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Photosynthesis controls of CO_2 efflux from maize rhizosphere

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Abstract

The effects of different shading periods of maize plants on rhizosphere respiration and soil organic matter decomposition were investigated by using a ^{13}C natural abundance and ^{14}C pulse labeling simultaneously. ^{13}C was a tracer for total C assimilated by maize during the whole growth period, and ^{14}C was a tracer for recently assimilated C. CO_2 efflux from bare soil was 4 times less than the total CO_2 efflux from planted soil under normal lighting. Comparing to the normal lighting control (12/12 h day/night), eight days with reduced photosynthesis (12/36 h day/night period) and strongly reduced photosynthesis (12/84 h day/night period) resulted in 39% and 68% decrease of the total CO_2 efflux from soil, respectively. The analysis of ^{13}C natural abundance showed that root-derived CO_2 efflux accounted for 82%, 68% and 56% of total CO_2 efflux from the planted soil with normal, prolonged and strongly prolonged night periods, respectively. Clear diurnal dynamics of the total CO_2 efflux from soil with normal day-night period as well as its strong reduction by prolonged night period indicated tight coupling with plant photosynthetic activity. The light-on events after prolonged dark periods led to increases of root-derived and therefore of total CO_2 efflux from soil. Any factor affecting photosynthesis, or substrate supply to roots and rhizosphere microorganisms, is an important determinant of root-derived CO_2 efflux, and thereby, total CO_2 efflux from soils. ^{14}C labeling of plants before the first light treatment did not show any significant differences in the $^{14}CO_2$ respired in the rhizosphere between different dark periods because the assimilate level in the plants was high. Second labeling, conducted after prolonged night phases, showed higher contribution of recently assimilated C (^{14}C) to the root-derived CO_2 efflux by shaded plants. Results from ^{13}C natural abundance showed that the cultivation of maize on Chromic Luvisol decreased soil organic matter (SOM) mineralization compared to unplanted soil (negative priming effect). A more important finding is the observed tight coupling of the negative rhizosphere effect on SOM decomposition with photosynthesis.

Introduction

Carbon dioxide efflux from soils, an important component of the global C cycle, is connected with global climatic change because of the enhanced greenhouse effect caused by the increasing atmospheric CO_2 concentration. A small alteration in the turnover intensity of soil organic matter (SOM) can lead to a large change of CO_2 concentration in the atmosphere since the amount of C in SOM is twice as large as that in the atmosphere. However, common changes of SOM decomposition are usually small compared to the high variability of SOM content (20–40%) inherent of most soils. Therefore, quantification of SOM changes during short-term investigations is most often carried out by measuring soil CO_2 efflux which is sensitive enough to detect small and actual changes, especially for recently altered ecosystems. However, most soils are covered with vegetation, which also contributes to the CO_2 efflux from soil. Therefore CO_2

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efflux originated from SOM decomposition in planted soils is 'masked' by root-derived CO_2. Root-derived CO_2, also called rhizosphere respiration, comes from root respiration *per se* and rhizomicrobial respiration of exudates and dead roots[1]. Root-derived CO_2 is thought to comprise 40–60% of total CO_2 flux (Raich and Schlesinger, 1992), although these values strongly depend on growth stage especially in agriculture soils. Root-derived CO_2 is not part of soil C loss, and must be separated from the total CO_2 efflux in studies of soil C sequestration or loss and SOM turnover. So, the total CO_2 efflux consists of two unknown sources and it is necessary to know one to estimate the other.

