Review: Factors affecting rhizosphere priming effects

Yakov Kuzyakov[1]*

[1]Institute of Soil Science and Land Evaluation, University of Hohenheim, Emil-Wolff-Straße 27, D-70599 Stuttgart, Germany

Accepted 31 May 2002

Summary – Zusammenfassung

Living plants change the local environment in the rhizosphere and consequently affect the rate of soil organic matter (SOM) decomposition. The rate may increase for 3- to 5-folds, or decrease by 10 % to 30 % by plant cultivation. Such short-term changes of rate (intensity) of SOM decomposition are due to the priming effect. In the presence of plants, a priming effect occurs in the direct vicinity of the living roots, and it is called rhizosphere priming effect (RPE). Plant-mediated and environmental factors, such as, plant species, development stage, soil organic matter content, photosynthesis intensity, and N fertilization which affect RPE are reviewed and discussed in this paper. It was concluded that root growth dynamics and photosynthesis intensity are the most important plant-mediated factors affecting RPE. Environmental factors such as amount of decomposable C in soil and N_{min} content are responsible for the switch between following mechanisms of RPE: concurrence for N_{min} between roots and microorganisms, microbial activation or preferential substrate utilization. Succession of mechanisms of RPE along the growing root in accordance with the rhizodeposition types is suggested. Different hypotheses for mechanisms of filling up the C amount loss by RPE are suggested.

The ecosystematic relevance of priming effects by rhizodeposition relates to the connection between exudation of organic substances by roots, the increase of microbial activity in the rhizosphere through utilization of additional easily available C sources, and the subsequent intensive microbial mobilization of nutrients from the soil organic matter.

Key words: carbon turnover / exudation / humus mineralization / soil organic matter decomposition / rhizosphere priming effect / rhizodeposition / root effects / ^{14}C / ^{13}C / ^{15}N

Einflussfaktoren auf Priming-Effekte in der Rhizosphäre

Wurzeln lebender Pflanzen verändern die lokale Umgebung in der Rhizosphäre und beeinflussen oft die Intensität des Abbaus der organischen Bodensubstanz (OBS). Beim Anbau von Pflanzen kann die OBS-Mineralisation um das 3- bis 5-fache im Vergleich zur Schwarzbrache ansteigen oder um 10 % bis 30 % abnehmen. Solche kurzfristigen Änderungen der Intensität des OBS-Abbaus gehören zum Phänomen des Priming-Effektes. Da beim Pflanzenwachstum die Priming-Effekte in unmittelbarer Nähe von lebenden Wurzeln stattfinden, werden sie Rhizosphäre-Priming-Effekte (RPE) genannt. Dieser Artikel gibt eine kritische Analyse und Diskussion des Erkenntnisstandes über die Faktoren, die die RPE beeinflussen. Dazu gehören Faktoren, die über die Pflanze bzw. die Umwelt wirken, wie Pflanzentyp und -entwicklung, Photosyntheseintensität, Gehalt an organischer Bodensubstanz und N-Düngung. Es kann geschlussfolgert werden, dass die Dynamik des Wurzelwachstums und die Intensität der Photosynthese die wichtigsten über die Pflanze wirkenden Faktoren sind. Die Umweltfaktoren wie der Gehalt an umsetzbarem Kohlenstoff und mineralischem Stickstoff (N_{min}) im Boden bedingen den Wechsel zwischen folgenden Mechanismen der RPE: (1) Konkurrenz für N_{min} zwischen den Wurzeln und den Mikroorganismen, (2) Aktivierung der Rhizosphärenmikroorganismen durch die Wurzelexsudate und (3) bevorzugte Nutzung der Rhizodeposite als leichtverfügbares Substrat und nicht der OBS. Dieser Wechsel wird, in Übereinstimmung mit den Typen der Rhizodeposite und der Sukzession der Mikroorganismen, durch die räumliche Abfolge der RPE entlang der wachsenden Wurzel erklärt. Unterschiedliche Mechanismen der Auffüllung der C-Verluste der OBS, die während der RPE entstehen, werden diskutiert. Die ökosystemare Bedeutung der Priming-Effekte durch die Rhizodeposition besteht in der Stimulation der Rhizosphärenmikroorganismen durch den leichtverfügbaren Kohlenstoff zum intensiven mikrobiellen Abbau der organischen Bodensubstanz und in der Mobilisation zusätzlicher Nährstoffe speziell in Perioden des intensiven Pflanzenwachstums.

1 Introduction

Carbon (C) input by plants into the soil is the primary source of soil organic matter (SOM). In the past decades, we have gained considerable insight into below-ground C allocation by plants (reviewed by *Lynch* and *Whipps*, 1990; *Whipps*, 1990; *Kuzyakov* and *Domanski*, 2000). About one-third to half of total assimilated C (net assimilated + shoot respiration) is allocated below-ground. Subsequently, between 10 and 15 % of below-ground allocated C is respired by roots to generate metabolic energy which is used for growth, maintenance and transport processes. About 15 % to 25 % of below-ground allocated C is exuded from the roots into the soil. These exuded organic substances induce fast C turnover in the vicinity of the roots. The rhizosphere is characterized by very intensive C turnover forced by microorganisms (*Hiltner*, 1904). Rhizosphere microorganisms utilize these substances as easily available C and energy sources for fast growth and reproduction. Because microorganisms are not limited by available C in rhizosphere, the number of microorganisms in the rhizosphere is 19- to 32-times larger than in the root-free soil

---

* Correspondence: Dr. Y. Kuzyakov; E-mail: kuzyakov@uni-hohenheim.de

1436-8730/02/0408-382 $17.50+.50/0

(*Bodelier* et al., 1997). However, this surplus of easily available source in the rhizosphere is typical only for C. Despite the exudation of some nitrogen- (N) containing organic compounds, mostly amino acids (*Merbach* et al., 1999; *Hütsch* et al., 2002), the C:N ratio of whole rhizodeposits is higher than that of microorganisms (bacteria), which have the C:N ratio of 5:1 to 6:1 (*Fenchel*, 1982). It is important to note, that most of the results about C:N ratio in rhizodeposits have been obtained from nutrient solution studies, in which only exudates (definition see below) having low C:N ratio are considered. The C:N ratio of exudates is about 2.5 to 13.0 (*Mench* and *Martin*, 1991; *Van de Geijn* and *Van Veen*, 1993). Other parts of rhizodeposition such as sloughed root cells, root hairs, lysates, and mucilage (all with high C:N) are strongly underestimated in nutrient solution studies compared to soil conditions. Therefore, the C:N ratio of rhizodeposits released under non-sterilized soil conditions is much higher than that of exudates. Consequently, compared to C, all other nutrients, including N, are strongly limited in the rhizosphere (*Kuikman* et al., 1990; *Liljeroth* et al., 1990; *Breland* and *Bakken*, 1991). Additionally, root uptake and intensive microbial growth on easily available C sources lead to temporary immobilization of all accessible nutrients into growing plant and microbial cells. In contrast, in a root-free soil easily available C is limiting for microbial growth and all nutrients are usually not limiting (*Wardle*, 1992). Both factors: **surplus of easily available C and strong nutrient limitation produce the local environment in the rhizosphere strongly different from that of the root-free soil.**

Fast turnover of C and microorganisms in the rhizosphere may locally change the rate of microbial SOM decomposition. The increasing or decreasing decomposition of SOM compared with the SOM decomposition in root-free soil (Fig. 1) belongs to the phenomena of priming effects (*Parnas*, 1976; Kuzyakov et al., 2000). A priming effect (PE) is a short-term change in the turnover intensity (e.g. decomposition) of SOM caused by different factors such as fertilization, plant cultivation etc. The mechanisms of PEs caused by mineral and organic fertilization have been reviewed earlier (*Jenkinson*, 1966; *Jenkinson* et al., 1985; *Kuzyakov* et al., 2000) and are not included in this review.

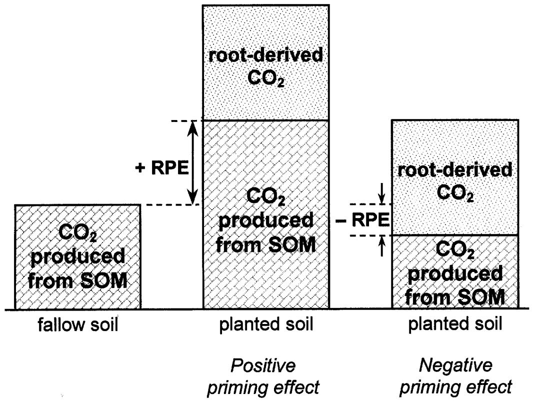

Figure 1: Schematization of the priming effect – non-additive interactions between root growth and decomposition of soil organic matter (SOM): (a) acceleration of SOM decomposition – positive priming effect; (b) retardation of SOM decomposition – negative priming effect (*Kuzyakov* et al., 2000, changed)

Abbildung 1: Vereinfachte Darstellung der Priming-Effekte – der nicht-additiven Wechselwirkungen zwischen dem Wurzelwachstum und dem Abbau der organischen Bodensubstanz (OBS): (a) Beschleunigung des OBS-Abbaus – positiver Priming-Effekt; (b) Verlangsamung des OBS-Abbaus – negativer Priming-Effekt (*Kuzyakov* et al., 2000, verändert)

In case of plant cultivation, PEs occur in the direct vicinity of living roots. Therefore, they are called rhizosphere priming effect (RPE). The negative RPE cannot be lower than –100 %, because 100 % decrease corresponds to the absence of SOM decomposition. However, in many studies negative RPE of about –10 % to –30 % were measured. Positive RPE could be much higher than 100 %. For example, in one of the pioneer priming effects study, 4- to 11-fold increase of SOM decomposition was recorded as CO$_2$ efflux after addition of ^{13}C labeled sudan grass (*Broadbent* and *Norman*, 1946). Also in later studies RPE of about 200 % to 400 % were frequently reported.

2 Mechanisms of rhizosphere priming effects

Seven possible mechanisms of rhizosphere priming effects caused by living root have been suggested:

1) **Drying effect or drying / rewetting hypothesis**: Compared to unplanted soil, water uptake by plants always results in drier soil conditions, which reduces SOM decomposition (*Van Schreven*, 1967; *Reid* and *Gross*, 1982a). However, drying-rewetting cycles in cultivated soil, and especially in the topsoil, could increase SOM decomposition compared to unplanted soil (*Sala* et al., 1992).

2) **Aggregate destruction hypothesis**: Growing roots may promote the destruction of aggregates more than their formation. Therefore, some portion of the physically protected labile SOM is then exposed to microbial attack, which may increase SOM decomposition (*Reid* and *Gross*, 1981, 1982b; *Helal* and *Sauerbeck*, 1984, 1986).

3) **Root uptake of soluble organic substances**: If roots take up the released exudates in a significant quantity, the microbial activity in the rhizosphere will be decreased because of reduction of C source; the SOM decomposition decreases subsequently (*Sparling* et al., 1982; *Reid* and *Goss*, 1982b; 1983).

