

Root Effects on Soil Organic Matter Decomposition

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Roots of higher plants, a key functional component of belowground systems and one of the main soil-forming agents (Jenny, 1941), interact with virtually all soil components. Processes that are largely controlled or directly influenced by roots and often occur in the vicinity of the root surface are often referred to as rhizosphere processes. These processes may include root production through growth and death (root turnover), rhizodeposition, root respiration, and rhizosphere microbial respiration that is a result of microbial utilization of rhizodeposits. Rhizosphere processes play an important role in the global C cycle (Fig. 7-1). Terrestrial ecosystems are intimately connected to atmospheric carbon dioxide (CO₂) levels through photosynthetic fixation of CO₂, sequestration of CO₂ into biomass and soils, and the subsequent release of C through respiration and decomposition of organic matter. Considering all the pools and fluxes of C within ecosystems, C cycling belowground is increasingly being recognized as one of the most significant components (Jackson et al., 1997; Zak and Pregitzer, 1998). Globally, the input of C to the soil has been estimated to be as great as $60 (10^{-5} \text{ g yr}^{-1})$ (Post et al., 1990). Thus, small changes in the equilibrium between inputs and decomposition could have a significant impact on atmospheric CO₂ concentrations, which may either exacerbate or reduce the consequence of burning of fossil fuels (Schimel, 1995).

Carbon dioxide efflux from the soil is a combination of two distinct processes: (i) rhizosphere respiration, including root respiration and microbial respiration from the metabolism of rhizodeposits and (ii) microbial decomposition of soil organic matter (SOM). The substrates for rhizosphere respiration come from C recently fixed through photosynthesis, whereas SOM decomposition is primarily a function of soil heterotrophic activities using soil C. The two processes act simultaneously and are also linked through rhizosphere interactions, which

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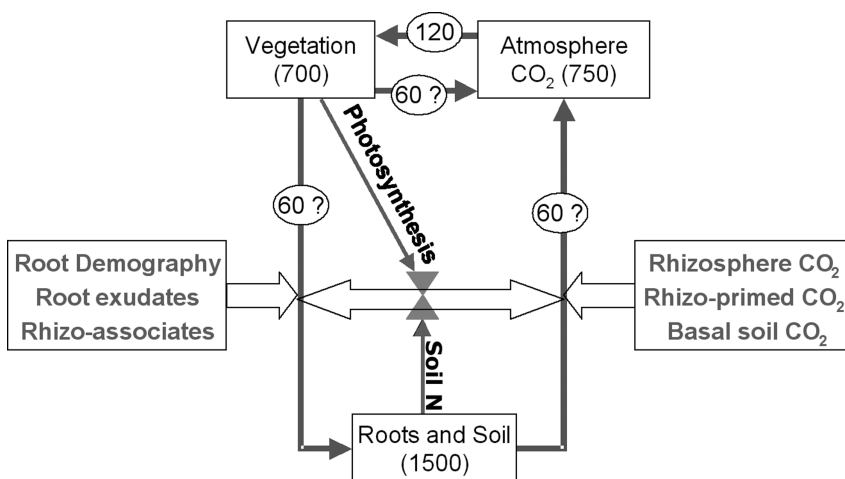


Fig. 7-1. A conceptual model depicting potential mechanisms controlling rhizosphere C dynamics. The unit of the numbers is 10^{15} g (annually for fluxes) (Based on Post et al., 1990).

may exert a stimulative (priming effect) or a suppressive influence on SOM decomposition (Cheng, 1999; Van Veen et al., 1991). The focus of this chapter is on this linkage and the associated rhizosphere interactions.

Large amounts of C and mineral nutrients contained in plants recycle back to the soil through rhizosphere processes (Pregitzer et al., 1995). A significant amount of work has been done quantifying root production (Vogt et al., 1986; Cheng et al., 1990; Hendrick and Pregitzer, 1993; Eissenstat and Yanai, 1997) and total rhizodeposition (Lynch and Whipps, 1990; Kuzyakov and Domanski, 2000). However, only limited effort has been made to link rhizosphere processes with soil processes such as organic matter decomposition and nutrient transformation. A recent report from the EUROFLUX project clearly illustrates the potential importance of rhizosphere processes in determining the net C gain or loss in 18 forest ecosystems in Europe (Janssens et al., 2001). It is challenging to link rhizosphere processes with soil processes such as organic matter decomposition. Although studies (e.g., Helal and Sauerbeck, 1984, 1986; Liljeroth et al., 1994) have indicated that input of labile substrates in the rhizosphere may significantly enhance SOM decomposition as a result of the priming effect (Dalenberg and Jager, 1989), rates of SOM decomposition are commonly assessed by laboratory incubations of soil samples with an often implicit assumption that rhizosphere processes have little impact on the results. However, the assumption has rarely been rigorously tested. Many questions remain to be answered. What is the potential effect of the rhizosphere on SOM decomposition? Is it significant enough to warrant serious investigation? How does the rhizosphere effect on SOM decomposition change through time? What biotic and abiotic factors (e.g., N, CO₂, light, soil types, and plant species) control or influence the level of root effects on SOM decomposition? Which kinds of rhizosphere mechanisms and interactions change the SOM

decomposition rate? By reviewing published results on this issue, we aim to address these questions and describe the current stage of understanding on the mechanisms that regulate these root effects.

METHODOLOGY

Studies of root effects on decomposition processes have been restricted by the limitation of existing methods. Carbon dioxide released by a respiring system of living roots and soil may have four origins (Fig. 7-2): (i) root respiration, (ii) microbial respiration using substrates from live roots (rhizo-microbial respiration), (iii) rhizosphere-stimulated (or suppressed) microbial respiration using SOM as the substrates, and (iv) microbial respiration using SOM without the influence of live roots (basal respiration), which is often measured in soil incubations. The third source is also called the “primed decomposition” or the “priming effect.” Total rhizosphere respiration is defined as the sum of root respiration and rhizo-microbial respiration. Carbon used in total rhizosphere respiration is all derived from photosynthesis or storage of living plants. Studying root effects on decomposition requires separation of decomposing sources of focus from sources of live roots. This has been mostly accomplished by using isotope techniques. Methods used in published studies can be grouped into five main categories: (i) labelled

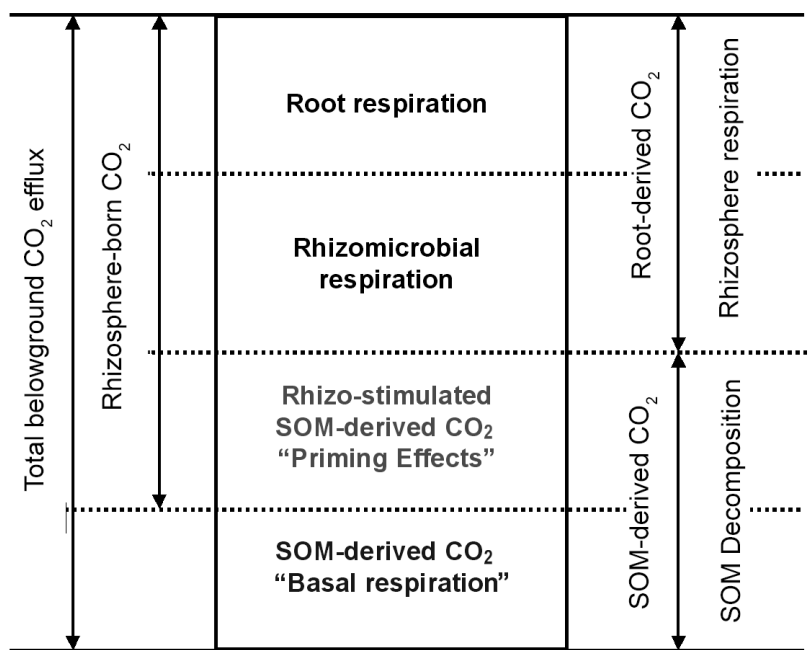


Fig. 7-2. The separation of different sources of carbon dioxide (CO₂) evolved from the belowground system.

litter, (ii) pulse-labelling of plants, (iii) continuous labelling of plants, (iv) natural ^{13}C tracers, and (v) N budgeting. Without C isotopic labelling and tracing, simple C budgeting approach is inadequate for studying root/rhizosphere effects on SOM decomposition because of the unavoidable mixing of C sources from roots and SOM. However, N budgeting has been used to evaluate the effect of roots on N mineralization with considerable success (e. g., Wang and Bakken, 1997; Merbach et al., 1999). Because the quantity of N deposition from living roots is often negligible compared to the amount of soil mineral N or N taken up by plants, total N mineralization can be a reasonable measure of SOM decomposition if microbial N immobilization is also negligible.

With the labelled-litter method, plants are grown in soils mixed with isotope-labelled (C or N) litter, so that the release of the labelled source between the planted treatment and an unplanted control can be compared. The difference in either CO_2 production or N release allows the determination of root effects on the rate of litter decomposition if other soil conditions have been kept the same. This method requires production of uniformly labelled litter before the start of the experiment. Some studies indicate that multiple pulse labelling is an acceptable alternative to continuous labelling to produce labelled litter for decomposition studies (Sparling et al., 1982; Sallih and Bottner, 1988). However, the degree of uniformity of the labelled litter has been an issue of concern because unevenly labelled litter may produce seriously biased results. Litter labelled with ^{14}C has been the most common form in published studies. This method is relatively easy to use. The major drawback of this method is that it only measures the change in the labelled components in litter, and does not necessarily represent the decomposition of SOM.