Different isotope methods have been used to separate root-derived CO_2 from SOM-derived CO_2 effluxes, such as continuous (Johnen and Sauerbeck, 1977; Whipps, 1987; Meharg, 1994) or pulse (Warembourg and Billes, 1979; Meharg and Killham, 1990; Cheng et al., 1993; Swinnen et al., 1994; Kuzyakov et al., 1999; 2001; Nguyen et al., 1999) labeling with ^{13}C or ^{14}C, and ^{13}C tracing using the natural difference in ^{13}C abundance between C_3 and C_4 plants (Cheng, 1996; Qian et al., 1997, Rochette and Flanagan, 1998). The advantages and limitations of these methods were reviewed by Kuzyakov and Domanski (2000). Using these C tracer techniques, it has been shown that root-derived CO_2 can contribute from 19% (Warembourg and Paul, 1977) to 80% (Martin and Merckx, 1992) of the total CO_2 efflux from planted soil. This high variation in the share of root-derived CO_2 indicates that measurement of total soil CO_2 efflux alone is not sufficient for the assessment of the contribution of soil C to the global atmospheric CO_2 because root-derived CO_2 comes from plant photosynthesis, not from soil C. Any alteration in the environmental factors controlling photoassimilation may potentially affect exudate release (Hodge et al., 1997) and root respiration, thereby changing the total CO_2 efflux from planted soils.

The first objective of our study was to investigate the relationship between plant photosynthesis and total and root-derived CO_2 efflux using both a ^{13}C natural abundance tracer method and a ^{14}C pulse labeling method.

[1] We prefer the term root-derived CO_2, because strictly speaking, the term 'rhizophere CO_2', frequently used in the literature, refers not to the origin of CO_2 production, but to its location. From this point of view it must include not only root respiration and CO_2 evolved by microbial utilization of exudates, but also the CO_2 derived by microbial decomposition of soil organic matter in the rhizophere.

In addition to the direct contribution of roots to total soil CO_2 efflux, roots can also affect soil microbial activities by exuding organic substrates for microorganisms and by altering the soil physical and chemical environment (i.e., pH, soil structure, water flow), consequently controlling SOM-derived CO_2 efflux. This can lead to either acceleration or retardation of SOM decomposition in the rhizosphere (Helal and Sauerbeck, 1986; 1989; Bottner et al., 1988; 1991; Mary et al., 1993; Swinnen et al., 1995; Cheng, 1996; Kuzyakov et al., 2000). It has been hypothesized that the intensity of rhizodeposition may be controlled by photosynthesis and below-ground assimilate allocation, so that the changes in light intensity or photoperiod may have an indirect effect on SOM decomposition. This hypothesis has been tested and confirmed in our previous study with wheat plants grown on C_4 Haplic Chernozem: prolonged darkness significantly decreases positive rhizosphere priming effect on SOM decomposition rate as compared to the normal light setting (Kuzyakov and Cheng, 2001). However, as shown in another experiment (Fu and Cheng, 2002) using four different plant – soil pairs, the direction of rhizosphere priming effect depends on the particular type of plant – soil pairs, e.g., the pair of a 'C_3-soil' with a C_4-plant results in no significant rhizosphere effect or a negative effect depending on plant growing stages, whereas the pair of a 'C_4-soil' with a C_3 plant consistently produces a significant positive rhizosphere priming effect. This result leads to our second objective of this study: to investigate the relationship between photosynthetic activity of a C_4-plant (maize) and the direction and the magnitude of the rhizosphere effect on the decomposition rate of SOM in a 'C_3-soil' taken from a coastal annual grassland.

Some investigations of CO_2 efflux from soils under natural conditions have shown diurnal patterns in the efflux rates (Baldocchi et al., 1986; Kim and Verma, 1992). Most investigators of these studies have attributed these diurnal fluctuations to diurnal soil temperature changes because soil temperature has repeatedly been shown to be one of the important controlling factors for soil CO_2 efflux. Plant photosynthesis has rarely been considered as an important controlling factor for the diurnal fluctuation of soil CO_2 efflux, even though substrate supply for rhizosphere processes is controlled by plant photosynthesis. High transport rates of assimilates from leaves into roots and their subsequent loss in the processes of root respiration and exudation in the rhizosphere have been

reported based on data from laboratory experiments (Biddulph, 1969; Gregory and Atwell, 1991; Cheng et al., 1993; Kuzyakov et al., 1999; 2001). Therefore, any short-term changes of assimilation rates caused by day/night light cycles may potentially control the diurnal dynamics of root-derived CO_2.