4) **Enhancing microbial turnover due to faunal grazing** (*Ingham* et al., 1985; *Clarholm*, 1985a, b; *Elliot* et al., 1988; *Kuikman* et al., 1990, 1991; *Griffiths*, 1994; *Alphei* et al., 1996). Faunal predation of microorganisms in the rhizosphere may increase microbial turnover, and consequently increase the release of mineral N (N$_{min}$) and CO$_2$. Strictly speaking, this mechanism is due the release of CO$_2$ and nutrients from dying microorganisms and not from SOM.

5) **Competition for N$_{min}$ between plant roots and rhizosphere microorganisms**: Microbial growth in the rhizosphere is limited by available N. Therefore, root uptake of N raises the competition for nutrients and decreases the microbial growth and metabolism, thereby depressing SOM decomposition (*Schimel* et al., 1989; *Wang* and *Bakken*, 1989, 1997; *Ehrenfeld* et al., 1997; *Bottner* et al., 1999).

6) **Preferential substrate utilization**: If two substrates with very different availability (e.g. exudates and SOM) are present at one location, microorganisms prefer to utilize at first the easily available rhizodeposits and then SOM, resulting in a decrease in SOM decomposition during the first period (*Sparling* et al., 1982; *Billes* et al., 1988).

7) **Microbial activation**: Easily available substances released by roots stimulate microbial growth in the rhizosphere and lead to an increased decomposition of SOM probably to get limiting N, or to "unintentional" co-metabolic decomposition of SOM (*Helal* and *Sauerbeck*, 1986; *Sallih* and *Bottner*, 1988; *Cheng* and *Coleman*, 1990). According to *Nobili* et al. (2001), even very low amount ($\mu g\ g^{-1}$) of some primers such as exudates, may stimulate microbial biomass to stronger SOM decomposition.

These mechanisms were reviewed in detail by *Dormaar* (1990) and *Cheng* and *Kuzyakov* (2002). It has been concluded, that biological rather than physical factors are responsible for RPE (*Dormaar*, 1990) and that (1) microbial activation, (2) preferential substrate utilization, and (3) concurrence of demand for mineral N between plant roots and microorganisms, are the most important mechanisms of rhizosphere priming (*Cheng* and *Kuzyakov*, 2002). Also it has been stated that easily decomposable C_{org} and N_{min} in the soil determine the presence and magnitude of these mechanisms. Beside these two parameters controlling mechanisms of RPE, there are some other environmental and plant-mediated factors responsible for RPE which have not been summarized before. Therefore, the first aim of this article is to discuss the factors affecting RPE.

It is important to note here, that not only microbial enhance of SOM decomposition, but also direct chemical effects, such as pH and redox change, complexation, chelatization, and solubilization of some elements (e.g. P, Fe, Mn, Zn, Cu, S etc.) by exuded substances (especially organic acids, exoenzymes) may increase availability of some nutrients in soil (*Jauregui* and *Reisenauer*, 1982; *Uren* and *Reisenauer*, 1988; *Marschner*, 1991, 1995; *Vaughan* et al., 1993; *Merbach* et al., 1999; *Gahoonia* et al., 1992; *Jungk* and *Claassen*, 1997; *Schilling* et al., 1998). These chemical causes of RPE are not reviewed in this article (see *Marschner*, 1995).

Positive PEs were observed in the most studies investigating effects of roots on the SOM decomposition (*Cheng* and *Kuzyakov*, 2002). It means that SOM decomposition in rooted soil is faster compared to that in root-free soil. Therefore, plant cultivation may lead to the depletion of SOM. In contrast, all long-term field experiments show that fallow plots always have lower C_t content compared to planted plots (*Körschens*, 1998; *Powlson* et al., 1998). Thus, the second aim was to suggest mechanisms explaining the replacement and rebuilding the losses of C and other nutrients induced by positive RPE.

3 Methods estimating rhizosphere priming effects

Several direct and indirect methods were used to estimate priming effects in the rhizosphere. The direct methods estimate either C_{org} changes or differences in mineral nutrients, mainly N, before and after cultivation and compare these changes with that of the fallow soil samples for the same investigation period. Simultaneous measurements of both (C_{org} and N_{min}) were used very seldom (*Sallih* et al., 1987; *Billes* et al., 1988; *Zagal*, 1994). High variability of C_{org} content and its very low changes during short-term experiments decrease the applicability of direct methods. Measuring dissolved organic C (DOC) or other forms of labile C could improve validity of the direct methods (*Martin*, 1987; *Lasserre-Joulin* et al., 2001) because the changes in decomposable labile C are much stronger than that of total C_{org}.

Indirect methods are based on the comparison between the SOM-derived CO_2 efflux from planted and unplanted soil. The total CO_2 efflux from planted soil consists of two main sources: i) root-derived CO_2 which is the sum of root respiration and microbial respiration decomposing rhizodeposits and ii) SOM-derived CO_2 evolved by microbial decomposition of SOM. Firstly, it is important to separate these two sources. Secondly, the CO_2 evolved by microbial decomposition of SOM from the planted soil is compared with the total CO_2 efflux from unplanted soil (consisting only from one source: microbial SOM decomposition).

Using different C isotopes techniques is the only way to separate root-derived and SOM-derived CO_2 evolved from the planted soil. Continuous labeling of plants during the whole plant development in $^{14}CO_2$ or $^{13}CO_2$ atmosphere with constant specific ^{14}C activity or ^{13}C enrichment and subsequent measuring of ^{14}C or ^{13}C in CO_2 evolved from soil is a reliable method for this aim (*Liljeroth* et al., 1990, 1994; *Helal* und *Sauerbeck*, 1981, 1983). The exact separation of SOM-derived and root-derived CO_2 occurs according to the reduction of specific ^{14}C activity of CO_2 evolved from soil compared to activity of CO_2 offered for assimilation. However, the equipment needed for continuous labeling is difficult and expensive, and it can be applied only in a few laboratories in the world.

An important modification for continuous labeling techniques was introduced by *Cheng* (1996) and *Rochette* and *Flanagan* (1997) using the differences in ^{13}C discrimination by C_3 and C_4 plants. Cultivation of C_3 plant on C_4 soil (*Cheng*, 1996) or vice versa (*Rochette* and *Flanagan*, 1997) and subsequent monitoring of $\delta^{13}C$ values of CO_2 from the soil allow the separation of SOM and root-derived CO_2 without special equipment for continuous ^{14}C or ^{13}C labeling. The ^{13}C natural abundance method has important advantages over other techniques (*Rochette* et al., 1999) since: (1) all C pools of the plant are labeled, (2) it is a non-intrusive method, and (3) it does not involve handling of radioactive material. This method can be used under field conditions (*Rochette* and *Flanagan*, 1997). Meanwhile, this method is used in many studies as standard procedure allowing separation of root-derived and SOM-derived CO_2 (*Qian* et al., 1997; *Rochette* et al., 1999; *Flessa* et al., 2000; *Kuzyakov* and *Cheng*, 2001; *Fu* et al., 2002; *Fu* and *Cheng*, 2002). The principle of the ^{13}C natural abundance method allows an exact calculation of the proportion of the root-derived and SOM-derived CO_2 in the total CO_2 efflux from soil. However, some important limitations of ^{13}C natural abundance method limit its application. Soil-plant pairs impose limitations to the ^{13}C natural abundance method through C_3 plants growing in a C_4 soil or *vice versa* are unusual. Hence, the field application of this method is restricted to places where soils developed under C_3 vegetation allow the growth of C_4 plants and vice versa. This limit of the $\delta^{13}C$ method was overcome by the use of the Free Air CO_2 Enrichment (FACE) experiment with shifted C isotopic composition (*Leavitt* et al., 1996; *Andrew* et al., 1999; *Kessel* et al., 2000). In most cases the CO_2 depletion in ^{13}C ($\delta^{13}C \approx 40$ ‰) produced by combustion of fossil sources of energy is used for FACE. High-resolution and high-sensitivity mass-spectrometry is necessary for ^{13}C analyses, because a maximal range of only ~14 ‰ is available for all variations of the $^{13}C : {}^{12}C$ ratio in CO_2 (it is calculated as the difference between the $\delta^{13}C$ value of cell tissue of C_3 and C_4 plants). At the same time, the variability of $\delta^{13}C$ value in soil or plant is at least about ± 1 ‰–2 ‰ (*Cheng*, 1996) or more (*Farquhar* et al., 1989). Additionally, the ^{13}C discrimination by plants is depending on the environmental conditions, such as temperature, water deficit (*Farquhar* et al., 1989; *Hogh-Jensen* and *Schjoerring*, 1997; *Lucero* et al., 2000), air humidity (*Ekblad* and *Hödberg*, 2001), N supply (*Hogh-Jensen* and *Schjoerring*, 1997), light intensity (*Pate* and *Arthur*, 1998), and specific root length (*Poorter* and *Farquhar*, 1994). Also CO_2 diffusion in soil leads to isotopes fractionation (*Cerling* et al., 1991). Similar to the labeling methods, application of ^{13}C natural abundance method require a gas-tight isolation of soil from the atmosphere, which have $\delta^{13}C$ of about 6 ‰ to 7 ‰. These limitations of the ^{13}C natural abundance method limit its wider application and an exact estimation of root-derived and SOM-derived CO_2.

There is another method for separating the root-derived from the SOM-derived CO_2 which is based on the pulse labeling of shoots in $^{14}CO_2$ atmosphere and calculation of the amount of root-derived and SOM-derived CO_2 according ^{14}C specific activity in different plant parts (*Kuzyakov* et al., 1999a, 2001). This method assumes that the partitioning pattern of assimilated C does not change significantly during the monitoring period. This assumption is accomplishable only during vegetative growth stages. The ^{14}C distribution applied at one growth stage cannot be applied to another because partitioning patterns undergo changes during plant growth, especially by transition to generative stage. Therefore, the pulse labeling allows only very rough estimation of the root derived CO_2 because of continual dilution of the labeled photosyntates with new unlabelled photosyntates. However, series of labeling pulses applied at regular intervals during plant growth have been found to provide a reasonable estimate of the cumulative belowground C input (*Keith* et al., 1986; *Gregory* and *Atwell*, 1991; *Jensen*, 1993; *Swinnen* et al., 1994; *Warembourg* and *Estelrich*, 2000; *Kuzyakov* et al., 1999a, 2001, 2002). The calculation of the root-derived CO_2 according to ^{14}C distribution after pulse labeling could not be used under conditions that rapidly change ^{14}C incorporation into the shoots (i.e. defoliation, strong reduced photosynthesis, etc.). As it has been shown by *Hodge* and *Millard* (1998) ^{14}C pulse chase methodology is an important physiological tool, although it should not be used in isolation.

In spite of the great variation between results observed in different laboratories, *Kuzyakov* and *Cheng* (2001) have shown that ^{13}C natural abundance method and ^{14}C pulse labeling produce similar values for separating the root-derived and SOM-derived CO_2. Each method separating root-derived and SOM-derived CO_2 has some limitations (*Killham* and *Yeomans*, 2001). Besides, results obtained with each of these three methods will be discussed in the following.

It is important to mention that the estimations of root-derived and SOM-derived CO_2 based on the root exclusion techniques (*Rochette* et al., 1999) primary accept that no RPE are induced by plant growth. Therefore these results cannot be reviewed here.