The pulse labelling method involves pulse-labelling plants with C isotopes so that C from the live roots can be separately monitored from the soil C (Kuzyakov et al., 2001; Kuzyakov and Cheng, 2001). Difference in the rates of soil C loss between the planted treatment and the unplanted control is a measure of root effect on the rate of SOM decomposition. This method has not been used often because it involves complicated calculations and some assumptions (Kuzyakov et al., 2001). One of the assumptions is that the specific activity of the root-derived CO_2 is the same as that of the roots sampled at the end of the experiment, which has not yet been critically tested. Another assumption is that plant shoots and roots grow linearly during the period of the experiment. A comparison of the pulse-labelling method of Kuzyakov and Cheng (2001) with the natural ^{13}C -tracer method of Cheng (1996) shows that the two methods may give similar results in terms of total rhizosphere respiration measurements. However, because pulse labelling does not uniformly label all plant C, total plant-derived C cannot be separated from soil-derived C in a pulse-labelling experiment.

The continuous labelling method has been used in several studies (e.g., Liljeroth et al., 1994; Helal and Sauerbeck, 1983, 1984, 1986). This method requires that plants are grown in an atmosphere with labelled C dioxide ($^{13}\text{CO}_2$ or $^{14}\text{CO}_2$) of a relatively constant specific activity or enrichment throughout an entire experiment so that all plants are uniformly labelled, because photosynthetically fixed CO_2 is the sole source of plant C. This continuous labelling method allows separation of plant-derived C from the soil C. The difference in the rates of soil C loss between

the planted treatment and the unplanted control is a measure of root effect on the rate of SOM decomposition. This method focuses on the mineralization of total soil organic C pool instead of on plant litter C only as in the case of the labelled litter method. Both ^{14}C pulse labelling and continuous labelling methods have limitations. Continuous ^{14}C labelling requires special facilities that are available at only a few places in the world. Also, the continuous ^{14}C labelling method often requires transplanting of seedlings which may have considerable unlabelled C reserves, therefore requiring some time for all plant parts to become uniformly labelled. Because of the safety issue due to the use of radioactive materials, most ^{14}C -labelling experiments have been of short duration. The safety issue can be avoided if $^{14}\text{CO}_2$ is replaced with $^{13}\text{CO}_2$ in the continuous labelling experiment. However, ^{13}C mass spectrometry analysis is much more expensive and time consuming than ^{14}C scintillation counting.

Natural ^{13}C abundance has also been used to trace root effects on SOM decomposition (Cheng, 1996; Qian et al., 1997; Rochette and Flanagan, 1997). The principle of the natural ^{13}C tracer method is based on two factors: (a) the difference in the ^{13}C : ^{12}C ratio (often reported in $\delta^{13}\text{C}$ value) between plants with the C_3 photosynthetic pathway whose mean $\delta^{13}\text{C}$ is -27‰ and plants with the C_4 pathway whose mean $\delta^{13}\text{C}$ is -12‰ (Smith and Epstein, 1971), and (b) the subsequent difference between SOM derived from the two types of plants. SOM derived from C_4 plant-dominated vegetation (C_4 -derived soil) such as tallgrass prairies and tropical grasslands may have $\delta^{13}\text{C}$ values ranging from -12 to -20‰ , whereas $\delta^{13}\text{C}$ values of SOM derived from cold and temperate forest (C_3 -derived soil) may range from -23 to -27‰ . By using C_4 -derived soil in a C_3 plant system or vice versa, the C entering the soil via live roots will have a different $\delta^{13}\text{C}$ value than the $\delta^{13}\text{C}$ value of SOM. Thus the total amount of C dioxide evolved from the root-soil system can be separated into the plant-derived source and the soil-derived source.

This natural ^{13}C method eliminates some of the major limitations of earlier labelling methods and offers a new opportunity for systematic studies of the mechanisms regulating the quantity and quality of rhizodeposition as well as the interactions between plant roots and SOM decomposition. As mentioned above, this method requires the switch of C_3 -plants from their original C_3 -soils to C_4 -derived soils or the switch of C_4 -plants from their original soils to C_3 -derived soils. Because of this switch, the composition of soil microbial communities may be different from the original one. Therefore, one untested assumption associated with this method is that the switches of plant species from their original soils do not substantially modify rhizosphere processes. Compared to the continuous ^{14}C -labelling approach, a major drawback of this method is the much higher cost associated with sample analysis for ^{13}C (Cheng, 1996). Another limitation of this method is its relatively low sensitivity and low accuracy.

SYNTHESIS OF CURRENT RESULTS

The labelled-litter method has been one of the most common methods used to study root effects on litter decomposition. This method was employed initially in several field studies (e.g., Jenkinson, 1977; Shields and Paul, 1973; Fuhr and

Sauerbeck, 1968). In these field studies, the rate of loss of ^{14}C -labelled C was measured in treatments of planted and unplanted fallow control. One common result of these studies was that planted treatments significantly reduced labelled litter decomposition as compared to the fallow control and that the soil moisture level in the planted treatment was also significantly reduced. Therefore, the reduction in the rates of litter decomposition was most likely caused by the drier soil conditions due to plant water uptake and transpiration. In other words, the effect of planting and root growth on litter decomposition was confounded by their effects on soil water conditions. In order to resolve this confounding outcome, soil water levels have to be maintained to a similar level between the planted treatment and the unplanted control by frequent watering or irrigation. In this synthesis, we exclude results generated from experiments that did not have adequate soil water control.

For comparisons between different studies, we calculated priming effect values as percents of the unplanted control (% priming) due to the presence of the rhizosphere based on the following formula:

$$\% \text{ priming} = \frac{R_P - R_{NP}}{R_{NP}} \times 100$$

where R_P is the SOM decomposition rate of the planted treatment and R_{NP} is the SOM decomposition rate of the unplanted treatment. The presence of the rhizosphere stimulates SOM decomposition when % priming is a positive value and suppresses decomposition when it is a negative value.

Labelled Litter Studies

The effect of roots on SOM decomposition, based on labelled litter methods under controlled water conditions, are summarized in Table 7-1. The % priming values from these studies ranged from 270% (Sparling et al., 1982) to 23% (Helal and Sauerbeck, 1987). These results demonstrated that the presence of roots may either enhance or suppress the decomposition of labelled litter, depending on the coupling of plant species with soil types, experimental conditions, and the duration of the experimental period (Sallih and Bottner, 1988). All these results were obtained from experiments under well-watered and well-aerated conditions and with limited plant types (all from the Monocotyledonae). The experimental duration for the studies was <2 mo except for one study that lasted 690 d. Some studies (Reid and Goss, 1982; Sparling et al., 1982) attempted to estimate root effects on SOM decomposition by incubating the labelled litter (shoots or roots) in the soil before planting. However, the labelled materials from the litter would not be incorporated into the SOM evenly. Therefore, the results should be interpreted as root effects on litter decomposition instead of SOM decomposition as a whole. In the report by Cheng and Coleman (1990), the influence of fertilization and microbial biomass was also assessed. They found that the amount of ^{14}C -labelled microbial biomass C was highly correlated with the amount of $^{14}\text{CO}_2$ released during their experiment, and thereby speculated that microbial biomass or activities were the main determinant of the outcomes of root effect on decomposition. Helal and Sauerbeck (1987) also indicated that there was less ^{14}C -labelled materials remaining at the end of the experiment in the planted soil zones than soil zones away from roots or the unplanted control. Sallih and Bottner (1988) noted that there was

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Table 7-1. Magnitude of the root effect on the decomposition of labeled litter added to the soil.

Plant type	Material of focus	Soil type, C %	PGC [†]	% Priming [‡]	Duration(d)	Reference
Rye	¹⁴ C rye litter	Typic Kanadult, 1.1%	GH	11	49	Cheng and Coleman (1990)
Maize	¹⁴ C maize litter	Luvisol/Chernozem	GC	23	25	Helal and Sauerbeck (1987)
Maize.	¹⁴ C barley roots	Sandy loam, 2%C	GH	-53	22	Reid and Goss (1982)
<i>Lolium perenne</i>	¹⁴ C barley roots	Sandy loam, 2%C	GH	-38	42	Reid and Goss (1982)
Maize	¹⁴ C barley roots	Sandy loam, 2%C	GH	-21	22	Reid and Goss (1983)
<i>Lolium perenne</i>	¹⁴ C barley roots	Sandy loam, 2%C	GH	-30	42	Reid and Goss (1983)
Wheat	¹⁴ C wheat litter	Fersiallitic calcic, 2.7%C	GH	-10 to 20	690	Sallih and Bottner (1988)
Barley	¹⁴ C rye litter	4.8% C	GH	-70	42	Sparling et al.. (1982)

[†]Plant growth conditions: GH = greenhouse; GC = growth chamber.

[‡]Each value is calculated as: (planted 2 unplanted)/unplanted × 100.

an inhibition effect of wheat (*Triticum aestivum* L.) roots during early period (0–200 d) of the experiment and a positive priming effect of roots during the later part (200–690 d) of the experiment. There were seven frequent harvests of shoots and roots during the whole experiment, which might have imposed a high degree of disturbance to the experimental system. Results of the negative priming effect were mostly reported by Reid and Goss (1982, 1983) and Sparling et al. (1982). These studies reported a significant amount of ^{14}C -labelled C was taken up by plant roots, which might have contributed to the negative priming effect of the roots on decomposition of the labelled materials.

