly *F. ovina* plants can also increase the mineralization of the soil organic matter.

The main question in this study was whether living plant species actively regulate the decomposition of litter. We found that in addition to the effects of differences in biomass production, biomass turnover time and litter decomposition (Berendse et al. 1989, Van Vuuren et al. 1993, Brevedan et al. 1996, Cadisch and Giller 1997) living plant roots may also have significant effects on the decomposition of litter. Our data show that living plants can accelerate dead root decomposition and subsequent mineralization. We conclude that living plants probably release carbon compounds that could stimulate the growth of soil microorganisms (Reid and Goss 1982, Van Veen et al. 1993, Nicolardot et al. 1995).

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References

Berendse, F. 1990. Organic matter accumulation and nitrogen mineralization during secondary succession in heathland ecosystems. – J. Ecol. 78: 413–427.

Berendse, F. 1998. Effects of dominant plant species on soils during succession in nutrient-poor ecosystems. – Biogeochemistry 42: 73–88.
Berendse, F., Bobbink, R. and Rouwenhorst, G. 1989. A comparative study on nutrient cycling in wet heathland ecosystems. II. Litter production and nutrient mineralization. – Oecologia 78: 338–348.
Berendse, F., Braakhekke, W. and Van der Krift, T. A. J. 1998. Adaptations of plant populations to nutrient-poor environments and implications for soil nutrient mineralization. – In: Lambers, H., Poorter, H. and Van Vuuren, M. M. I. (eds), Inherent variation in plant growth. Physiological mechanisms and ecological consequences. Backhuys, pp. 503–514.
Bremer, E. and Kuikman, P. J. 1997. Influence of competition for nitrogen in soil on net mineralization of nitrogen. – Plant Soil 190: 119–126.
Brevedan, R. E., Busso, C. A., Montani, T. and Fernandez, O. A. 1996. Production and nitrogen cycling in an ecosystem of *Eragrostis curvula* in semiarid Argentinia. II Nitrogen content and transfer. – Acta Oecol. 17: 211–223.
Cadisch, G. and Giller, K. E. 1997. Driven by nature: plant litter quality and decomposition. – CAB, Wallingford, UK.
Clarholm, M. 1985. Interactions of bacteria, protozoa and plants leading to mineralization of soil nitrogen. – Soil Biol. Biochem. 17: 181–187.
Eissenstat, D. M. and Yanai, R. D. 1997. The ecology of root lifespan. – Adv. Ecol. Res. 27: 1–60.
Grayston, S. J., Vaughan, D. and Jones, D. 1996. Rhizosphere carbon flow in trees, in comparison with annual plants: the importance of root exudation and its impact on microbial activity and nutrient availability. – Appl. Soil Ecol. 5: 29–56.
Janzen, H. H. and Radder, G. D. 1989. Nitrogen mineralization in a green manure-emended soil as influenced by cropping history and subsequent crop. – Plant Soil 120: 125–131.
Jenkinson, D. S. 1977. Studies on the decomposition of plant material in soil. V. The effects of plant cover and soil type on the loss of carbon from ^{14}C labelled ryegrass decomposing under field conditions. – J. Soil Sci. 28: 424–434.
Liljeroth, E., Van Veen, J. A. and Miller, H. J. 1990. Assimilate translocation to the rhizosphere of two wheat cultivars and subsequent utilization by rhizophere microorganisms at two soil nitrogen levels. – Soil Biol. Biochem. 22: 1015–1021.
Magid, J., Kjærgaard, C., Gorissen, A. and Kuikman, P. J. 1999. Drying and rewetting of a loamy sand soil did not increase the turnover rate of native organic matter, but retarded the decomposition of added ^{14}C-labelled plant material. – Soil Biol. Biochem. 31: 595–602.
Nicolardot, B., Denys, D., Lagacherie, B. et al. 1995. Decomposition of ^{15}N-labelled catch-crop residues in soil: evaluation of N mineralization and plant-N uptake potentials under controlled conditions. – Eur. J. Soil Sci. 46: 115–123.
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. – J. Soil Sci. 33: 387–395.
Robinson, D., Griffiths, B., Ritz, K. and Wheatley, R. 1989. Root-induced nitrogen mineralisation: a theoretical analysis. – Plant Soil 117: 185–193.
Seneviratne, G. 2000. Litter quality and nitrogen release in tropical agriculture: a synthesis. – Biol. Fertil. Soils 31: 60–64.
Sparling, G. P., Cheshire, M. V. and Mundie, C. M. 1982. Effect of barley plants on the decomposition of ^{14}C-labelled soil organic matter. – J. Soil Sci. 33: 89–100.
Swinnen, J., Van Veen, J. A. and Merckx, R. 1994a. ^{14}C pulse-labelling of field-grown spring wheat: an evaluation of its use in rhizosphere carbon budget estimations. – Soil Biol. Biochem. 26: 161–170.
Swinnen, J., Van Veen, J. A. and Merckx, R. 1994b. Rhizosphere carbon fluxes in field-grown spring wheat: model calculations based on ^{14}C partitioning after pulse-labelling. – Soil Biol. Biochem. 26: 171–182.
Van Schreven, D. A. 1967. The effect of intermittent drying and wetting of a calcareous soil on carbon and nitrogen mineralization. – Plant Soil 26: 14–32.
Van Veen, J. A., Kuikman, P. J. and Bremer, E. 1993. The regulation of carbon and nitrogen turnover in the rhizosphere. – In: Guerrero, R. and Pedros-Alio, C. (eds), Trends in microbial ecology. Spanish Society for Microbiology, pp. 239–242.
Van Vuuren, M. M. I., Berendse, F. and de Visser, W. 1993. Species and site differences in the decomposition of litters and roots from wet heathlands. – Can. J. Bot. 71: 167–173.
Vinton, M. A. and Burke, I. C. 1995. Interactions between individual plant species and soil nutrient status in shortgrass steppe. – Ecology 76: 1116–1133.
Vitousek, P. M., Turner, D. R., Parton, W. J. and Sanford, R. L. 1994. Litter decomposition on the mauna loa environmental matrix, Hawai'i: patterns, mechanisms, and models. – Ecology 75: 418–429.
Wardle, D. A., Barker, G. M., Bonner, K. I. and Nicholson, K. S. 1998. Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? – J. Ecol. 86: 405–420.
Wedin, D. A. and Tilman, D. 1990. Species effect on nitrogen cycling: a test with perennial grasses. – Oecologia 84: 433–441.