4 Rhizodeposition components in respect to rhizosphere priming effects

Total input of organic C by plant roots into the soils consists of two main forms: (1) root biomass which contribute to C budget of the soils after the plant has died, and (2) rhizodeposition including whole organic C released by living roots into the soil (exudations, secretions, sloughed off cells, C released by root turnover). The contribution of the first source is well known and there are many studies on decomposition, mineralization, and humification rates of root residues in the soil. Compared to rhizodeposits, roots are decomposed much slower. Therefore, they do not induce strong PE. Moreover, a wide C:N ratio of roots can provoke N immobilization or negative PE during their decomposition (*Kuzyakov* et al., 1999b).

The lack of simple methods limit the estimation of the second source, the rhizodeposition under undisturbed soil conditions. The difficulties are connected with fast decomposition of the most rhizodeposits, their losses by common separation methods (e.g. root washing) and their disregarding by some optical methods (rhizotron studies), as well as difficult differentiation between the SOM-derived and root-derived organic substances. Different isotopic methods which allow distinguishing between SOM-derived C and C deposited by roots into the soil have been used successfully (see above). The amounts of C released as rhizodeposits and estimated by isotopic methods are reviewed earlier (*Lynch* and *Whipps*, 1990; *Whipps*, 1990; *Kuzyakov* and *Domanski*, 2000; *Kuzyakov*, 2001).

It is generally accepted that rhizodeposition comprise of several groups, depending on the mode of release and their chemical composition (*Lynch* and *Whipps*, 1990; *Whipps*, 1990; *Marschner*, 1995; *Graystone* et al., 1996):

(1) **Water soluble exudates**, consisting of low molecular weight substances (mainly sugars and molecular organic acids), which are lost passively along a concentration gradient without metabolic activity (*Burström*, 1955; *Bowen* and *Rovira*, 1991);

(2) **Secretions** comprising mostly of higher molecular weight substances (carbohydrates, lipids, and proteins), released depending on the metabolic processes against

electrochemical potential and chemical gradients (*Hale* et al., 1978);

(3) **Mucilage** which covers the plant roots and is composed mainly of polysaccharides and polygalacturonic acids of high molecular weight (*Watt* et al., 1993; *Marschner*, 1995);

(4) **Lysates** released from cells after autolysis and comprise the components of sloughed-off cells, and within time, the whole root (*Whipps*, 1990);

(5) **Gases** such as CO_2, ethylene etc. evolved by roots may also be accepted as rhizodeposits (*Rovira*, 1969, 1973; *Graystone* et al., 1996). According to the definition, that only organic substances belong to rhizodeposits, these gases are not considered here. Also, gases evolved by roots play a marginal role in the C turnover in the rhizosphere.

These rhizodeposits groups were arranged above according to their availability for microorganisms as C source and correspond to their possibility to induce RPE. Thus, low molecular weight exudates (group 1) are utilized by microorganisms during few hours (*Kuzyakov* and *Demin*, 1998). Their solubility in water, mobility, as well as ability to direct incorporation in growing microbial cells make exudates most important primer in the rhizosphere. As shown by *Nobili* et al. (2001), almost very low amounts of glucose and amino acids could trigger biomass activation and 2- to 5-fold increase of SOM decomposition. High relevance of exudates for microorganisms shows the fact that exudates are the group of rhizodeposits which is mostly increased in non-sterile conditions compared to other rhizodeposits groups (*Schönwitz* and *Ziegler*, 1982; *Kloss* et al., 1984). Secretes and mucilage (group 2 and 3) need longer time for uptake and utilization by microorganisms. Lysates (group 4), especially cell walls and other high molecular organic substances cannot be consumed within a few hours. Therefore, lysates are less important for priming microbial biomass.

Dalenberg and *Jager* (1989) also divided the organic substances they studied into two classes. Substances belonging to the first class (amino acid, glutamate, aspartate) lead to positive C priming effects when decomposed. These substances are similar to exudates. Substances of the second class, which are similar to cell lysates and mucilage, were high molecular and slowly decomposable substances such as cellulose or wheat straw caused negative priming effects.

5 Factors affecting rhizosphere priming effects

Different factors can influence the physical and chemical conditions in the rhizosphere and thereby change the C utilization by microorganisms. Because RPEs depend on the rhizodeposition and especial on the exudation intensity, all factors affecting rhizodeposition as well as microbial turnover in the rhizosphere should also affect RPE. In the following, results from the literature and own studies will be discussed to outline the effects of shoot and root growth, plant species and soil types, soil fertility and N_{min} content, and photosynthesis intensity on C and N release during plant induced changes of SOM decomposition.

5.1 Plant-mediated factors

5.1.1 Shoot and root growth

Shoot and root development are the most important plant-mediated factors controlling rhizodeposition. Most studies observed the maximal exudation intensity for young roots (*Fu* et al., 2002). Root senescence leads to the decrease of the amount of exuded substances related to the root mass unit. However, the decrease of exudation intensity at the beginning is slower than the root growth and therefore the total amount of exuded substances increases. For most annual plants, the total rhizodeposition increases until the end of tillering. In the generative stage the amount of exudates decrease rapidly (*Warembourg* and *Esterlich*, 2001). In this context, the RPE must increase until begin of generative stage, and then they must decrease very fast.

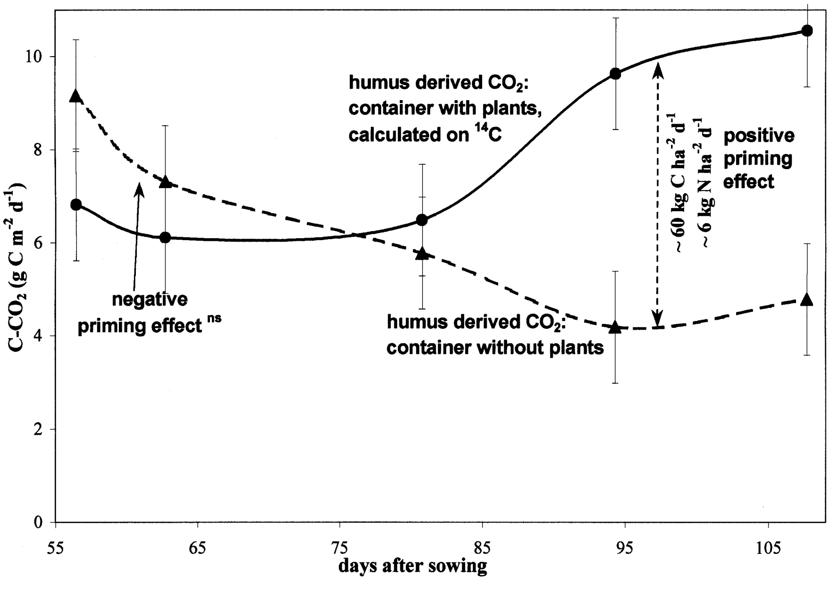

Figure 2: SOM-derived CO_2 efflux from the soil with *Lolium perenne* and from the bare soil and positive priming effect induced by plants (*Kuzyakov* et al., 2000a).

Abbildung 2: CO_2-Fluss aus dem Boden durch die Mineralisation der OBS (C_t = 4,7 %) mit und ohne *Lolium perenne* und positiver Priming-Effekt, der durch die Pflanzen induziert wird (*Kuzyakov* et al., 2000a).

According to this statement, *Kuzyakov* et al. (2001) found an increase of RPE induced by *Lolium* during 3.5 months (Fig. 2). During first half of the observation period a small non-significant negative PE was observed. After 2.5 month of vegetative growth of *Lolium*, the RPE became positive and 60 kg CO_2-C ha^{-1} d^{-1} was released additionally. Similar dynamics of RPE was measured during the whole development of wheat by *Cheng* (1996), *Cheng* and *Johnson* (1998), and *Kuzyakov* and *Cheng* (2001). At the beginning of wheat growth a negative PE of about 30 % was observed, followed by a strong increase up to 300 % at the end of the second month, and leveling out at 50 % of the control (*Cheng* and *Kuzyakov*, 2002).

Earlier investigated combination of three soils and two plants (*Kuzyakov* et al., 1999a, 2001; *Siniakina* and *Kuzyakov*, 2002) allowed to study the dependence of the extra decomposition of SOM on the plant age (Fig. 3). The decrease of decomposition of SOM was measured in our experiments only in a few cases. The fully developed plants increase the extra decomposition of SOM more strongly than the younger plants. This seems to disagree with the well-known fact, that young roots exude organic substances more intensively than old roots. This apparent contradiction can be explained by larger occupation of much more soil space by roots of fully developed plants compared to the young seedlings. It overcompensates the decreased exudation per root mass unit by old plants. In conclusion, exudation of organic substances during fast root growth phases may lead to strong SOM decomposition and mobilization of nutrients.

5.1.2 Plant and soil types

There are only a few studies investigating the effects of different plants or soils on the decomposition of soil organic matter in one experiment. Therefore a direct comparison of results obtained under different conditions is difficult. From this point of view, it is being promised to compare studies obtained in the same laboratory, because equipment, methods, and environmental conditions are frequently the same. Using a natural abundance ^{13}C method, *Fu* and *Cheng* (2002) and *Fu* et al. (2002) showed that two C_3 plants, soybean and sunflower, growing on a C_4 Haplic Chernozem induce 40 % to 70 % faster SOM decomposition. Under the same experimental conditions two C_4 plants, sorghum and amaranthus, slightly decreased the mineralization of organic matter of a C_3 Chromic Luvisol for about 5 % to 10 %. Furthermore, the RPE depended on the plant development stage. The authors concluded that in a C_4 soil – C_3 plant system positive priming will be observed and in a system C_3 soil – C_4 plant the direction of priming effect depends on plant development stage. However, the content of decomposable C in both soils, responsible for the direction of RPE, was not considered in this study. Probably the Haplic Chernozem had a higher amount of decomposable C, and root exudates induced some additional mineralization of the decomposable C. Inert C in Chromic Luvisol could hardly be used by rhizosphere microorganisms. Therefore, they switched on to easily available exudates and the SOM decomposition decreased. This means that the amount of decomposable C in soil determines the direction of RPE.

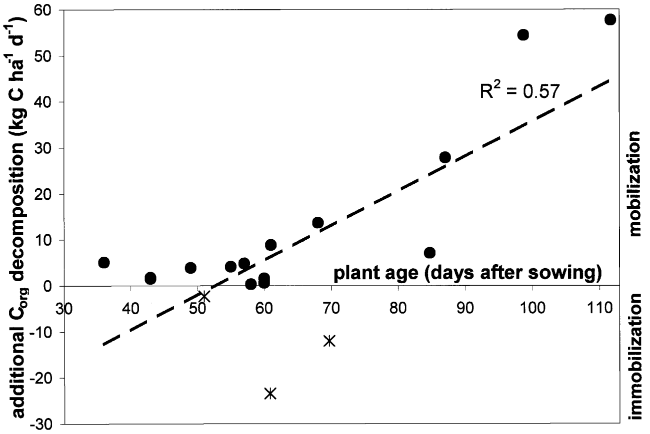

Figure 3: Effect of plant age (presented as days after sowing) of *Lolium perenne* and lettuce on the decomposition intensity of SOM (combined from *Kuzyakov* et al., 1999a, 2001; *Siniakina* and *Kuzyakov*, 2002).