Continuous Labelling Studies

The magnitude of root effects on SOM decomposition was assessed in four published studies using continuous labelling methods as found in a literature search (Table 7–2). In all these studies, soil water was controlled to a similar level between the planted treatment and the unplanted control by frequent watering. The potential effect of soil drying in planted treatments was at a minimum. The values of % priming were estimated using the data/figures reported in these studies. The % priming values ranged from 33% to as high as 332%. These results demonstrated that the presence of roots enhanced the decomposition rate of original SOM in all four studies. The experimental duration was short for all studies (<55 d). Nitrogen fertilization reduced the priming effect of roots on SOM decomposition rates from 196% priming to 33% for wheat and from 196 to 133% for maize (*Zea mays* L.) (Liljeroth et al., 1994). Studies by Helal and Sauerbeck (1984, 1986) reported much higher % priming values (336 and 432%). These higher values were indirectly derived from soil C budgets (^{12}C -C) instead of direct measurements of soil C loss as $^{12}\text{CO}_2$ as in the case of Liljeroth et al. (1990, 1994). The approach of total soil C budgeting has much lower sensitivity and accuracy than directly measuring soil C loss in the form of $^{12}\text{CO}_2$ because the inherently high variability of total soil C contents often buries treatment differences in terms of soil C loss. However, the consistently lower amount of soil C remaining in the soil sections with roots or closer

Table 7–2. Magnitude of the root effect on soil organic matter (SOM) decomposition as assessed by continuous ^{14}C -labeling of plants.

Plant type	Treatment	Soil type,	C %	PGC†	% Priming‡	Time (d)	Reference
Wheat	High N	Loamy sand	2% C	GC	33	54	Liljeroth et al. (1990)
Maize	High N	Loamy sand	2% C	GC	133	47	Liljeroth et al. (1994)
Wheat	High N	Loamy sand	2% C	GC	33	47	Liljeroth et al. (1994)
Maize	Low N	Loamy sand	2% C	GC	196	47	Liljeroth et al. (1994)
Wheat	Low N	Loamy sand,	2% C	GC	196	47	Liljeroth et al. (1994)
Maize		Chernozemic sandy loam	1.5%	GC	236	25	Helal and Sauerbeck (1984)
Maize		Chernozemic sandy loam	1.5%	GC	332	30	Helal and Sauerbeck (1986)

†Plant growth conditions: GH = greenhouse; GC = growth chamber.

‡Each value is calculated as: (planted 2 unplanted)/unplanted \times 100.

to the rooting zone than sections away from the rooting zone, also indicated a priming effect by roots in their studies. Soil aggregate destruction by growing roots was mentioned as the main cause of the priming effect by Helal and Sauerbeck (1987). These continuous labelling studies were able to assess the root effects on SOM decomposition, not just litter decomposition. However, the required use of special continuous labelling facility might have prevented comprehensive investigation of the root priming effect both because of the short experimental duration permitted by such facility and because of the limited plant growth space.

Studies Using Natural ^{13}C Tracers

The results of root effects on SOM decomposition were given in Table 7–3 based on six published studies using natural ^{13}C -tracer methods under controlled soil water conditions. The % priming values were mostly positive, ranging from –37% to as high as 164%. In a very short (16 d) experiment using soils from a continuous corn field, the presence of wheat roots was shown to reduce the SOM decomposition rate by about 37% (Cheng, 1996). In another short (28 d) experiment (Cheng and Johnson, 1998), wheat plants grown under elevated CO_2 increased rhizosphere priming effects on SOM decomposition when the soil received additional N, but decreased rhizosphere priming effects without N addition. Sunflower (*Helianthus annuus* L.) plants grown under elevated CO_2 without N fertilization also produced less rhizosphere priming effects than ambient CO_2 as shown by the results from a mesocosm-scale experiment lasting for 53 d (Cheng et al., 2000). The highest degree of rhizosphere priming effects in this set was reported from the greenhouse study that lasted for 119 d (Cheng et al., 2003); the rate of SOM decomposition under the influence of soybean [*Glycine max* (L.) Merr.] rhizosphere was 164% higher than the no-plant control and 96% higher with the presence of wheat rhizosphere. Two kinds of plant-soil couplings (C_3 -plants grown in a “ C_4 -soil” and C_4 -plants grown in a “ C_3 -soil”) were compared in the greenhouse study by Fu and Cheng (2002). The two C_4 plant species grown in the “ C_3 -soil” (a coastal annual grassland soil) produced a lower rhizosphere effect (29 and 27%) on SOM decomposition than the two C_3 plant species grown in the “ C_4 -soil” (a tallgrass prairie soil). This difference could be due to the two soil types, to the different plant species with two different photosynthetic pathways, or both. As has been pointed out by Kuzyakov et al. (2000), soils with higher amounts of labile SOM are more likely to produce priming effects than soils with less labile SOM. As indicated by its lower basal respiration rate, the coastal grassland “ C_3 -soil” probably contained less labile SOM than the tallgrass prairie soil (C_4 -soil). It is also possible that plant species with the C_4 -photosynthetic pathway produced less rhizosphere-priming than C_3 plants (Epstein et al., 1998). However, similar rhizosphere priming effects were reported between maize (a C_4 species) and wheat (a C_3 species) when both received the low level of N fertilization (Liljeroth et al., 1994). In a controlled shading experiment (Kuzyakov and Cheng, 2001), plant photosynthesis, as modified by different day-night cycles, was shown to exert an important control on rhizosphere priming effects. The SOM decomposition rate of the planted treatment under a regular day-night cycle (12 h light/12 h dark) increased 100% above the no-plant control but decreased to a level of 50%

Table 7-3. Magnitude of the root effect on soil organic matter (SOM) decomposition by the natural ^{13}C tracer method.

Plant type	Treatment	Soil type, C %	PGC [†]	% Priming [‡]	Time (d)	Reference
Wheat	Ambient CO ₂ , No-N	Typic Fragiudalf	GC	-37	16	Cheng (1996)
Wheat	Elevated CO ₂ , No-N	Mollisol, clay loam, 2%	GC	44	28	Cheng and Johnson (1998)
Wheat	Ambient CO ₂ , No-N	Mollisol, clay loam, 2%	GC	17	28	Cheng and Johnson (1998)
Wheat	Elevated CO ₂ , +N	Mollisol, clay loam, 2%	GC	42	28	Cheng and Johnson (1998)
Sunflower	Ambient CO ₂	Mollisol, clay loam, 2%	GC	73	28	Cheng and Johnson (1998)
Sunflower	Elevated CO ₂	Mollisol, clay loam, 2%	Mesocosm	55	53	Cheng et al. (2000)
Soybean		Mollisol, clay loam, 2%	Mesocosm	31	53	Cheng et al. (2000)
Wheat		Mollisol, clay loam, 2%	GH	164	119	Cheng et al. (2003)
Soybean	Tallgrass prairie soil (C ₄)	Mollisol, clay loam, 2%	GH	96	119	Cheng et al. (2003)
Sunflower	Tallgrass prairie soil (C ₄)	Mollisol, clay loam, 2%	GH	70	120	Fu and Cheng (2002)
Sorghum	Coastal grassland soil (C ₃)	Mollisol, clay loam, 2%	GH	39	120	Fu and Cheng (2002)
<i>Amaranthus</i>	Coastal grassland soil (C ₃)	Sandy loam, 1.9%	GH	-9	120	Fu & Cheng (2002)
Wheat	12/12 h light/dark cycle	Sandy loam, 1.9%	GH	-5	120	Fu & Cheng (2002)
Wheat	12/60 h light/dark cycle	Mollisol, clay loam, 2%	GC	100	38	Kuzyakov and Cheng (2001)
		Mollisol, clay loam, 2%	GC	-50	38	Kuzyakov and Cheng (2001)

[†]Plant growth conditions: GH = greenhouse; GC = growth chamber.[‡]Each value is calculated as: (planted—unplanted)/unplanted × 100.

below the no-plant control after two long dark periods (60 h dark each, with a 12-h light period in between) were imposed. The study indicated that plant photosynthesis controlled total rhizosphere respiration and exudation directly, thereby influencing the priming effect indirectly by changing the amount of easily decomposable organic substances in the rhizosphere.

Based on data from several experiments, timing of plant growth or plant phenological stages seems to be a very important factor influencing the magnitude of the rhizosphere priming effect (Fig. 7-3) (Cheng et al., 2003; Fu and Cheng, 2002). Rhizosphere priming effects seem low or even negative during the early growth stages, increases to the highest point at approximately 60 d after planting or around the flowering stage, and declines to lower levels afterwards. This is logical since the release of substrates in the rhizosphere is also controlled by the timing of plant growth or plant phenological stages (Warembourg and Estelrich, 2000).

MECHANISMS

As shown in the previous sections, plant roots may strongly influence SOM decomposition. These root effects can be in the forms of decreasing mineral nutrient availability to soil microorganisms due to plant uptake (Schimel et al., 1989; Schimel and Chapin, 1996), changing the physical and chemical environment in the rhizosphere (i.e., water, pH, etc.) (Fuhr and Sauerbeck, 1968; Shields and Paul, 1973; Jenkinson, 1977), increasing organic substrates (i.e., exudates, other rhi-

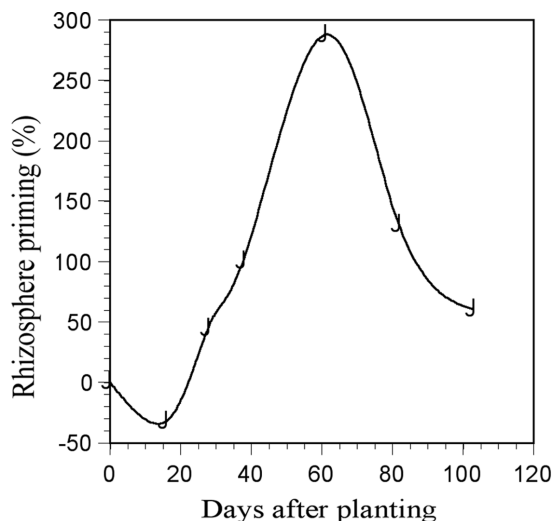


Fig. 7-3. Change of rhizosphere priming through time of wheat growth. The data points on the left shorter than 40 d are from three separate experiments using growth chambers (Cheng, 1996; Cheng and Johnson, 1998; Kuzyakov and Cheng, 2001), and the three data points on the right longer than 40 d are from one greenhouse experiment (Cheng et al., 2003).

zodeposition) for rhizosphere microorganisms, and enhancing microbial turnover due to faunal grazing (Ingham et al., 1985; Elliott et al., 1979; Clarholm, 1985a, 1985b; Kuikman et al., 1990). However, direct mechanistic investigations of these root effects are still sparse.