The third objective of our study was to investigate the diurnal dynamics of root-derived CO_2 and its possible dependence on light-dark cycles.

Materials and methods

Soil

The soil used in the experiment was taken from the Ah horizon of coastal annual grassland within the campus reserve of the University of California, Santa Cruz, California, USA. The soil was a clay loamy Chromic Luvisol. The soil pH was 5.49. The soil contained 1.9% C_{org} and 0.17% N. Vegetation at this site has consisted of C_3 grasses for possibly thousands of years. The $\delta^{13}C$ value of the soil organic matter was $-24.16‰ \pm 0.13$ (SD), and the $\delta^{13}C$ value of SOM-derived CO_2 (from bare soil) was $-24.45‰ \pm 0.57$. By growing maize (C_4) plants in this soil, we used natural ^{13}C abundance as a tracer to separately measure root-derived C from SOM-derived C (Cheng, 1996).

Plants and growth conditions

Polyvinyl chloride (PVC) containers 76 mm in diameter and 190 mm in height were used for growing plants. Each container was fitted with plastic tubing for air circulation first, and was filled with 1 kg of dry soil before planting (1.16 g cm^{-3} soil density). Seeds of maize (*Zea mays* L, var. Rugosa, 63 d to maturity) were germinated in Petri dishes for 2 d. Four germinated seedlings were transplanted in each pot and grown at a distance of 2 cm from each other. After 5 d the weakest plant in each pot was thinned out, so only three plants per pot were maintained. The plants were grown in a growth chamber at a constant (25 ± 0.5 °C) day and night temperature with PAR light intensity of approximately 800 μmol m^{-2} s^{-1} at the top of the plant canopy. The air in the growth chamber was continuously mixed with the room air by a forced circulation. Before the start of light treatments (14 d after germination, see below) the plants were grown under 12/12 h day/night periods. The soil water content of each container was controlled gravimetrically and was adjusted daily with deionized water to 70% of field capacity. Eight and 13 days after germination 0.05 g N as KNO_3 was added to each container.

Three day/night settings were investigated in this study. The first setting (normal day/night period) had a day-length of 12 h and a night-length of 12 h. The second day/night setting (prolonged night) had a day-length of 12 h and a prolonged night of 36 h (12 h light + 12 h without light + one full day without light). The third day/night setting (strongly prolonged night) had a day-length of 12 h and a prolonged night of 84 h (12 h light + 12 h without light + three full days without light). Eight normal cycles (8×24 h), four prolonged (4×48 h) and 2 strongly prolonged (2×96 h) day/night periods were investigated. The light treatments were started at 14 d after germination.

To compare soil CO_2 evolution with or without maize, a treatment of soil without plants was also included at the same water content as vegetated pots. Each container without plants received 0.025 g N at 8 and 13 d after germination.

^{14}C labeling

A day before labeling, the top of each pot was sealed first with a thin layer of low melting point (42 °C) paraffin and then with Silicon paste NG 3170 from Thauer & Co. (Dresden, Germany). The seal was tested for air leaks. Then CO_2 accumulated during the plant growth was flushed out from the soil column with CO_2-free air. After sealing, water was added once daily through upper tubing for air circulation. Fresh CO_2-free air was added to each container twice daily to compensate for O_2 consumed by soil microorganisms and roots.

The plants were labeled with $^{14}CO_2$ twice: in the morning of the 14^{th} and 18^{th} days after germination. The first ^{14}C pulse labeling began at the beginning of the first period of prolonged nighttime periods. The second ^{14}C pulse labeling started at the beginning of the third prolonged and second strongly prolonged nighttime periods. Sealed pots with plants for labeling were put into a plexiglas chamber as described in details by Cheng et al. (1993). Briefly, $^{14}CO_2$ was introduced to the chamber by circulating air through a flask containing 2.5 M H_2SO_4 in which the $Na_2^{14}CO_3$ solution was added. The total ^{14}C input was 1.542 MBq per pot. The duration of pulse labeling was 30 min. During the labeling, the CO_2 concentration in the chamber was monitored by an Infrared Gas analyzer (Model CI-301, CID, Inc., Vancouver, Washington). Shortly before the start of the labeling period, the CO_2 concentration in the chamber was 380 μmol mol^{-1},