Abbildung 3: Einfluss des Pflanzenalters (Tage nach der Aussaat) von *Lolium perenne* und Kopfsalat (*Lactuca sativa*) auf die Intensität des OBS-Abbaus (kombinierte Ergebnisse aus *Kuzyakov* et al., 1999a, 2001; *Siniakina* and *Kuzyakov*, 2002).

Nevertheless, the physiological differences between C_3 and C_4 plants may probably have an effect on rhizosphere processes due to different amount and probably quality of exuded substances. C_4 plants have a higher efficiency of nutrient use. It means that they need fewer nutrients for the production of the same amount of organic substances compared to C_3 plants. Therefore, C_4 plants invest less C in the below ground processes, and probably exude less organic substances from the roots. However, this remains a hypothesis until the amounts and quality of organic substances released by roots of C_3 and C_4 plants will be investigated comparatively.

Regarding the variation between plants, the amount of roots, and the type of root system must have an effect of SOM decomposition. Most experiments were conducted with plants having fibrous root system. However, studies were found in which plants with different root systems were compared in one experiment. *Fu* and *Cheng* (2002) found positive correlation between root biomass and the amount of primed C (only for C_4 soil – C_3 plant system). Therefore plants with well-developed and branched root system must stronger increase SOM decomposition.

5.2 Environmental factors

5.2.1 C_{org} content in the soil

Two contrasting hypotheses could explain the effects of C_{org} content in a soil on the amount of RPE. (1) The high content of organic substances leads to high amounts of easily available C which can be mineralized by microorganisms during RPE. (2) N and other nutrients are not so strongly limited as compared with a low fertile soil. Therefore, plants as well as microorganisms growing on a soil rich in C_{org} are less dependent on enhanced SOM mineralization to obtain nutrient surplus.

Experiments that were conducted in our laboratory showed that a fine loamy Gleyic Cambisol containing 4.7 % of C_{org}

had 30- to 100-times higher RPE compared to a sandy Gleyic Camisol with 0.7 % C_{org} (*Kuzyakov* et al., 2001; *Siniakina* and *Kuzyakov*, 2002). However, different plants (*Lolium* and lettuce) were used in these experiments which limits the comparability.

Warembourg and *Esterlich* (2001) showed that in a soil poor in C_{org}, grasses allocated a higher portion of net assimilated C below ground and released more C as exudates compared to soil richer in C_{org}. The ecological application of this fact is that plants try to stimulate rhizosphere microorganism to increase SOM mineralization and nutrient mobilization due to the higher exudation especially in the low fertile soils.

5.2.2 Photosynthesis intensity

Up to now, only few studies have investigated the effect of photosynthesis on below-ground processes and C turnover in the rhizosphere. They have shown that the intensity of photosynthesis is the main factor controlling below-ground C allocation, exudation, as well as CO_2 efflux from the soil (*Whipps*, 1984; *Zagal*, 1994; *Todorovic* et al., 1999; *Craine* et al., 1999; *Högberg* et al., 2001; *Kuzyakov* and *Cheng*, 2001). An increase in the total CO_2 efflux from the soil with using plants growing under better light conditions was observed in all these studies. An important portion of the CO_2 increase is explained by the higher transfer of easy available organic compounds in the rhizosphere by roots at better light conditions (*Whipps*, 1984). However, the SOM decomposition could also be changed. Using the natural ^{13}C abundance method, *Kuzyakov* and *Cheng* (2001) separated root-derived and SOM-derived CO_2 and observed a strong RPE that was induced by wheat grown on a C_4 Haplic Chernozem (C_{org} rich soil) under normal light conditions (Fig. 4, left part). In this soil, microbial activation must be responsible for the positive RPE. Three days without light led to an exhaust of exudates as C and energy sources for microorganisms and to a decrease of RPE to zero. New light-on event after 2.5 days darkness led to a fast release of easily available organic compounds in the rhizosphere and resulted in a switch of microbial biomass from SOM decomposition to the utilization of easily available organic compounds. Probably, preferential substrate utilization was responsible for the negative PE observed after light-on event from the day 4 (Fig. 4). Diurnal dynamics of CO_2 efflux from the soil with a constant day/night temperature is also an indirect evidence of photosynthesis effects on SOM decomposition (*Kuzyakov* and *Cheng*, 2001). Similar diurnal cycles and effect of photosynthesis on processes in rhizosphere of *Glyceria maxima* was observed by lengthening photoperiod for the O_2 release by roots, induced denitrification and a higher C exudation (*Bodelier* et al., 1997).

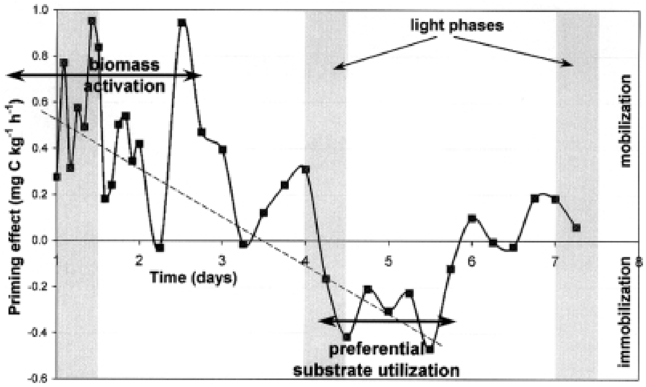

Figure 4: Effect of easily available rhizodeposits as controlled by photosynthesis intensity on the rhizosphere priming effect and its mechanisms (*Kuzyakov* and *Cheng*, 2001, changed).
Abbildung 4: Mechanismen der Rhizosphäre-Priming-Effekte in Abhängigkeit von der Photosynthese (*Kuzyakov* und *Cheng*, 2001, verändert).

Reduction of light intensity changes the amount of root-derived ^{14}C in the rhizosphere and in microorganisms reflecting a deficiency of energy and C needed by heterotrophic microflora. This results in a decrease of ^{15}N mineralization from SOM and, consequently, a lower N uptake by barley was measured (*Zagal*, 1994). A shorter photoperiod has a similar effect and results additionally in smaller numbers of bacteria in the rhizosphere (*Whipps*, 1984).

It could be concluded that the absence of light for plants or worse assimilation conditions can change the direction of RPE from strongly positive (under normal light conditions) to no RPE or negative (without light) only during 4–5 days. This causal relationship holds for short periods (days). Longer lasting changes in light condition could have a physiological effect. For instance, perennial grasses begin to store more C below-ground under a shorter day period which simulates autumn (*Todorovic* et al., 1999).

5.2.3 N_{min} content in soil and N fertilization

Mineral N fertilization changes the local environment in the rhizosphere directly and indirectly. Directly, added mineral N reduces the N limitation in the rhizosphere. Therefore, the concurrence for N_{min} between the roots and microorganisms is weaker, the growth conditions for microorganisms become better, the number of microorganisms increases (*Marschner*, 1995), and the C use efficiency of exudates increases (*Liljeroth* et al., 1990). Therefore, less SOM is necessity to be decomposed mobilizing additional N.

The indirect changes occur due to the response of plants to a better N supply. On one side, the net assimilation increases (*Warembourg* and *Esterlich*, 2001) and plants grow faster. On the other side, the portion of C allocated below-ground decreases (*Paterson* and *Sim*, 1999; *Chapin*, 1980; *Coleman* et al., 1983; *Warembourg* and *Estelrich*, 2001). These opposite tendencies of (1) a higher photosynthesis and (2) a lower portion of below-ground translocated C by better N supply complicate the prediction of total C transferred into the rhizosphere by N fertilization. Frequently, the increase of total assimilation by higher N_{min} supply over-compensates the reduction of the C part translocated below-ground and the increase in total rhizodeposition (*Liljeroth* et al., 1994; *Van der Krift* et al., 2001).

If one accepts that the total amount of C allocated into the soil by mineral N input remains similar as without N fertilization, then the RPE will decrease after fertilization, because the local N limitation decrease. This means that additional SOM mineralization in the planted unfertilized soil (= natural ecosystem) will be higher than in the fertilized soil (= agricultural ecosystem). Such reduction of rhizosphere priming effect by application of N fertilizer was observed in many studies (*Cheng* and *Coleman*, 1990; *Liljeroth* et al., 1994). Additionally, low N_{min} content alters root morphology. Much more fine roots were produced, the specific root length increased by about three times, and the exudation related to root mass increased (*Hodge* et al., 1996; *Paterson* and *Sim*, 1999). Therefore, the local C surplus, especially rhizodeposits inducing PE (see above), and N limitation are much higher pronounced in the rhizosphere of unfertilized plants than that of fertilized ones. Therefore RPE must be stronger in an unfertilized soil. This was confirmed by *Kessel* et al. (2000) who showed in FACE with depleted $\delta^{13}C$ that *Lolium perenne*, which cannot fix N_2, induced a stronger SOM decomposition than *Trifolium repens* which symbiotically fix N_2.

However, a very low N_{min} amounts in the soil may have an opposite effect. Under strong N_{min} limitation, additional N_{min} depletion by root uptake leads to a decrease of microbial biomass (*Merckx* et al., 1985, 1987; *Hu* et al., 2001; *Wang* and *Bakken*, 1997; *Bottner* et al., 1999). Roots are strongly effective competitors with microorganisms for N (*Hodge* et al., 2000) and are winning during long-term periods. Under this strong concurrence for N_{min}, rhizosphere microorganisms cannot benefit from organics released by roots (*Merckx* et al., 1985, 1987; *Van Veen* et al., 1989). Thus the immobilization of N_{min} after straw addition also decreased the additional SOM decomposition and N mineralization induced by wheat roots (*Bremer* and *Kuikman*, 1997; *Wang* and *Bakken*, 1997).

5.2.4 N mineralization by extra decomposition of SOM

In the previous discussion the RPE for C was reviewed. However, the extra SOM decomposition leads to the release of N_{min}. Probably, N acquisition is most the important goal for microorganisms which decompose SOM in the rhizosphere. *Clarholm* (1989) showed that about 21 % of total N in barley plants originated from root-induced N mineralization of SOM. Experimental evidence showing that plants can enhance the net mineralization of soil organic N has been reported by several workers (*Billes* et. al., 1988; *Clarholm*, 1985b; *Haider* et al., 1987, 1991; *Kuikman* and *Van Veen*, 1989; *Wheatley* et al., 1990). The N mineralization in the rhizosphere was associated with an increase in casein-hydrolyzing and L-histidine-deaminating activities (*Badalucco* et al., 1997). In contrast to C, mineralized N can remain in soil, be taken up by plants, immobilized by microbial biomass, or leached. Therefore, processes of N turnover in the rhizosphere are more complicated compared to those of C, and many pools have to be considered in investigating the priming effect for N (= extra N mineralization from SOM). Additionally, ^{15}N fertilizers frequently used as tracer showed an apparent increase in the SOM-derived N (apparent N priming effect) by processes of pool substitution or isotopic exchange (*Jenkinson* et al., 1985; *Kuzyakov* et al., 2000).