There are controversies about the mechanisms of root effects on the intensity of SOM decomposition. Some hypotheses have been given in reconciling these controversies. Plant roots may have dual and counteracting effects on soil microbial activities and thereby SOM decomposition (Van Veen et al., 1989). The following mechanisms have been suggested to explain the effect of roots on SOM decomposition:

- Drying effect hypothesis
- Aggregate destruction hypothesis
- Competition hypothesis
- Preferential substrate utilization hypothesis
- Microbial activation hypothesis
- C uptake hypothesis

These mechanisms are presented and discussed below.

Drying Effect Hypothesis

Water uptake by plants always results in drier soil conditions in planted treatments than unplanted controls. Although frequent watering can be carried out to compensate the water difference between the two kinds of treatments, drying–rewetting cycles occur inevitably more in the planted treatment than the no-plant control, especially in the topsoil (Sala et al., 1992). According to the results from some experiments investigating soil drying–rewetting cycles, the change in water regime tends to induce an increased SOM mineralization (Van Schreven, 1967; Lundquist et al., 1999). This effect has been attributed to (i) enhanced solubility of humic substances, (ii) increased microbial death during desiccation and osmotic shock caused by rewetting followed by an acceleration in decomposition and mineralization rates during microbial regrowth, and (iii) release of protected organic matter by disruption of macroaggregates during rewetting due to ‘slaking’ (Magid et al., 1999). Since root hairs are responsible for water uptake as well as for the exudation of readily available organic substances, these locations contain high density of bacteria. Therefore the drying of soil particles on the root surface can also lead to dehydration of some microbial cells. Subsequent rewetting may enhance the utilization of dead cells and an increased C and N mineralization (Van Gestel et al., 1993). This mechanism may explain the increased CO₂ efflux and N mineralization in the presence of the rhizosphere. On the other hand, low soil moisture may decrease microbial activities. So, under prolonged dry soil conditions (not a rapid change), the SOM decomposition must decrease. Therefore, under certain conditions the negative effect of water limitations on microbial activities and the positive effect of enhanced substrate availability (as mentioned above) can be balanced out, resulting in little change in SOM decomposition when soils are exposed to the drying–rewetting regime (Degens and Sparling, 1995). This possibility is clearly demonstrated by the results of a recent study (Magid et

al., 1999), indicating that drying and rewetting a loamy sand soil did not significantly alter the rate of native SOM decomposition but reduced plant litter decomposition, as compared to the constant soil moisture regime. These balancing mechanisms in the drying–rewetting regime may lower the magnitude of the enhanced SOM decomposition compared to the degree of rhizosphere priming effect. However, the potential contribution of the drying–rewetting in the rhizosphere to the priming of SOM decomposition warrants further investigations.

Aggregate Destruction Hypothesis

Some studies have shown that a portion of labile SOM may be physically protected from microbial utilization due to the formation of soil aggregates (Beare et al., 1994; Elliott, 1986; Tisdall and Oades, 1982). If the presence of live roots promotes the destruction of aggregates rather than their formation, some portion of the physically protected labile SOM is further exposed to microbial attack, thereby resulting in positive priming effects of roots on SOM decomposition. Helal and Sauerbeck (1984, 1986) first put out this hypothesis to explain the positive priming effect of live roots on SOM decomposition. According to this mechanism, destroying aggregates increases the SOM mineralization. Indeed, roots promote the reorganization of the soil structure: they can destroy some old aggregates as well as contribute to the formation of new ones. However, live roots tend to promote aggregate formation more than aggregate destruction (Haynes and Beare, 1997). Roots tend to occupy existing soil pores instead of creating new ones. This feature of root growth is particularly prevalent in soils or horizons with fine texture such as clay or clayey loam. However, extreme drying–rewetting cycles, more likely to occur in the presence of live roots than no-root controls in some experiments, may result in aggregate destruction more than aggregate formation, thereby leading to priming effects on SOM decomposition. In most of the studies cited in the above section, extreme drying–rewetting cycles were avoided by frequent watering. Therefore, aggregate destruction may not have been the main cause of root priming effects on SOM decomposition. However, published studies of root priming effects on SOM decomposition rarely include assessment of root effects on soil aggregates simultaneously. Further studies on this issue are needed before a general conclusion can be reached.

Competition Hypothesis

It is hypothesized that, when plants are grown in soils with low nutrient concentrations, nutrient uptake by roots will intensify the competition for mineral nutrients in the rhizosphere and decrease microbial growth and metabolism, thereby depressing SOM decomposition. A similar hypothesis was proposed by Cheng (1999) to explain how rhizosphere processes change when plants are grown under elevated CO₂ conditions. This mechanism has been suggested indirectly by Schimel et al. (1989) and Ehrenfeld et al. (1997), but the hypothesis has never been directly tested. The competition hypothesis has been used to explain the negative effects of roots on SOM decomposition in several studies (e.g., Bottner et al., 1999). This hypothesis is based on the assumption that N is the most limiting nu-

trient for plants and microorganisms in terrestrial ecosystems (Vitousek and Howarth, 1991). Microbial growth in the rhizosphere is especially limited by available N as well as by some other nutrients (Schimel et al., 1989; Jackson et al., 1989; Liljeroth et al., 1990). Therefore, under conditions of limited soil mineral nutrient supply, plant roots and microorganisms compete strongly for available N resources (Wang and Bakken 1997; Jackson et al., 1989). However, the winner in this competition may depend on the time period considered. In the short-term (hours to days), soil microorganisms can capture ammonia (NH_4^+) or nitrate (NO_3^-) two to five times faster than the plant roots (Jackson et al., 1989), because microorganisms have high substrate affinities, rapid growth rates, and high surface/volume ratios (Rosswall, 1982; Jackson et al., 1989). The short-term immobilization of N added in the form of mineral fertilizer is one of the frequently observed results of this competition (e. g., Bremer and Kuikman, 1997). However, in the longer-term (weeks to months), plant roots may take up more N from the soil even in the presence of microbial competition. This competition mechanism can be represented by a simple model (Fig. 7–4). Because soil microorganisms normally grow and die (or turnover) at a much faster rate than do most plant roots, mineral nutrients taken up by microorganisms in the short-term are returned to the mineral nutrient pool as microorganisms die and decompose, whereas nutrients taken up by roots are mostly transported to other parts of the plant and little returns to the soil mineral pool within a growing season. Root exudation of N containing compounds usually does not exceed 5% of total plant N uptake (Merbach et al., 1999), which is one to two orders of magnitude lower than the amount of N mineralized from microbial biomass turnover. Root turnover can be another source of plant N loss to the soil within a growing season and should be a small portion of the total plant N uptake. Because of this difference in turnover rates between plant materials and soil microbial biomass, the flow between the microbial pool and the mineral N pool is bi-directional and the flow between the mineral N pool to roots is unidirectional. In such a system (Fig. 7–4), plants win the competition in terms of net N uptake in the longer-term, and the amount of net N uptake by microorganisms can be either positive, zero, or negative depending on other sources of N and C substrates in the system. If the mechanism presented in this simple model operates widely in natural ecosystems in the longer-term, plants always win the competition for net N uptake as long as soil microorganisms turnover at a faster rate. Under N limiting conditions, the removal of available N from the soil pool by roots may reduce microbial growth due to N limitation, resulting in a decreased rate of SOM decomposition. This mechanism has been suggested by several stud-

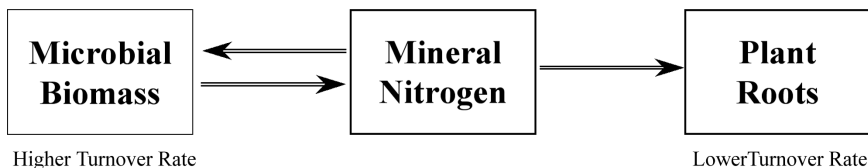


Fig. 7–4. The box and arrow diagram represents a mechanism of competition for mineral nitrogen (N) between plant roots and soil microbes.

ies (Jackson et al., 1989; Schimel et al., 1989; Kaye and Hart, 1997; Hodge et al., 2000a) and supported by the results of Hodge et al. (2000b). A similar hypothesis has also been used to explain the competition between soil microorganisms and forest plant communities (Hobbie, 1992). It has been shown that phosphorus (P) limitations may also reduce the rate of SOM decomposition (Hobbie and Vitousek, 2000). This competition hypothesis postulates that root effects on SOM decomposition depend on the level of soil mineral nutrition: (i) under nutrient limiting conditions, SOM decomposition decreases due to competition between roots and soil microorganisms for mineral nutrients; and (ii) the effect of roots on SOM decomposition increases when soil mineral nutrients are abundant (Fig. 7–5).