The priming effect for N strongly depends on the N_{min} content of soil or on the added N fertilizer. In accordance to this point of view, *Bremer* and *Kuikman* (1997) observed a strong decrease in N mineralization from SOM after $^{15}NO_3^-$ addition to wheat. The extent of N priming effect decreases during the plant development of ryegrass by rising N supplies (Fig. 5). The extra N mineralization from SOM increases without N fertilization from 40 up to more than 100 kg N ha^{-1}. This phenomenon is connected with a decrease in the exudation amount by increasing N supply. The same effect of decreasing portion of below-ground translocated C or exuded organic substances was observed in some investigations for N (*Merckx* et al., 1987; *Johansson*, 1992; *Zagal* et al., 1993; *Zagal*, 1994; *Swinnen* et al., 1995; *Van Ginkel* et al., 1997; *Stewart* and *Metherell*, 1999; *Kuzyakov* et al., 1999a), for potassium (*Kraffczyk* et al., 1984), and for phosphorus (*Foehse* and *Jungk*, 1983; *Wittenmayer* et al., 1995; *Schilling* et al., 1998; *Stewart* and *Metherell*, 1999). These studies have shown that in soils well supplied with all nutrients, the necessity for plants to invest C for the below-ground organs and exudation decreases.

5.2.5 Elevated atmospheric CO_2 concentrations

Many studies have shown that the amount of assimilated C as well as C allocated below-ground was increased under elevated CO_2. Additionally, it was observed frequently that the rhizodeposition and root-derived CO_2 increased stronger than the C allocation to roots. Therefore, the C surplus and N limitation in the rhizosphere under elevated CO_2 concentrations were stronger pronounced than under ambient CO_2. From these relationships it can be expected that an increased amount of C in the rhizosphere could have an effect on the SOM decomposition. However, in contrast to PE, changes in SOM content induced by elevated CO_2 concentrations will

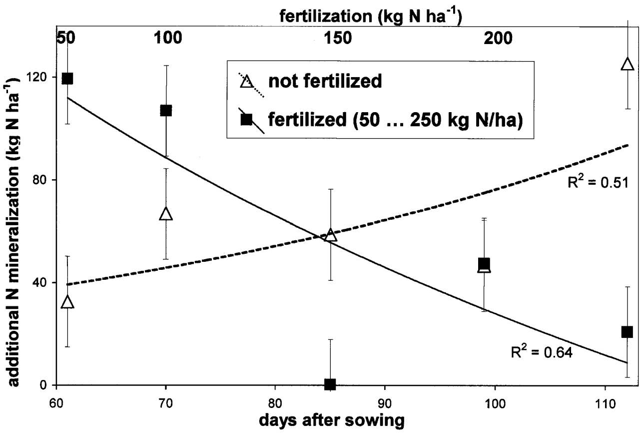

Figure 5: Effect of N fertilization on the additional N mineralization from SOM by growing *Lolium perenne* (unpublished data from the experiment *Kuzyakov* et al., 2001).

Abbildung 5: Einfluss der N-Düngung auf die zusätzliche N-Mineralisierung aus der OBS während des Wachstums von *Lolium perenne* (nicht veröffentlichte Ergebnisse aus dem Experiment *Kuzyakov* et al., 2001).

have a rather long-term effect. Strictly speaking, a new equilibrium between high C input by plants into the soil, its humification rates and SOM mineralization can be expected. The PE is a short-term change according to the definition in the introduction. As shown earlier, positive and/or negative PE were leveled out, when longer observation periods were considered (*Führ* and *Sauerbeck*, 1968; *Bottner* et al., 1999). Therefore, long-term changes of SOM decomposition rates under elevated CO_2 concentrations do not belong to the priming effect and, thus, will not be described here. Other reviews could be recommended for this aim (*Kirschbaum*, 2000).

6 Synthesis

6.1 Mechanisms of RPE depending on the amount of decomposable C and N_{min} in soil

As it is shown above, decomposable organic C in soil and the N_{min} content are the most important soil factors determining the direction and the amplitude of the RPE. Now, suggestions are given how the mechanisms of RPE can switch depending on the amount of decomposable organic C and N_{min} in soil (Fig. 6). Two axes represent incremental amounts of decomposable C and N_{min} in the soil, and the mechanisms of RPE are placed according to the both environmental factors.

(1) At low contents of both nutrients (C and N_{min}), a strong concurrence for mineral N between roots and microorganisms retard SOM decomposition (**concurrence for N_{min} between roots and microorganisms**).

(2) Higher amounts of decomposable C correspond to a better C availability for microorganisms and to their high activity. Additional input of easily available rhizodeposits with low C:N ratio primes microorganisms to decompose SOM for achieving additional N (**microbial activation**).

(3) At the low contents of decomposable C and high N_{min} contents, SOM decomposition is not necessary for obtaining additional N. Therefore, the input of easily available rhizodeposits leads to a switch from the SOM decomposition to the decomposition of recent rhizodeposits (**preferential substrate utilization**).

(4) If both factors, decomposable organic C and N_{min}, are not limited in soil, no RPE will be observed because microorganisms have optimal growth conditions and additional rhizodeposits cannot stimulate or suppress them.

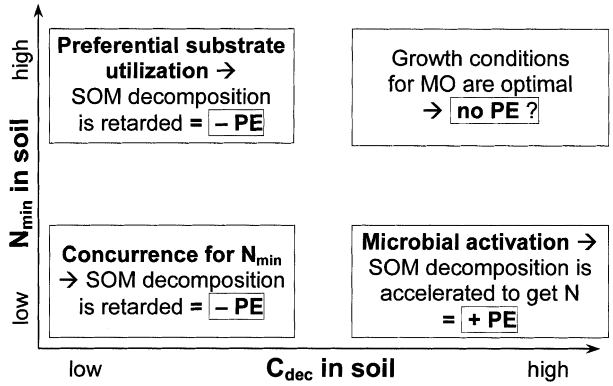

Figure 6: Hypothesized dominating mechanism of priming effects (PE) in the rhizosphere under different combination of decomposable C (C_{dec}) and N_{min} in soil. MO: microorganisms; SOM: soil organic matter.

Abbildung 6: Dominierende Mechanismen der Priming-Effekte (PE) in der Rhizosphäre bei unterschiedlicher Kombination des umsetzbaren C (C_{dec}) und N_{min} im Boden. MO: Mikroorganismen; SOM: organische Bodensubstanz.

As described in the introduction, low contents of N_{min} and other nutrients as well as a surplus of easily available C are typical for rhizosphere conditions. Therefore, activation of microorganisms by rhizodeposits (mechanism 2) is most common for RPE in natural ecosystems. Frequent ploughing, exhausting decomposable C, and high N input in agricultural soils favor a switch of the main mechanism of RPE. Probably, preferential substrate utilization is the main mechanism controlling RPE in agricultural ecosystems. Further research is required to quantify the threshold values of decomposable C and N_{min} which lead to the switch from one kind of mechanisms to the others.

6.2 Mechanisms of RPE depending on localization along the roots

In the most soil ecology studies investigating the distribution of organic substances, enzymes etc. depending on the distance from the roots, it is tacitly accepted that different part of the roots have similar exudation activity. So, the distribution of substances in the root-free soil is usually investigated depending on the distance from the rooted soil layer. However, the maximum rhizodeposition occurs in the most active root parts, not far from the root tip (*Marschner*, 1995). Additionally, various root zones release different rhizodeposite types. Dead root cap cells will be sloughed from the root cap (Fig. 7). Mucilage and slime are secreted around the root cap and the cell division zone. Low molecular weight organic substances are exuded in the elongation zone. In the root hair zone, and cork zone cell lysates are typical rhizodeposits (*Marschner*, 1995).

According to this scheme as well as to the microbial growth intensity, different effects of substances that are released by roots could be expected. As it is shown in Fig. 7, the most easily decomposable substances are released between root tips and the beginning of the root hair zone. Therefore, the maximum intensity of the microbial growth is also typical for this zone. Usually, this zone is located at places firstly occupied by roots. Mineral N is not depleted by root uptake. Surplus of available C and fast microbial growth lead to fast immobilization of N in rhizosphere microorganisms in this zone. Because of sufficient amounts of decomposable C (assumed for Fig. 7) and the growth of microorganisms in this zone, microorganisms begin to decompose intensively SOM to obtain N (microbial activation). Consequently, a positive RPE is expected in the first zone.

In the second zone, protozoa feed microorganisms, and a part of N stored in microorganisms is released. Roots take up this mineral N in this as well as in the next zone. In the second zone, the concurrence between microorganisms and roots for N_{min} is maximal. The amount of easily available exudates decreases and exudates are replaced by slowly

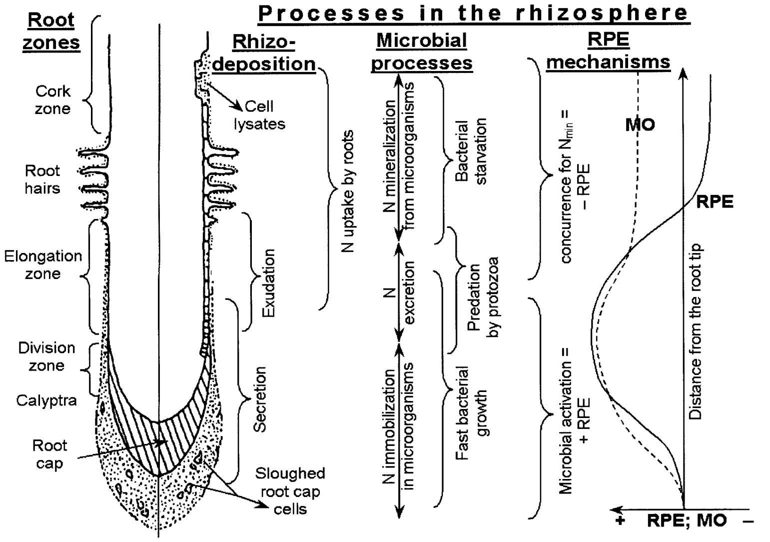

Figure 7: Types of rhizodeposits, microbial growth, C and N turnover processes, and rhizosphere priming effects (RPE) along the growing root. RPE and change of microorganisms (MO) amount compared to the fallow soil is shown on the right (high content of decomposable C is accepted, see Fig. 6).
Abbildung 7: Typen der Rhizodeposition, mikrobielles Wachstum, C- und N-Umsatzprozesse, und Rhizosphäre-Priming-Effekte (RPE) entlang der wachsenden Wurzel. RPE und die Veränderungen der Menge der Mikroorganismen (MO) im Vergleich zu wurzelfreiem Boden sind rechts dargestellt (hoher Gehalt an umsetzbarem C ist für die RPE-Mechanismen vorausgesetzt, siehe Abb. 6).

decomposable cell lysates. Hence, strong concurrence and bacterial starvation lead to a decrease of SOM decomposition (= negative RPE).

Similar wavelike patterns of microbial populations in the rhizosphere along the growing roots were experimentally observed by *Semenov* et al. (1999) and *Bruggen* et al. (2000), and were modeled according growing root as a moving source of easily available C (*Zelenev* et al., 2000).

This scheme shows, that different mechanisms are replaced during the root growth. It is important, that especially the young roots induce the priming effect. Usually the volume occupied by roots is about 1 % in the upper soil horizons (*Marschner*, 1995) and about 10 % in the rhizosphere. Therefore, the values of RPE that are presented in the first part of the review must be actually related to the small soil volume around the young roots rather than to the whole soil volume. Consequently, the local increase of SOM decomposition intensity will be at least 5- to 10-times higher!

6.3 Hypotheses for replenishing of C losses induced by RPE

As mentioned in the introduction and shown by *Cheng* and *Kuzyakov* (2002), positive RPEs were observed in most short-term studies and were pronounced much stronger than negative RPEs. This means, that the plant growth decreases the content of soil C_{org}. Contrary, all long-term field experiments show an accumulation or stationary level of SOM by cultivation (*Körschens*, 1998; *Powlson* et al., 1998). This apparent controversy needs to be explaned.

It is undoubted that plants accelerate the turnover of SOM (*Zagal*, 1994). On the one hand, plants induce mostly positive RPE and, thus, an accelerated SOM decomposition. On the other hand, plant-derived organic C that remained in soil after plant death and C exuded during the life are the most important sources for humification. Therefore, accelerated decomposition and higher C input result in an acceleration of SOM turnover by cultivation.

Not only high C inputs, but also other mechanisms are responsible for the replenishment of C losses that are induced by RPE. I suggest three different mechanisms:

1) **Time** hypothesis: positive PE (increased decomposition) and preferred humification occur at different time periods. Most studies investigating RPE were conducted for a short time period, usually 2 to 4 months, simulating the spring season. In this period (spring under natural conditions) the root growth is mostly intensive, the required nutrient amounts are at maximum, and the roots exude the maximum quantity of organic substances to stimulate microorganisms for SOM decomposition (Fig. 8). Further plant development and transition in the generative stage (occurring in summer or autumn under natural conditions) strongly decrease root growth as well as the exudation. Hence, the plant-mediated decomposition of SOM decreases. More dead plant residues (slowly

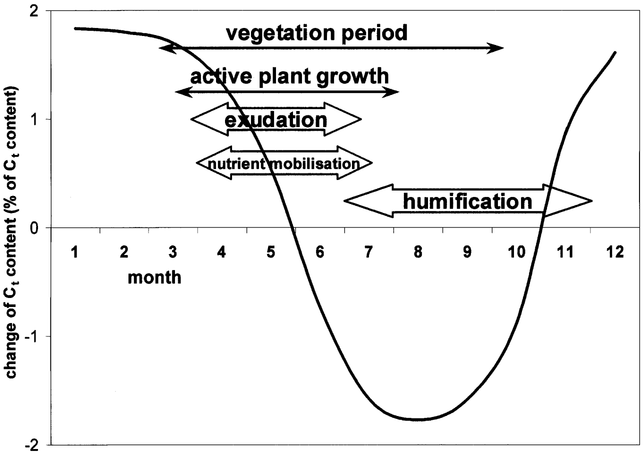

Figure 8: Annual SOM dynamics as explained by RPE and humification of plant residues dominating in SOM turnover at different time periods. Explanation in text.
Abbildung 8: Jährliche OBS-Dynamik erklärt durch die RPE und Humifikation der Pflanzenreste, die zu unterschiedlichen Zeitperioden dominieren. Erklärungen im Text.

decomposable compared to rhizodeposits) remain in the soil and are preferably converted to SOM (Fig. 8). This stage of plant development (simulating late summer and autumn) was very seldom investigated in the scope of RPE studies. This hypothesis explains annual dynamics of many parameters measured in some long-term studies such as SOM (*Dormaar* et al., 1984; *Leinweber* et al., 1994), easily available organic C (*Leinweber* et al., 1995), microbial biomass (*Diaz-Ravina* et al., 1993), enzyme activities (*Dormaar* et al., 1984), and nutrient content (*Vaughn* et al., 1986; *Diaz-Ravina* et al., 1993). In these studies, the decrease of SOM similar to that presented on Fig. 8 was measured in the spring and in the beginning of summer. Thereafter, an increase in SOM content and its maximum in the winter period were observed.

2) **Localization** hypothesis: SOM decomposition occurs preferably in the rhizosphere and humification mostly in the root-free soil. This hypothesis corresponds to many studies showing that living plants stimulate SOM decomposition in the rhizosphere compared to the decomposition in the root-free soil.

3) **Quality** hypothesis: different qualities of organic substances referred to humification:
   a. Easily decomposable N-free, low-molecular weight organic substances such as sugars, organic acids etc. induce a fast microbial growth and provoke a positive PE.
   b. Some substances could be incorporated chemically in humus molecules (e.g. amino acids) or will be decomposed slowly and will be stronger humified compared to group “a”.

   This hypothesis assumes that the humification coefficients of different substance classes are different. It means that some substances, probably more important for the ecosystem, were preferably selected by humification. A similar approach, concerning priming effects and not humification, was suggested by *Dalenberg* and *Jager* (1989), who divided some organic substances into two classes, causing either positive or negative priming effects.

7 Conclusions

There are no doubts that plants change the environment at each level, the global, the ecosystem, the soil horizon, and the rhizosphere level. In most ecosystems, plants modify soils making and maintaining the habitat more favorable for growth and surviving in stress conditions (*Van Breemen*, 1993). These biotic changes of abiotic environment include some new processes and also modify the rates of existing processes. Concerning C turnover in soil, plants may increase or decrease the rate of microbial SOM decomposition compared to that in root-free soil. In most cases an acceleration of SOM turnover by plant cultivation was observed. This C turnover is especially intensive in the rhizosphere, and differs from root-free soil by a high amount of C that is easily available for microorganisms, and by a low content of N_{min} and other nutrients.

Since photosynthesis intensity and root growth rate are the most important plant-mediated factors controlling rhizodeposition, plants may directly influence synchronization between nutrient demand during intensive growth phases and nutrient mobilization. “This synchronization occurs by stimulating N mineralization during active growth by stimulating microbial activity and suppressing N mineralization during periods of inactivity by depositing N-deficient residues” (*Bremer* and *Kuikman*, 1997). Therefore, exudation of organic substances by roots in the rhizosphere is not a wasteful C and energy losses for the plants, but an evolutionary developed mechanism of indirect symbiosis with rhizosphere microorganisms. The ecosystematic relevance of PEs by rhizodeposition relates to the connection between exudation of organic substances by roots, the increase of microbial activity in the rhizosphere through utilization of additional easily available C sources, and the subsequent intensive microbial mobilization of nutrients from SOM. Also the plants compensate C losses in the rhizosphere by increasing nutrients uptake and photosynthesis intensity. Plants also benefit from the increased mobilization through the indirect additional nutrient acquisition. Similar symbiosis between N_2 fixing bacteria and legume plants is accepted for a long time (*Warembourg* and *Roumet*, 1989; *Lynch* and *Whipps*, 1990). Probably, RPE is an important mechanism for nutrient mobilization especially in natural ecosystems that have high levels of decomposable C in the soil and strong interspecific concurrence for nutrients. N fertilization and frequently exhausted soil fertility in ploughed soils diminish the importance of RPE in agricultural ecosystems or lead to negative RPE (preferential substrate utilization).

Easily decomposable C in the soil as a part of SOM and the N_{min} amount determine the mechanism that dominates in the specific conditions. Preferential substrate utilization and concurrence between roots and microorganisms for N_{min} are other mechanisms crucial for RPEs. The triggers of these and possibly some other mechanisms of nutrient mobilization in the rhizosphere remain unknown and need further investigation. The amounts of C lost during RPE is replaced by the C remaining for humification in the cultivated soil after plant death, different qualities of substances for humification, different C turnover in cultivated and fallow soil as well as shift of periods with preferred mobilization and humification.

References

Alphei, 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.

Badalucco, L., *P. J. Kuikman*, and *P. Nannipieri* (1997): Protease and deaminase activities in wheat rhizosphere and their relation to bacterial and protozoan populations. Biol. Fert. Soils 23, 99–104.

Bazin, M. J., P. Markham, E. M. Scott, and *J. M. Lynch* (1990): Population dynamics and rhizosphere interactions. In Lynch, J. M. (ed.): The Rhizosphere. Wiley, Chichester, p. 99–127.

Billes, G., *P. Bottner*, and *N. Gandais-Riollet* (1988): Effet des raciness de graminees sur la mineralization nette de l'azote du sol. Rev. Ecol. Biol. Sol 25, 261–277.

Bodelier, P. L. E., *A. G. Wijlhuizen*, *C. W. P. M. Blom*, and *H. J. Laanbroek* (1997): Effects of photoperiod on growth of and denitrification by Pseudomonas chlororaphis in the root zone of Glyceria maxima, studied in a gnotobiotic microcosm. Plant Soil. 190, 91–103.

Bottner, P., *M. Pansu*, and *Z. Sallih* (1999): Modelling the effect of active roots on soil organic matter turnover. Plant Soil 216, 15–25.

Bowen, G. D., and *A. D. Rovira* (1991): The rhizosphere, the hidden half of the hidden half. In Waisel, Y., Eshel, A., and U. Kafkafi (eds.): Plant Roots – The Hidden Half. Marcel Dekker, New York, p. 641–649.

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

Bremer, E., and *P. Kuikman* (1997): Influence of competition for nitrogen in soil on net mineralization of nitrogen. Plant Soil 190, 119–126.

Broadbent, F. E., and *A. G. Norman* (1946): Some factors affecting the availability of the organic nitrogen in soil – A preliminary report. Soil Sci. Soc. Am. Proc. 11, 264–267.

Bruggen, A. H. C., *A. M. Semenov*, and *V. V. Zelenev* (2000): Wavelike distributions of microbial populations along an artificial root moving through soil. Microbial Ecol. 40, 250–259.

Burström, H. G. (1955): The physiology of plant roots. In Baker, K. F., and W. C. Snyder (eds): Ecology of Soil-Borne Plant Pathogenes. University California Press, Berkeley, p. 154–166.

Cardon, Z. G., *B. A. Hungate*, *C. A. Cambardella*, *F. S. Chapin, III.*, *C. B. Field*, *E. A. Holland*, and *H. A. Mooney* (2001): Contrasting effects of elevated CO_2 on old and new soil carbon pools. Soil Biol. Biochem. 33, 365–373.

Cerling, T. E., *D. K. Solomoin*, *J. Quade*, and *J. R. Bowman* (1991): On the isotopic composition of carbon in soil carbon dioxide. Geochim. Cosmochim. Acta 55, 3403–3405.

Chapin, III., F. S. (1980): The mineral nutrition of wild plants. An. Rev. Ecol. Systematics 11, 233–260.

Cheng, W. (1996): Measurement of rhizosphere respiration and organic matter decomposition using natural ^{13}C. Plant Soil 183, 263–268.

Cheng, W., and *D. C. Coleman* (1990): Effect of living roots on soil organic matter decomposition. Soil Biol. Biochem. 22, 781–787.

Cheng, W., and *Y. Kuzyakov* (2002): Root effects on decomposition of organic matter. In S. Wright (ed.): Roots and Soil Management: Interactions Between Roots and Soil. Soil Sci. Soc. Am. Book Series, Soil Sci. Soc. Am., Inc., Madison, Wisconsin. (in press).

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.

Clarholm, M. (1985a): Possible role for roots, bacteria, protozoa and fungi in supplying nitrogen to plants. In Fitter, A. H. (ed.): Ecological interactions in soil. Blackwell Science, Oxford. p. 355–365.