Preferential Substrate Utilization Hypothesis

This hypothesis states that, given abundant mineral nutrient supply, soil microbes prefer labile root-derived C to SOM-derived C, resulting in a decreased SOM decomposition in the rhizosphere and that, if mineral nutrients are in short supply, soil microbes prefer nutrient-rich SOM to root-derived C, resulting in increased SOM decomposition in the rhizosphere (Fig. 7–6). A similar hypothesis has been given in a review (Cheng, 1999). This hypothesis focuses on the role of soil mineral nutrition and assumes that all root-derived materials have a much wider C/N ratio than the SOM. The initial supporting data for this hypothesis comes from some studies using the continuous ^{14}C -labelling approach (Merckx et al., 1987; Van Veen et al, 1989; Liljeroth et al., 1994). The decomposition rate of ^{14}C -labelled materials from the current season rhizodeposition appeared to be higher under the treatment receiving N fertilization (or abundant mineral nutrient supply) than under the unfertilized treatment (or mineral nutrient limited), and the decomposition rate of original SOM decreased under the fertilized treatment. These results seem to support the idea that the microbial preference for substrate

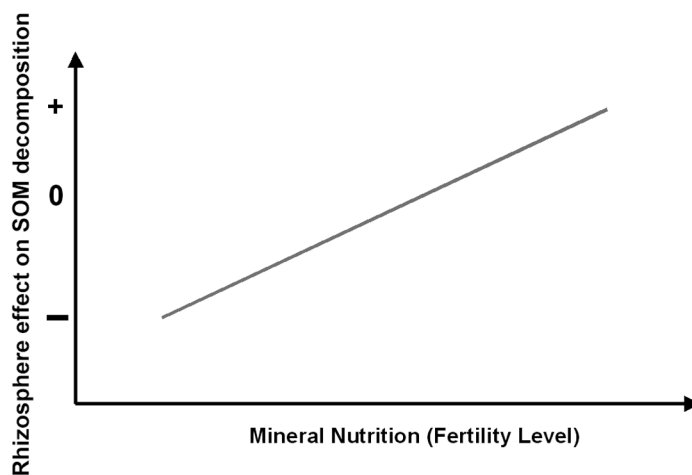


Fig. 7–5. A graphical presentation of the competition hypothesis in relation to mineral nutrient levels.

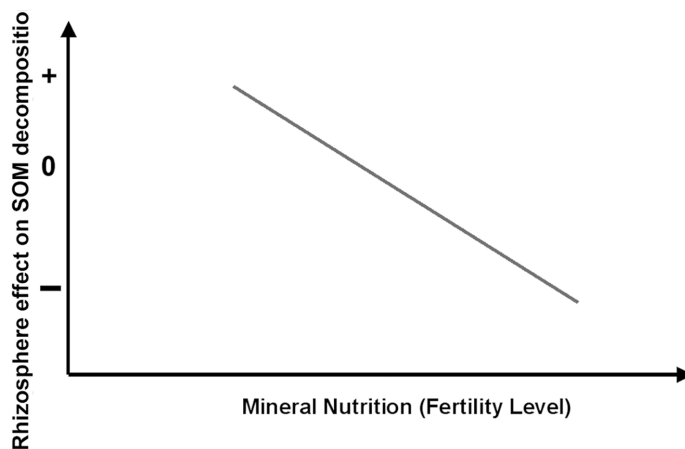


Fig. 7-6. A graphical presentation of the preferential substrate utilization hypothesis in relation to the level of soil mineral nutrients.

utilization switches depending on the level of soil mineral nutrients. This preferential substrate utilization hypothesis seems contradictory to the competition hypothesis at the first glance but may be explained if both are shown on a gradient of mineral nutrition (Fig. 7-7). Since the competition hypothesis is primarily based on results from experiments in nutrient poor soils (pine forests in Ehrenfeld et al. [1997] and dry grasslands in Schimel et al. [1989]), it belongs to the lower part of the mineral nutritional gradient (or the very left part of the X-axis). The substrate-preference hypothesis can be placed to the right part of the X-axis because the evidence supporting the hypothesis mainly came from experiments using very fer-

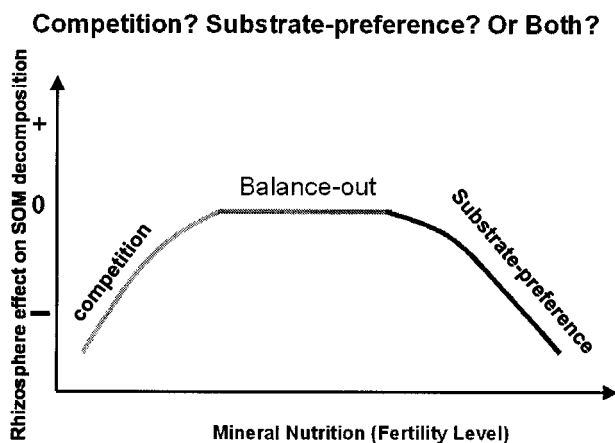


Fig. 7-7. A reconciliation of the preferential substrate utilization hypothesis and the competition hypothesis.

tile soils from agricultural fields. In other words, the mechanism of competition dominates under the condition of severe mineral nutrient limitation, the substrate-preference mechanism dominates when soil mineral nutrients are not so limiting, and the two mechanisms may balance out in the intermediate level of soil mineral nutrients. Further work is needed to verify these possibilities.

Microbial Activation Hypothesis

This hypothesis has previously been described by Kuzyakov et al. (2000). Substances released by roots are readily available for rhizosphere microorganisms. These substrates normally stimulate microbial growth in the rhizosphere. This increased microbial growth may further lead to an increased co-metabolic decomposition of SOM, thereby resulting in an increased rate of SOM decomposition. Microorganisms are the key players for producing this rhizosphere priming effect, because no real priming effects have been observed under sterile conditions (Jansson, 1958). Also, the close relationship between microbial growth and the increased mineralization rate indicates a real connection between the dynamics of microbial activities and real priming effects (Dalenberg and Jager, 1989). There is also a significant correlation between the amount of N released from SOM and the level of exocellular enzyme activities, especially the total and soluble protease, as shown in an experiment studying the effect of glucose addition to the soil (Asmar et al., 1994). In experiments using soils of high N levels, Schmitt et al. (1991) reported that a pulse input of available substrates such as glucose enhances dehydrogenase activity and increases the number of ammonifying and protolytic bacteria but decreases the concentration of total organic C in the soil solution. An increased microbial substrate availability induces enzyme production or increases enzyme activity, further leading to a co-metabolic decomposition of SOM.

Some studies have suggested that the response of total microbial metabolism determines the effect of roots on SOM decomposition (Fig. 7–8) (Cheng and Coleman, 1990). Increased microbial biomass is reported when a stimulatory effect of roots on SOM decomposition occurs (Helal and Sauerbeck, 1986; Sallih and Bottner, 1988; Cheng and Coleman, 1990). Decreased microbial biomass is indicated when a negative effect of roots on SOM decomposition is found (Reid and Goss, 1982; 1983; Sparling et al., 1982; Sallih and Bottner, 1988).

The input of labile root-derived C in the rhizosphere initially may decrease SOM decomposition due to the increase of microbial growth and immobilization. But later it may stimulate SOM decomposition and nutrient release due to the turnover of this newly grown microbial biomass (Fig. 7–9). The quality of the root-derived substrates is an important determinant of the timing and the magnitude of the priming effect. This hypothesis emphasizes the temporal microbial dynamics and the quality of the root-derived substrates. This hypothesis can be used to potentially explain all the results mentioned above if the information on microbial dynamics and the quality of root exudates is available and correct. Unfortunately, such information is difficult to obtain and rarely available. Studies using ^{14}C -labelled substrates have also shown that the priming effect of added labile substrates on SOM decomposition is mainly due to the stimulation of microbial growth and subsequent microbial turnover (death) (Dalenberg and Jager, 1989;

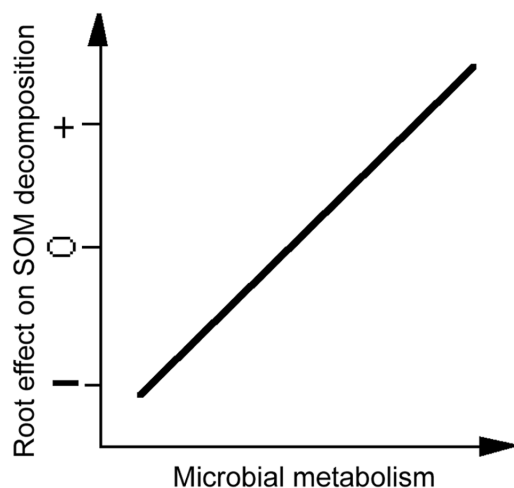


Fig. 7-8. Rhizosphere priming affects soil organic matter (SOM) decomposition by changing soil microbial metabolism. If soil microbial biomass and metabolism are increased by the presence of the rhizosphere, SOM decomposition is stimulated.

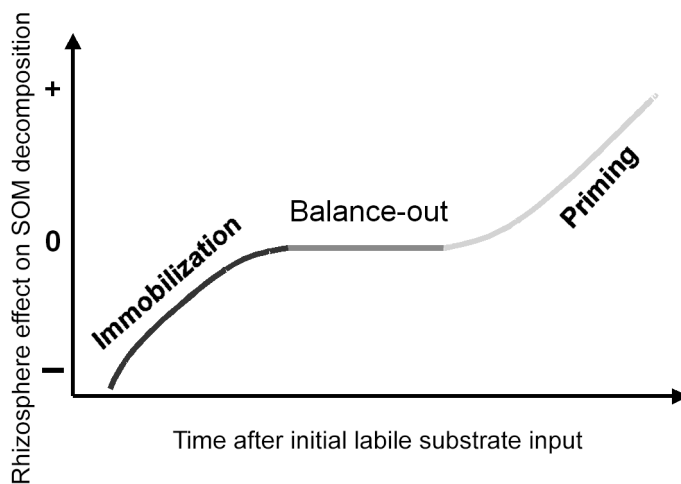


Fig. 7-9. A graphical presentation of the microbial activation hypothesis and the time course of the priming effect.

Nicolardot et al., 1994). Microbial biomass turns over faster in the rhizosphere than in the bulk soil, often resulting from intensified predation by rhizospheric fauna (Elliott et al., 1988; Clarholm, 1985a; Ingham et al., 1985; Griffiths, 1994). Interactions between soil microorganisms, soil fauna, and roots are regarded as one of the keys for understanding SOM decomposition in the rhizosphere (Alpeh et al., 1996). Plant roots increase the microbial activity in the rhizosphere through

rhizodeposition and thus can enhance N mineralization via activated foodweb interactions in the rhizosphere (Elliott et al., 1979; Clarholm, 1985b; Haider et al., 1987; Kuikman et al., 1991; Zagal, 1994; Zwart et al., 1994; Kuzyakov et al., 2001).

Carbon Uptake Hypothesis

If live roots take up SOM in a significant quantity, the SOM absorbed by the live roots will be removed temporarily from microbial decomposition, resulting in a lower rate of SOM decomposition compared to SOM decomposition without the presence of live roots. This mechanism has been suggested in some studies as a possible cause of the negative rhizosphere effect on SOM decomposition (Sparling et al., 1982; Reid and Goss, 1982; 1983). However, later studies indicate that the amount of soil C absorbed by roots is often <1% of the total decomposed SOM (as often measured by CO₂ efflux) and is too small to be a significant factor influencing rhizosphere effects (Sallih and Bottner, 1988; Cheng and Coleman, 1990; Hodge et al., 2000a). Results from experiments using solution cultures under sterile conditions suggest that plant roots tend to absorb or re-absorb some quantity of soluble root exudates (Jones and Darrah, 1992, 1993, 1996) and limited quantity of dissolved organic N (e.g., amino acids) (Chapin et al., 1993; Kielland, 1994). However, the quantitative significance of such absorption under realistic conditions remains debatable. The rapid turnover of soluble organic substrates by soil microorganisms and the poor competitive ability of plant roots may constrain the quantity of root absorption of soluble organic materials to a relatively low level (Jones, 1999; Owen and Jones, 2001; Jones and Kielland, 2002).

Mechanism Interactions-A hypothesis

Based on the evidence obtained so far, the most important mechanisms controlling the rhizosphere effect on SOM mineralization are: preferential substrate utilization, competition for mineral nutrients, and microbial activation. In reality these mechanisms may operate individually or in combination, and dominate depending on the availability of soil C and N at different spatial and temporal scales. Four scenarios can be given depending on which nutrient (C or N) is limiting the microbial growth (Table 7–4). Microbial growth in non-rhizosphere soils is often limited by the C_{available} (e.g., Wardle, 1992; Grayston et al., 1996), but, under certain conditions, C_{available} in the rhizosphere may surpass the threshold of limitation

Table 7–4. Hypothesized dominating mechanism under different combination of carbon (C) and nitrogen (N) availability to microbial growth.

Soil conditions	N limited	N not limited
C _{available} limited	Competition dominates (negative rhizosphere priming)	Substrate preference dominates (negative rhizosphere priming)
C _{available} not limited	Microbial activation or Nutrient competition dominates (+ or – rhizosphere priming)	Microbial activation dominates (+ or – rhizosphere priming)

to microbial growth (Cheng et al., 1996) and then N_{\min} becomes a limiting factor (Merckx et al., 1987; Van Veen et al., 1989). If soil microbial growth is limited by both $C_{\text{available}}$ and N_{\min} , the competition between plants and microorganisms for N_{\min} dominates, leading to a decreased microbial activity, and, as a result, SOM decomposition decreases. If only $C_{\text{available}}$ limits microbial growth, microbes may preferentially use rhizodeposits instead of SOM decomposition, then the mechanism of the preferential substrate utilization dominates. In the case that microbial growth is limited by N_{\min} but not limited by $C_{\text{available}}$, the rhizodeposition of easily available organic compounds may either activate total microbial activity or provoke competition for mineral nutrients between roots and microbes, or both. When both $C_{\text{available}}$ and N_{\min} are not limiting microbial growth, the fast microbial growth invokes an enhanced faunal predation in the rhizosphere, resulting in an increased SOM decomposition and the domination by the microbial activation mechanism.

SUMMARY AND FUTURE RESEARCH

Based on results from experiments under laboratory or greenhouse conditions, root effects on the rate of SOM decomposition can range from negative 70% to as high as 330% above the unplanted control. It is clear that the rhizosphere significantly controls SOM decomposition. In all real terrestrial ecosystems, SOM decomposition always occurs with plant roots, thereby inevitably entangles with both the soil component and the plant component. This entanglement seriously challenges the reliability of existing assessments on the rates of SOM decomposition that often come from measurements using root exclusions or soil incubations without the presence of plant roots (e. g., Bolker et al., 1998; Dalias et al., 2001; Parton et al., 1987).

Virtually all published data cited in this chapter come from experiments using herbaceous plant species. How tree roots may affect SOM decomposition remains to be investigated. Since forests constitute a major portion of the global C cycle, understanding tree root effects on SOM decomposition may bear more significance in terms of quantifying the potential of C sequestration into forest ecosystems at the global scale. Therefore, the effect of tree roots on SOM decomposition warrants future research.

Based on scattered studies, both biotic and abiotic factors, for example, N, CO_2 , soil moisture, light, soil types, plant species, and plant phenological stages, are found to significantly control or influence the level of root effects on SOM decomposition. Because rhizosphere processes are intimately connected with both the plant system and the soil system (Högberg et al., 2001; Kuzyakov and Cheng, 2001), any environmental conditions that affect either the plant functions or the soil functions or both, inevitably modulate root effects on SOM decomposition. Comprehensive future studies are clearly needed to integrate all these important factors into a general model of understanding on this issue.

Studies of root effects on SOM decomposition have mostly been constrained by the availability of research methods. What emerges from the discussion on methods is the need for the development of innovative methods that allow realistic investigation of root effects on SOM decomposition in situ. Before such

new methods become available, our understanding of root effects on SOM decomposition will have to rely on results from either greenhouse or laboratory studies. Natural ^{13}C tracers have been used in field-based studies for separating rhizosphere respiration from soil respiration (e.g., Rochette and Flanagan, 1997; Andrews et al., 1999). It is logical that these natural tracers can also be used for investigating root effects on SOM decomposition if soil moistures can be adequately controlled in both the rooted plots and the no-plant control plots.

The six mechanisms identified as potentially responsible for causing root effects on SOM decomposition are preliminary in nature, and need to be rigorously tested. For example, relevant to the drying effect hypothesis, the issue of differential drying or wetting between the no-plant control and the planted treatments remains to be carefully investigated. Does frequent (e.g., daily) watering adequately eliminate the drying/wetting effect on SOM decomposition with or without roots? This potential drying/wetting effect may also disturb soil aggregate structures, thereby further influence SOM decomposition. The soil structure aspect of root effects on decomposition definitely needs more research before a general understanding can be achieved. Microbial dynamics are either directly or indirectly involved in the six mechanistic hypotheses discussed above. Therefore, measurements of microbial community structure, growth and turnover, substrate use, and the level of root-microbe associations are essential for reliable testing of these hypotheses in the future.

Evidence from studies cited in this review supports a general belief that the root effect on SOM decomposition can be large in magnitude and significant in mediating plant-soil interactions. However, very little is known about the role of the rhizosphere effect in shaping plant adaptation to various soil environments in the long-term. If the rhizosphere effect are closely connected to plant photosynthesis and rhizodeposition (Högberg et al., 2001; Kuzyakov and Cheng, 2001), it is conceivable that the rhizosphere effect should be largely beneficial to plants, and thereby enhancing their fitness. Among possible benefits, enhanced nutrient acquisition is often suggested (Clarholm, 1985a; Ingham et al., 1985). Other benefits may include suppression of root pathogens by supporting healthy microbial communities (Hu et al., 1997), conditioning of soil paths for root growth, and improving soil structures and chemical environment such as pH adjustment (Schaller, 1987; Gahoonia and Nielsen, 1992). If all these benefits are true, the rhizosphere effect on SOM decomposition should be a result of evolutionary processes operating between plants and soil organisms in the overall rhizosphere continuum from incidental to highly symbiotic. Different rhizosphere mechanisms should be selected under different plant and soil environments. This argument seems to be supported by the fact that different plant-soil couplings produce different rhizosphere effects on SOM decomposition (Fu and Cheng, 2002; Cheng et al., 2003). Future research is needed to fully illuminate the evolutionary aspects of the rhizosphere effect.