Clarholm, M. (1985b): Interactions of bacteria, protozoa and plants leading to mineralization of soil nitrogen. Soil Biol. Biochem. 17, 181–187.

Clarholm, M. (1989): Effects of plant-bacterial-amoebal interactions on plant uptake of nitrogen under field conditions. Biol. Fert. Soils 8, 373–378.

Coleman, D. C., *C. P. P. Reid*, and *C. V. Cole* (1983): Biological strategies of nutrient cycling in soil systems. Adv. Ecol. Res. 13, 1–54.

Craine, J. M., *D. A. Wedin*, and *F. S. Chapin III.* (1999): Predominance of ecophysiological controls on soil CO_2 flux in a Minnesota grassland. Plant Soil 207, 77–86.

Dalenberg, J. W., and *G. Jager* (1989): Priming effect of some organic additions to ^{14}C-labeled soil. Soil Biol. Biochem. 21, 443–448.

Dormaar, J. F. (1990): Effect of active roots on the decomposition of soil organic materials. Biol. Fert. Soils 10, 121–126.

Dormaar, J. F., *A. Johnston*, and *S. Smoliak* (1984): Seasonal changes in carbon content, and dehydrogenase, phosphatase, and urease activities in mixed prairie and fescue grassland Ah horizons. J. Range Manag. 37, 31–35.

Diaz-Ravina, M., *M. J. Acea*, and *T. Carballas* (1993): Seasonal fluctuations in microbial populations and available nutrients in forest soils. Biol. Fert. Soils 16, 205–210.

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.

Ekblad, A., and *P. Hödberg* (2001): Natural abundance of ^{13}C in CO_2 respired from forest soils reveals speed of link between tree photosynthesis and root respiration. Oecologia 127, 305–308.

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.

Farquhar, G. D., *J. R. Ehleringer*, and *K. T. Hubick* (1989): Carbon isotope discrimination and photosynthesis. An. Rev. Plant Phys. Plant Molec. Biol. 40, 503–537.

Fenchel, T. (1982): Ecology of heterotrophic microflagelates. II. Bioenergetics and growth. Marine Ecol. Prog. Ser. 8, 225–231.

Flessa, H., *B. Ludwig*, *B. Heil*, and *W. Merbach* (2000): The origin of soil organic C, dissolved organic C and respiration in a long-term maize experiment in Halle, Germany, determined by ^{13}C natural abundance. J. Plant Nutr. Soil Sci. 163, 157–163.

Foehse, D., and *A. Jungk* (1983): Influence of phosphate and nitrate supply on root hair formation of rape, spinach and tomato plants. Plant Soil 74, 359–368.

Fu, S., and *W. Cheng* (2002): Rhizosphere priming effects on the decomposition of soil organic matter in C_4 and C_3 grassland soils. Plant Soil 238, 289–294.

Fu, S., *W. Cheng*, and *R. Susfalk* (2002): Rhizosphere respiration varies with plant species and phenology: A greenhouse pot experiment. Plant Soil 239, 133–140.

Führ, F., and *D. Sauerbeck* (1968): Decomposition of wheat straw in the field as influenced by cropping and rotation. In: Isotopes and radiation in soil organic matter studies. Proc. Symp. Intern. Atomic. Energy Agency, Food and Agriculture Organization and Intern. Soil Sci. Soc. in Vienna, July 15–19, 1968. Inter Atomic Energy Agency, Vienna. p. 241–250.

Gahoonia, T. S., *N. Claassen*, and *A. Jungk* (1992): Mobilization of phosphate in different soils by ryegrass supplied with ammonium or nitrate. Plant Soil 140, 241–248.

Graystone, 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.

Gregory, P. J., and *B. J. Atwell* (1991): The fate of carbon in pulse labelled crops of barley and wheat. Plant Soil 136, 205–213.

Griffiths, B. S. (1994): Soil nutrient flow. In Darbyshire, J. F. (ed.): Soil Protozoa. Wallingford, CAB International, p. 65–92.

Haider, K., *A. Mosier*, and *O. Heinemeyer* (1987): The effect of growing plants on denitrification at high soil nitrate concentrations. Soil Sci. Soc. Am. J. 51, 97–102.

Haider, K., *A. Mosier*, and *O. Heinemeyer* (1991): Effects of plants on nitrogen and carbon turnover in soil. In Berthelin, J. (ed.): Diversity of

Environmental Biogeochemistry. Developments in Geochemistry 6, Elsevier, Amsterdam, p. 419–426.

Hale, M. G., L. D. Moore, and *G. J. Griffin* (1978): Root exudates and exudation. In Dommergues, Y. R., and S. V. Krupa (eds): Interactions between Non-pathogenic Soil Microorganisms and Plants. Elsevier, Amsterdam 163–203

Helal, H. M. und *D. R. Sauerbeck* (1981): Ein Verfahren zur Trennung von Bodenzonen unterschiedlicher Wurzelnähe. Z. Pflanzenernähr. Bodenkd. 144, 524–527.

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. Sauerbeck* (1989): Carbon Turnover in the Rhizosphere. Z. Pflanzenernähr. Bodenkd. 152, 211–216.

Hiltner, L. (1904): Über neuere Erfahrungen und Probleme auf dem Gebiet der Bodenbakteriologie und unter besonderer Berücksichtigung der Gründüngung und Brache. Arb. Deutsch. Landw. Gesell. 98, 59–78.

Hodge, A., and *P. Millard* (1998): Effect of elevated CO_2 on carbon partitioning and exudate release from *Plantago lanceolata* seedlings. Phys. Plantarum 103, 280–286.

Hodge, A., *S. J. Graystone*, and *B. G. Ord* (1996): A novel method for characterization and quantification of plant root exudates. Plant Soil 184, 97–104.

Hodge, A., *J. Stewart*, *D. Robinson*, *B. S. Griffiths*, and *A. H. Fitter* (2000): 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. Hogberg*, *G. Nyberg*, *M. Ottosson-Lofvenius*, and *D. J. Read* (2001): Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature-London. 411, 6839, 789–792.

Hogh-Jensen, H., and *J. K. Schjoerring* (1997): Effects of drought and inorganic N form on nitrogen fixation and carbon isotope discrimination in *Trifolium repens*. Plant Phys. Biochem. 35, 55–62.

Hu, S., *F. S. Chapin, III.*, *M. K. Firestone*, *C. B. Field*, and *N. R. Chiariello* (2001): Nitrogen limitation of microbial decomposition in a grassland under elevated CO_2. Nature 409, 188–191.

Hütsch, B. W., *J. Augustin*, and *W. Merbach* (2002): Plant rhizodeposition – an important source for carbon turnover in soils. J. Plant Nutr. Soil Sci. 165, 397–407.

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.

Jauregui, M. A., and *H. M. Reisenauer* (1982): Dissolution of oxides of manganese and iron by root exudate components. Soil Sci. Soc. Am. J. 46, 314–317.

Jenkinson, D. S. (1966): The priming action. In: The Use of Isotopes in Soil Organic Matter Studies. Report of Food and Agriculture Organization and International Atomic Energy Agency, Technical Meeting: Braunschweig-Völkenrode 1963, p. 199–207.

Jenkinson, D. S., *R. H. Fox*, and *J. H. Rayner* (1985): Interactions between fertilizer nitrogen and soil nitrogen – the so called 'priming' effect. J. Soil Sci. 36, 425–444.

Jensen, B. (1993): Rhizodeposition by $^{14}CO_2$-pulse-labelled spring barley grown in small field plots on sandy loam. Soil Biol. Biochem. 25, 1553–1559.

Johansson, G. (1992): Release of organic C from growing roots of meadow fescue (*Festuca pratensis* L.). Soil Biol. Biochem. 24, 427–433.

Jungk, A., and *N. Claassen* (1997): Ion diffusion in the soil-root system. Adv. Agron. 61, 53–110.

Keith, H., *J. M. Oades*, and *J. K. Martin* (1986): Input of carbon to soil from wheat plants. Soil Biol. Biochem. 18, 445–449.

Kessel, C., *J. Nitschelm*, *W. R. Horwath*, *D. Harris*, *F. Walley*, *A. Luscher*, and *U. Hartwig* (2000): Carbon-13 input and turn-over in a pasture soil exposed to long-term elevated atmospheric CO_2. Global Change Biology 6, 123–135.

Killham, K., and *C. Yeomans* (2001): Rhizosphere carbon flow measurement and implications: from isotopes to reporter genes. Plant Soil 232, 91–96.

Kirschbaum, M. U. F. (2000): Will changes in soil organic carbon act as a positive or negative feedbyck on global warming? Biogeochem. 48, 21–51.

Kloss, M., *K.-H. Iwannek*, *I. Fendrik*, and *E. G. Niemann* (1984): Organic acids in the root exudates of *Diplachne fusca* (Linn.). Beauv. Environ. Exp. Bot. 24, 179–188.

Körschens, M. (1998): Soil organic matter and sustainable land use. Adv. Geoecol. 31, 423–430.

Kraffczyk, I., *G. Trolldenier*, and *H. Beringer* (1984): Soluble root exudates of maize: influence of potassium suply and rhizosphere microorganisms. Soil Biol. Biochem. 16, 315–322.

Kuikman, P. J., and *J. A. Van Veen* (1989): The impact of protozoa on the availability of bacterial nitrogen to plants. Biol. Fert. Soils 8, 13–18.

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.

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.

Kuzyakov, Y. V. (2001): Tracer studies of carbon translocation by plants from the atmosphere into the soil (a review). Eurasian Soil Sci. 34, 28–42.

Kuzyakov, Y., and *V. Demin* (1998): CO_2 efflux by rapid decomposition of low molecular organic substances in soils. Sciences of Soils 3. http://link.springer.de/link/service/journals/10112/ fpapers/8003001/80030002.htm

Kuzyakov, Y., and *G. Domanski* (2000): Carbon input by plants into the soil. Review. J. Plant Nutr. Soil Sci. 163, 421–431.

Kuzyakov, Y., and *W. Cheng* (2001): Photosynthesis controls of rhizosphere respiration and organbic matter decomposition. Soil Biol. Biochem. 33, 1915–1925.

Kuzyakov, Y., *A. Kretzschmar*, and *K. Stahr* (1999a): Contribution of *Lolium perenne* rhizodeposition to carbon turnover of pasture soil. Plant and Soil 213, 127–136.

Kuzyakov, Y., *G. Yilmaz*, and *K. Stahr* (1999b): Abbau der Rückstände von *Lolium perenne* und dadurch initiierte Priming-Effekte in Böden unterschiedlicher Nutzung. Agrobiol. Res. 52, 25–34.

Kuzyakov, Y., *J. K. Friedel*, and *K. Stahr* (2000): Review of mechanisms and quantification of priming effects. Soil Biol. Biochem. 32, 1485–1498.

Kuzyakov, Y., *H. Ehrensberger*, and *K. Stahr* (2001): Rhizodeposition of *Lolium perenne* on two nitrogen levels and enhance of humus decomposition. Soil Biol. Biochem. 33, 61–74.

Kuzyakov, Y., O. V. Biryukova, T. V. Kuznetzova, K. Mölter, E. Kandeler, and *K. Stahr* (2002): The response of C partitioning and CO_2 fluxes to cutting of ryegrass. Biol. Fert. Soils, 35, 348–358.