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REFERENCES

- Alpei, J., M. Bonkowski, and S. Scheu. 1996. Protozoa, Nematoda and Lumbricidae in the rhizosphere of *Hordelymus europaeus* (Poaceae): Faunal interactions, response of micro-organisms and effects on plant growth. *Oecologia* 106:111–126.
- Andrews, J.A., K.G. Harrison, R. Matamala, and W.H. Schlesinger. 1999. Separation of root respiration from soil respiration using carbon-13 labeling during free-air carbon dioxide enrichment (FACE). *Soil Sci. Soc. Am. J.* 63:1429–1435.
- Asmar, F., F. Eiland, and N.E. Nielsen. 1994. Effect of extracellular-enzyme activities on solubilization rate of soil organic nitrogen. *Biol. Fertil. Soils* 17:32–38.
- Beare, M.H., M.L. Cabrera, P.F. Hendrix, and D.C. Coleman. 1994. Aggregate-protected and unprotected organic matter pools in conventional-tillage and no-tillage soils. *Soil Sci. Soc. Am. J.* 58:787–795.
- Bolker, B.M., S.W. Pacala, and W.J. Parton, Jr. 1998. Linear analysis of soil decomposition: Insights from the CENTURY model. *Ecol. Appl.* 8:425–439.
- Bottner, P., M. Pansu, and Z. Sallih. 1999. Modelling the effect of active roots on soil organic matter turnover. *Plant Soil* 216:15–25.
- Bremer, E., and P. Kuikman. 1997. Influence of competition for nitrogen in soil on net mineralization of nitrogen. *Plant Soil* 190:119–126.
- Chapin, F.S., L. Moilanen, and K. Kielland. 1993. Preferential use of organic nitrogen for growth by a nonmycorrhizal arctic sedge. *Nature (London)* 361:150–153.
- Cheng, W. 1996. Measurement of rhizosphere respiration and organic matter decomposition using natural ^{13}C . *Plant Soil* 183:263–268.
- Cheng, W. 1999. Rhizosphere feedbacks in elevated CO_2 . *Tree Physiol.* 19:313–320.
- Cheng, W., and D.C. Coleman. 1990. Effect of living roots on soil organic matter decomposition. *Soil Biol. Biochem.* 22:781–787.
- Cheng, W., D.C. Coleman, and J.E. Box, Jr. 1990. Root dynamics, production and distribution in agroecosystems on the Georgia Piedmont using minirhizotrons. *J. Appl. Ecol.* 27:592–604.
- Cheng, W., and D.W. Johnson. 1998. Effect of elevated CO_2 on rhizosphere processes and soil organic matter decomposition. *Plant Soil* 202:167–174.
- Cheng, W., D.W. Johnson, and S. Fu. 2003. Rhizosphere priming effects on decomposition: Controls of fertilization, plant species, and phenology. *Soil Sci. Soc. Am. J.* 67:1418–1427.
- Cheng, W., D.A. Sims, Y. Luo, D.W. Johnson, J.T. Ball and J.S. Coleman. 2000. Carbon budgeting in plant-soil mesocosms under elevated CO_2 : Locally missing carbon? *Global Change Biol.* 6: 99–110.
- Cheng, W., Q. Zhang, D.C. Coleman, C.R. Carroll and C.A. Hoffman. 1996. Is available carbon limiting microbial respiration in the rhizosphere? *Soil Biol. Biochem.* 28:1283–1288.
- Clarholm, M. 1985a. Possible role for roots, bacteria, protozoa and fungi in supplying nitrogen to plants. p. 355–365. *In* A.H. Fitter (ed.) *Ecological interactions in soil*. Blackwell Science, Oxford.
- Clarholm, M. 1985b. Interactions of bacteria, protozoa and plants leading to mineralization of soil nitrogen. *Soil Biol. Biochem.* 17:181–187.
- Dalenberg, J.W., and G. Jager. 1989. Priming effect of some organic additions to ^{14}C -labelled soil. *Soil Biol. Biochem.* 21:443–448.
- Dalias, P., J.M. Anderson, P. Bottner, and M.M. Coûteaux. 2001. Temperature responses of carbon mineralization in conifer forest soils from different regional climates incubated under standard laboratory conditions. *Global Change Biol.* 7:181–192.
- Degens, B., and G. Sparling. 1995. Repeated wet-dry cycles do not accelerate the mineralization of organic C involved in the macro-aggregation of a sandy loam soil. *Plant Soil* 175:197–203.
- Ehrenfeld, J.G., W.F.J. Parsons, X. Han, R.W. Parmelee, and W. Zhu. 1997. Live and dead roots in forest soil horizons: Contrasting effects on nitrogen dynamics. *Ecology* 78:348–362.
- Eissenstat, D.M., and R.D. Yanai. 1997. The ecology of root lifespan. *Adv. Ecol. Res.* 27: 1–60.
- Elliott, E.T. 1986. Aggregate structure and carbon, nitrogen, and phosphorus in native and cultivated soils. *Soil Sci. Soc. Am. J.* 50:627–633.

- Elliott, E.T., D.C. Coleman and C.V. Cole. 1979. The influence of amoebae on the uptake of nitrogen by plants in gnotobiotic soil. p. 221–229. In J.L. Harley and R.S. Russel (ed.) The soil-root interface. Academic Press, London.
- Elliott, E.T., H.W. Hunt, and D.E. Walter. 1988. Detrital food-web interactions in North American grassland ecosystems. *Agric. Ecosys. Environ.* 24:41–56.
- Epstein, H.E., I.C. Burke, and A.R. Mosier. 1998. Plant effects on spatial and temporal patterns of nitrogen cycling in shortgrass steppe. *Ecosystems* 1:374–385.
- Fu, S., and W. Cheng. 2002. Rhizosphere priming effects on the decomposition of soil organic matter in C4 and C3 grassland soils. *Plant Soil* 238:289–294.
- Fuhr, F., and D.R. Sauerbeck. 1968. Decomposition of wheat straw in the field as influenced by cropping and rotation. p. 241–250. In *Isotopes and radiation in soil organic matter studies*, IAEA, Vienna.
- Gahoonia, T.S., and N.E. Nielsen. 1992. Control of pH at the soil-root interface. *Plant Soil* 140:49–54.
- Grayston, S.J., D. Vaughan, and D. Jones. 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.
- Griffiths, B.S. 1994. Soil nutrient flow. p. 65–92. In J.F. Darbyshire (ed.) *Soil Protozoa*. CAB Int., Wallingford, Oxon, UK.
- Haider, K., A. Mosier, and O. Heinemeyer. 1987. The effect of growing plants on denitrification at high nitrate concentrations. *Soil Sci. Soc. Am. J.* 51:97–102.
- Haynes, R.J. and M.H. Beare. 1997. Influence of six crop species on aggregate stability and some labile organic matter fractions. *Soil Biol. Biochem.* 29:1647–1653.
- Helal, H.M., and D.R. Sauerbeck. 1983. Method to study turnover processes in soil layers of different proximity to roots. *Soil Biol. Biochem.* 15:223–225.
- Helal, H.M., and D.R. Sauerbeck. 1984. Influence of plant root on C and P metabolism in soil. *Plant Soil* 76:175–182.
- Helal, H.M., and D.R. Sauerbeck. 1986. Effect of plant roots on carbon metabolism of soil microbial biomass. *Z. Pflanzenernaehr. Bodenkd.* 149:181–188.
- Helal, H.M., and D.R. Sauerbeck. 1987. Direct and indirect influence of plant roots on organic matter and phosphorus turnover in soil. *INTECOL Bull.* 15:49–58.
- Hendrick, R.L., and K.S. Pregitzer. 1993. The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood systems. *Can. J. For. Res.* 23:2507–2520.
- Hobbie, S.E. 1992 Effects of plant-species on nutrient cycling. *Trends Ecol. Evol.* 7:336–339.
- Hobbie, S.E., and P.M. Vitousek. 2000. Nutrient limitation of decomposition in Hawaiian forests. *Ecology* 81:1867–1877.
- Hodge, A., D. Robinson, and A. Fitter. 2000a. Are microorganisms more effective than plants at competing for nitrogen? *Trends Plant Sci.* 5:304–308.
- Hodge, A., J. Stewart, D. Robinson, B.S. Griffiths, and A.H. Fitter. 2000b. Competition between roots and soil micro-organisms for nutrients from nitrogen-rich patches of varying complexity. *J. Ecol.* 88:150–164.
- Högberg, P., A. Nordgren, N. Buchmann, A.F.S. Taylor, A. Ekblad, M.N. Högberg, G. Nyberg, M. Ottosson-Lofvenius, and D.J. Read. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature (London)* 411:789–792.
- Hu, S., A.H.C. van Bruggen, R.J. Wakeman, and N.J. Grünwald. 1997. Microbial suppression of in vitro growth of *Pythium ultimum* and disease incidence in relation to soil C and N availability. *Plant Soil* 195:43–52.
- Ingham, R.E., J.A. Trofymow, E.R. Ingham, and D.C. Coleman. 1985. Interactions of bacteria, fungi and their nematode grazers: Effects on nutrient cycling and plant growth. *Ecol. Monogr.* 55: 119–140.
- Jackson, L.E., J.P. Schimel, and M.K. Firestone. 1989. Short-term partitioning of ammonium and nitrate between plants and microbes in an annual grassland. *Soil Biol. Biochem.* 21:409–415.
- Jackson, R.B., H.A. Mooney, and E.D. Schulze. 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proc. Natl. Acad. Sci. USA* 94:7362–7366.
- Janssens, I.A., H. Lankreijer, G. Matteucci, A.S. Kowalski, N. Buchmann, D. Epron, K. Pilegaard, W. Kutsch, B. Longdoz et al.. 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biol.* 7:269–278.
- Jansson, S.L. 1958. Tracer studies on nitrogen transformations in soil with special attention to mineralisation immobilisation relationship. *Ann. R. Agric. Coll. Swed.* 24:101–361.
- Jenkinson, D.S. 1977. Studies on decomposition of plant material in soil.5: Effects of plant cover and soil type on loss of carbon from C-14-labeled ryegrass decomposing under field conditions. *J. Soil Sci.* 28: 424–434.

- Jenny, H. 1941. Factors of soil formation: A system of quantitative pedology. McGraw-Hill, Mineola, NY.
- Jones, D.L. 1999. Amino acid biodegradation and its potential effects on organic nitrogen capture by plants. *Soil Biol. Biochem.* 31:613–622.
- Jones, D.L., and P.R. Darrah. 1992. Re-sorption of organic components by roots of *Zea mays* L. and its consequences in the rhizosphere. I. Resorption of ^{14}C labelled glucose, mannose and citric acid. *Plant Soil* 143:259–266.
- Jones, D.L., and P.R. Darrah. 1993. Re-sorption of organic components by roots of *Zea mays* L. and its consequences in the rhizosphere. II. Experimental and model evidence for simultaneous exudation and re-sorption of soluble C compounds. *Plant Soil* 153:47–59.
- Jones, D.L., and P.R. Darrah. 1996. Re-sorption of organic components by roots of *Zea mays* L. and its consequences in the rhizosphere. III. Characteristics of sugar influx and efflux. *Plant Soil* 178: 153–160.
- Jones, D.L. and K. Kielland. 2002. Soil amino acid turnover dominates the nitrogen flux in permafrost-dominated taiga forest soils. *Soil Biol. Biochem.* 34:209–219.
- Kaye, J.P., and S.C. Hart. 1997. Competition for nitrogen between plants and soil microorganisms. *Trends Ecol. Evol.* 12:139–143.
- Kielland, K. 1994. Amino acid absorption by arctic plants: Implications for plant nutrition and nitrogen cycling. *Ecology* 75:2372–2383.
- Kuikman, P.J., A.G. Jansen, and J.A. Van Veen. 1991. ^{15}N -nitrogen mineralization from bacteria by protozoan grazing at different soil moisture regimes. *Soil Biol. Biochem.* 23:193–200.
- Kuikman, P.J., A.G. Jansen, J.A. Van Veen, and A.J.B. Zehnder. 1990. Protozoan predation and the turnover of soil organic carbon and nitrogen in the presence of plants. *Biol. Fert. Soils* 10:22–28.
- Kuzyakov, Y., and W. Cheng. 2001. Photosynthesis controls of rhizosphere respiration and organic matter decomposition. *Soil Biol. Biochem.* 33:1915–1925.
- Kuzyakov, Y. and G. Domanski. 2000. Carbon input by plants into the soil: Review. *J. Plant Nutr. Soil Sci.* 163:421–431.
- Kuzyakov, Y., H. Ehrensberger, and K. Stahr. 2001. Carbon partitioning and below-ground translocation by *Lolium perenne*. *Soil Biol. Biochem.* 33:61–74.
- Kuzyakov, Y., J.K. Friedel, and K. Stahr. 2000. Review of mechanisms and quantification of priming effects. *Soil Biol. Biochem.* 32:1485–1498.
- Liljeroth, E., P. Kuikman, and J.A. Van Veen. 1994. Carbon translocation to the rhizosphere of maize and wheat and influence on the turnover of native soil organic matter at different soil nitrogen levels. *Plant Soil* 161:233–240.
- Liljeroth, E., J.A. Van Veen, and H.J. Miller. 1990. Assimilate translocation to the rhizosphere of two wheat lines and subsequent utilization by rhizosphere microorganisms at two soil-nitrogen concentrations. *Soil Biol. Biochem.* 22:1015–1021.
- Lundquist, E.J., L.E. Jackson, and K.M. Scow. 1999. Wet-dry cycles affect dissolved organic carbon in two California agricultural soils. *Soil Biol. Biochem.* 31:1031–1038.
- Lynch, J.M., and J. M. Whipps. 1990. Substrate flow in the rhizosphere. *Plant Soil* 129:1–10.
- Magid, J., C. Kjaergaard, A. Gorissen, and P. J. Kuikman. 1999. Drying and rewetting of a loamy sand soil did not increase the turnover of native organic matter, but retarded the decomposition of added C-14-labelled plant material. *Soil Biol. Biochem.* 31:595–602.
- Merbach, W., E. Mirus, G. Knof, R. Remus, S. Ruppel, R. Russow, A. Gransee, and J. Schulze. 1999. Release of carbon and nitrogen compounds by plant roots and their possible ecological importance. *J. Plant Nutr. Soil Sci.* 162:373–383.
- Merckx, R.A., A. Dijkstra, A. den Hartog, and J.A. Van Veen. 1987. Production of root-derived materials and associated microbial growth in soil at different nutrient levels. *Biol. Fert. Soils* 5: 126–132.
- Nicolardot, B., G. Fauvet, and D. Cheneby. 1994. Carbon and nitrogen cycling through soil microbial biomass at various temperatures. *Soil Biol. Biochem.* 26:253–261.
- Owen, A.G. and D.L. Jones. 2001. Competition for amino acids between wheat roots and rhizosphere microorganisms and the role of amino acids in plant N acquisition. *Soil Biol. Biochem.* 33: 651–657.
- Parton, W.J., D.S. Schimel, C.V. Cole, and D.S. Ojima. 1987. Analysis of factors controlling soil organic matter level in Great Plains grasslands. *Soil Sci. Soc. Am. J.* 51:1173–1179.
- Post, W.M., T-H Peng, W.R. Emmanuel, A.W. King, V.H. Dale, and D.L. DeAngelis. 1990. The global carbon cycle. *Am. Sci.* 78:310–326.
- Pregitzer, K.S., D.R. Zak, P.S. Curtis, M.E. Kubiske, J.A. Teeri, and C.S. Vogel. 1995. Atmospheric CO_2 , soil nitrogen and turnover of fine roots. *New Phytol.* 129:579–585.

- Qian, J.H., J.W. Doran, and D.T. Walters. 1997. Maize plant contributions to root zone available carbon and microbial transformation of nitrogen. *Soil Biol. Biochem.* 29:1451–1462.
- Reid, J.B., and M.J. Goss. 1982. Suppression of decomposition of ¹⁴C-labelled plant roots in the presence of living roots of maize and perennial ryegrass. *J. Soil Sci.* 33:387–395.
- Reid, J.B., and M.J. Goss. 1983. Growing crops and transformations of ¹⁴C-labelled soil organic matter. *Soil Biol. Biochem.* 15:687–691.
- Rochette, P., and L.B. Flanagan. 1997. Quantifying rhizosphere respiration in a corn crop under field conditions. *Soil Sci. Soc. Am. J.* 61:466–474.
- Rosswall, T. 1982. Microbial regulation of the biogeochemical nitrogen cycle. *Plant Soil* 67:15–34.
- Sala, O.E., W.K. Lauenroth, and W.J. Patron. 1992. Long-term soil water dynamics in the shortgrass steppe. *Ecology* 73:1175–1181.
- Sallih, Z., and P. Bottner. 1988. Effect of wheat (*Triticum aestivum*) roots on mineralization rates of soil organic matter. *Biol. Fert. Soils* 7:67–70.
- Schaller, G. 1987. pH changes in the rhizosphere in relation to the pH-buffering of soils. *Plant Soil* 97:439–444.
- Schimel, D.S. 1995. Terrestrial ecosystems and the carbon cycle. *Global Change Biol.* 1:77–91.
- Schimel, J.P., and F.S. Chapin, III. 1996. Tundra plant uptake of amino acid and NH₄ nitrogen in situ: Plants complete well for amino acid N. *Ecology* 77:2142–2147.
- Schimel, J.P., L.E. Jackson, and M.K. Firestone. 1989. Spatial and temporal effects on plant microbial competition for inorganic nitrogen in a California annual grassland. *Soil Biol. Biochem.* 21:1059–1066.
- Schmitt, L., K. Muller, and E. Ahrens. 1991. Chemical and microbiological changes in a Regosol after mineral fertilization in long-term field experiments and short-term aerobic incubation trials. *Z. Pflanzenernahr. Bodenk.* 154:189–194.
- Shields, J.A. and E.A. Paul. 1973. Decomposition of ¹⁴C-labelled plant material under field conditions. *Can. J. Soil Sci.* 53:297–306.
- Smith, B.N., and S. Epstein. 1971. Two categories of ¹³C/¹²C ratios for higher plants. *Plant Physiol.* 47:380–384.
- Sparling, G.S., M.V. Cheshire, and C.M. Mundie. 1982. Effect of barley plants on the decomposition of ¹⁴C-labelled soil organic matter. *J. Soil Sci.* 33:89–100.
- Tisdall, J.M., and J.M. Oades. 1982. Organic matter and water stable aggregates in soils. *J. Soil Sci.* 33:141–161.
- Van Gestel, M., R. Merckx, and K. Vlassak. 1993. Microbial biomass responses to soil drying and rewetting—The fate of fast growing and slow-growing microorganisms in soils from different climates. *Soil Biol. Biochem.* 25:109–123.
- 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., E. Liljeroth, L.J.A. Lekkerkerk, and S.C. Van de Geijn. 1991. Carbon fluxes in plant-soil systems at elevated atmospheric CO₂ levels. *Ecol. Appl.* 1:175–181.
- Van Veen, J.A., R. Merckx, and S.C. Van De Geijn. 1989. Plant- and soil-related controls of the flow of carbon from roots through the soil microbial biomass. *Plant Soil* 115:179–188.
- Vitousek, P.M., and R.W. Howarth. 1991. Nitrogen limitation on land and in the sea—How can it occur. *Biogeochemistry* 13:87–115.
- Vogt, K.A., C.C. Grier, and D.J. Vogt. 1986. Production, turnover and nutrient dynamics of above- and belowground detritus of world forests. *Adv. Ecol. Res.* 15:303–378.
- Wang, J.G., and L.R. Bakken. 1997. Competition for nitrogen during decomposition of plant residues in soil: Effect of spatial placement of N-rich and N-poor plant residues. *Soil Biol. Biochem.* 29:153–162.
- Wardle, D.A. 1992. A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. *Biol. Rev.* 67:321–358.
- Warembourg, F.R., and D.H. Estelrich. 2000. Towards a better understanding of carbon flow in the rhizosphere: a time-dependent approach using carbon-14. *Biol. Fert. Soils* 30:528–534.
- Zagal, E. 1994. Influence of light intensity on the distribution of carbon and consequent effects on mineralization of soil nitrogen in a barley (*Hordeum vulgare* L.)—Soil system. *Plant Soil* 160:21–31.
- Zak, D.R., and K.S. Pregitzer. 1998. Integration of ecophysiological and biogeochemical approaches to ecosystem dynamics. p. 372–403. *In* M.L. Pace and P.M. Groffman (ed.) *Successes, limitations, and frontiers in ecosystem science*. Springer-Verlag, New York.
- Zwart, K.B., P.J. Kuikman, and J.A. Van Veen. 1994. Rhizosphere protozoa: Their significance in nutrient dynamics. p. 93–122. *In* J.F. Darbyshire (ed.) *Soil protozoa*. CAB Int., Wallingford, Oxon, UK.