Lasserre-Joulin, F., P. C. Vong, and *A. Guckert* (2001): Evolution of soluble organic carbon in the rhizosphere and in corresponding non-rhizosphere soil in field-grown oilseed rape and barley. Immobilisation and turnover of sulphur-35 in the rhizosphere soil. In Horst W. J., Schenk, M. K., Burkert, A., Claassen, N., Flessa, H., Frommer, W. B., Goldbach, H., Olfs, H. W., and V. Romheld (eds): Plant Nutrition: Food Security and Sustainability of Agro-Ecosystems through Basic and

Applied Research. Kluwer Academic Publishers, Dordrecht, Netherlands, p. 624–625.

Leavitt, S. W., *E. A. Paul*, *A. Galadima*, *F. S. Nakayama*, *S. R. Danzer*, *H. Johnson*, and *B. A. Kimball* (1996): Carbon isotopes and carbon turnover in cotton and wheat FACE experiments. Plant Soil 187, 147–155.

Leinweber, P., *H. R. Schulten*, and *M. Körschens* (1994): Seasonal variations of soil organic matter in a long-term agricultural experiment. Plant Soil 160, 225–235.

Leinweber, P., *H. R. Schulten*, and *M. Körschens* (1995): Hot water extracted organic matter: chemical composition and temporal variations in a long-term field experiment. Biol. Fert. Soils 20, 17–23.

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.

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.

Lucero, D. W., *P. Grieu*, and *A. Guckert* (2000): Water deficit and plant competition effects on growth and water-use efficiency of white clover (*Trifolium repens*, L.) and ryegrass (*Lolium perenne*, L.). Plant Soil 227, 1–15.

Lynch, J. M., and *J. M. Whipps* (1990): Substrate flow in the rhizosphere. Plant Soil 129, 1–10.

Marschner, H. (1991): Plant-soil relationships: acquisition of mineral nutrients by roots from soils. In Porter, J. R., and D. W. Lawror (eds): Plant Growth: Interaction with Nutrition and Environment. Cambridge University Press, p. 125–155.

Marschner, H. (1995): Mineral Nutrition of Higher Plants. 2nd edn. Academic Press, London

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

Mench, M., and *E. Martin* (1991): Mobilization of cadmium and other metals from two soils by root exudates of *Zea mais* L., *Nicotania tabacum* L. and *Nicotania rustica* L. Plant Soil 132, 187–196.

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. Den Hartog*, and *J. A. Van Veen* (1985): Turnover of root-derived material and related microbial biomass formation in soils of different texture. Soil Biol. Biochem. 17, 565–569.

Merckx, R., *A. Dijkstra*, *A. Den Hartog*, and *J. A. Van Veen* (1987): Production of root-derived material and associated microbial growth in soil at different nutrient levels. Biol Fert Soils 5, 126–132.

Nobili, M., *M. Contin*, *C. Mondini*, and *P. C. Brookes* (2001): Soil microbial biomass is triggered into activity by trace amounts of substrate. Soil Biol. Biochem. 33, 1163–1170.

Pate, J., and *D. Arthur* (1998): δ^{13}C analysis of phloem sap carbon: novel means of evaluating seasonal water stress and interpreting carbon isotope signatures of foliage and trunk wood of *Eucaliptus globules*. Oecologia 117, 301–311.

Parnas, H. (1976): A theoretical explanation of the priming effect based on microbial growth with two limited substrates. Soil Biol. Biochem. 8, 139–144.

Paterson, E., and *A. Sim* (1999): Rhizodeposition and C-partitioning of Lolium perenne in axenic culture affected by nitrogen supply and defoliation. Plant Soil 216, 155–164.

Poorter, H., and *G. D. Farquhar* (1994): Transpiration, intracellular carbon dioxide concentration and carbon-isotope discrimination of 24 wild species differing in relative growth rate. Austral. J. Plant Phys. 21, 507–516.

Powlson, D. S., *P. Smith*, *K. Coleman*, *J. U. Smith*, *M. J. Glendining*, *M. Körschens*, and *U. Franko* (1998): A European network of long-term sites for studies on soil organic matter. Soil Tillage Res. 47, 263–274.

Qian, J. H., *J. W. Doran*, and *D. T. Walters* (1997): Maize plant contributions to root zone available carbon and microbial transformations of nitrogen. Soil Biol. Biochem. 29, 1451–1462.

Reid, J. B., and *M. J. Goss* (1981): Effect of living roots of different plant species on the aggregate stability of two arable soils. J. Soil Sci. 32, 521–541.

Reid, J. B., and *M. J. Goss* (1982a): 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.

Reid, J. B., and *M. J. Goss* (1982b): Interactions between soil drying due to plant water use and decreases in aggregate stability caused by maize roots. J. Soil Sci. 33, 47–53.

Reid, J. B., and *M. J. Goss* (1983): Growing crops and transformations of ^{14}C-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.

Rochette, P., *L. B. Flanagan*, and *E. G. Gregorich* (1999): Separating soil respiration into plant and soil components using analyses of the natural abundance of carbon-13. Soil Sci. Soc. Am. J. 63, 1207–1213.

Rovira, A. D. (1969): Plant root exudates. Bot. Rev. 35, 35–57.

Rovira, A. D. (1973): Zones of exudation along plant roots and spatial distribution of micro-organisms in the rhizosphere. Science 4, 361–366.

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.

Sallih, Z., *P. Bottner*, *G. Billes*, and *P. Soto* (1987): Interaction racines-microorganismes: carbone et azote de la biomasse microbienne developpée en presence de racines. Rev. Ecol. Biol. Sol. 24, 459–471.

Schönwitz, R., and *H. Ziegler* (1982): Exudation of water soluble vitamins and of some carbohydrates by intact roots of maize seedlings (*Zea mays* L.). Z. Pflanzenphysiol. 107, 7–14.

Schilling, G., *A. Gransee*, *A. Deubel*, *G. Lezovic*, and *S. Ruppel* (1998): Phosphorus availability, root exudates, and microbial activity in the rhizosphere. J. Plant Nutr. Soil Sci. 161, 465–478.

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.

Semenov, A. M., *A. H. C. Bruggen*, and *V. V. Zelenev* (1999): Moving waves of bacterial populations and total organic carbon along roots of wheat. Microbial Ecol. 37, 116–128.

Siniakina S. V., and *Y. Kuzyakov* (2002): Contribution of lettuce to carbon turnover in soil. Eurasian Soil Sci. (in press).

Smith, P., *D. S. Powlson*, *J. U. Smith*, and *E. T. Elliot* (1997): Evaluation and comparison of soil organic matter models. Geoderma, Special Issue, 81, 1–2.

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

Stewart, D. P. C., and *A. K. Metherell* (1999): Carbon (^{13}C) uptake and allocation in pasture plants following field pulse-labelling. Plant Soil 210, 61–73.

Swinnen, J., *J. A. Van Veen*, and *R. Merckx* (1994): ^{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., *J. A. Van Veen*, and *R. Merckx* (1995): Carbon fluxes in the rhizosphere of winter wheat and spring barley with conventional vs integrated farming. Soil Biol. Biochem. 27, 811–820.

Todorovic, C., *C. Nguyen*, *C. Robin*, and *A. Guckert* (1999): ^{14}C-assimilate partitioning within white clover plant – soil system: effects of photoperiod/temperature treatments and defoliation. Eur. J. Agron. 11, 13–21.

Uren, N. C., and *H. M. Reisenauer* (1988): The role of root exudates in nutrient acquisition. In Tinker, P.B., and Lauchli, A. (eds): Advanced in Plant Nutrition. Praeger, New York, p. 79–114.

Van Breemen, N. (1993): Soils as biotic constructs favoring net primary productivity. Geoderma 57, 183–211.

Van Ginkel, J. H., *A. Gorissen*, and *J. A. Van Veen* (1997): Carbon and nitrogen allocation in Lolium perenne in response to elevated atmospheric CO_2 with emphasis on soil carbon dynamics. Plant Soil 188, 299–308.

Van Schreven, D. A. (1967): The effect of dreying and wetting of a calcareous soil on carbon and nitrogen mineralization. Plant Soil 26, 14–32.

Van de Geijn, C. S., and *J. A. Van Veen* (1993): Implications of increased carbon dioxide levels for carbon input and turnover in soils. Vegetatio 104/105, 283–292.

, Van der Krift, T. A. J., *P. J. Kuikman*, *F. Moller*, and *F. Berendse* (2001): Plant species and nutritional-mediated control over rhizodeposition and root decomposition. Plant Soil 228, 191–200.

Vaughan, D., *D. G. Lumsdon*, and *D. J. Linehan* (1993): Influence of dissolved organic matter on the bio-availability and toxicity of metals in soils and aquatic systems. Chem. Ecol. 8, 185–201.

Vaughn, C. E., *D. M. Center*, and *M. B. Jones* (1986): Seasonal fluctuations in nutrient availability in some northern California annual range soils. Soil Sci. 141, 43–51.

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

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 *C. Roumet* (1989): Why and how to estimate the cost of symbiotic N2 fixation. A progressive approach based on the use of ^{14}C and $_{15}$N isotopes. Plant Soil 115, 167–177.

Warembourg, F. R., and *H. D. Esterlich* (2000): Towards a better understanding of carbon flow in the rhizosphere: a time-dependent approach using carbon-14. Biol. Fert. Soils 30, 528–534.

Warembourg, F. R., and *H. D. Esterlich* (2001): Plant phenology and soil fertility effects on below-ground carbon allocation for an annual (*Bromus madritensis*) and a perennial (*Bromus erectus*) grass species. Soil Biol. Biochem. 33, 1291–1303.

Watt, M., *M. E. McCully*, and *C. E. Jeffree* (1993): Plant and bacterial mucigels of the maize rhizosphere – comparison of their soil binding properties and histochemistry in a model system. Plant Soil 151, 151–165.

Wheatley, R., *K. Ritz*, and *B. Griffins* (1990): Microbial biomass and mineral N transformations in soil planted with barley, ryegrass, pea and turnip. Plant Soil 127, 157–167.

Whipps, J. M. (1990): Carbon economy. In Lynch, J. M. (ed): The rhizosphere. John Wiley, Chichester, p. 59–97.

Whipps, J. M. (1984): Environmental factors affecting the loss of carbon from the roots of wheat and barley seedlings. J. Exp. Bot. 35, 767–773.

Wittenmayer, L., *A. Gransee*, and *G. Schilling* (1995): Untersuchungen zur quantitativen und qualitativen Bestimmung von organischen Wurzelabscheidungen bei Mais und Erbsen. Mitteilgn. Dtsch. Bodenkundl. Gesellsch. 76, 971–974.

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.

Zagal, E., *S. Bjarnason*, and *U. Olsson* (1993): Carbon and nitrogen in the root zone of barley (*Hordeum vulgare* L.) supplied with nitrogen fertilizer at two rates. Plant Soil 157, 51–63.

Zelenev, V. V., *A. H. C. Bruggen*, and *A. M. Semenov* (2000): "BACWAVE," a spatial-temporal model for traveling waves of bacterial populations in response to a moving carbon source in soil. Microbial Ecol. 40, 260–272.

[P99/4B]