and dropped exponentially to 18 μmol mol^{-1} (near compensation point) at the end of the 30 min labeling period. After labeling the air inside the chamber was pumped through 5 M NaOH solution to remove unassimilated CO_2. Then the top of the labeling chamber was removed and trapping of CO_2 from the soil-root column began.

Sample analysis

After the start of light treatments until the end of the experiment, the CO_2 evolved from the soil was completely trapped in 50 ml of 0.5 M NaOH solution by closed continuous air circulation (100 ml min^{-1}) with a diaphragm pump. The NaOH trap was changed every 12 h during the observation period. The replacement of NaOH traps was timed at 2 hours after the light on/off event with normal day/night period. The two-hour delay period was used here to collect CO_2 evolved in the rhizosphere during day-time or night-time. NaOH traps were analyzed for total carbonate content, ^{14}C activity and $\delta^{13}C$ value. The total carbonate content was measured with 1/10 dilution on an automatic analyzer (Model TOC-5050A, Shimadzu Scientific Instruments, Inc., Columbia, Maryland) using $NaHCO_3$ as standards. The ^{14}C activity was measured in 1-ml aliquots of NaOH with 3.5 ml of the scintillation cocktail EcoLite$^+$ (ICN) after the decay of chemiluminescence by a liquid scintillation counter (Beckmann 6500 LS) using a standard ^{14}C quenching library.

For ^{13}C analysis 1 ml of 2 M $SrCl_2$ was added to the remaining NaOH trapping solution to form a precipitate of $SrCO_3$. The $SrCO_3$ precipitate was carefully washed 7 times with deionized water until pH of 7 was achieved. Washed $SrCO_3$ was dried at 60 °C and 5.0 mg of dried $SrCO_3$ together with 6 mg of V_2O_5 as catalyst was analyzed for $\delta^{13}C$ value with a continuous flow isotope ratio mass spectrometer ('Hydra 20–20', PDZ Europa, Cheshire, UK) at the isotope facility of University of California at Davis.

Calculations and statistics

The total CO_2 efflux from the root-soil columns was partitioned into the root-derived and the SOM-derived parts using ^{13}C natural abundance method.

The ^{13}C natural abundance method uses the following equation (Cheng, 1996):

$$C_4{}^* = C_t \times (\delta_t - \delta_3)/(\delta_4 - \delta_3), \quad (1)$$

where $C_t = C_3^* + C_4^*$, is the total C from below ground CO_2, C_3^* is the amount of C-CO_2 derived from the C_3 soil, C_4^* is the amount of C-CO_2 derived from C_4 plants, δ_t is the $\delta^{13}C$ value of the C_t, δ_4 is the $\delta^{13}C$ value of the C_4 plant root C ($= -14.10‰$, measured at the end of the experiment), and δ_3 is the $\delta^{13}C$ value of the C-CO_2 evolved from the C_3 soil without plants ($= -24.45‰$). In contrast to Rochette and Flanagan (1998), we assumed that there was no isotopic discrimination during CO_2 diffusion and trapping (Ekblad et al., 2002), because trapping was carried out by a forced-air circulation with pumps. Based on Cheng (1996), Lin and Ehleringer (1997), as well as on the $\delta^{13}C$ values of SOM and respired CO_2 (see 'Soil'), there was no significant isotopic fractionation in processes of root respiration and microbial decomposition of exudates and SOM.

The SOM-derived CO_2 efflux was calculated as the difference between total CO_2 efflux and root-derived CO_2 obtained by the ^{13}C natural abundance method. The rhizosphere priming effect was calculated as the difference between SOM-derived CO_2 from planted soil and from unplanted soil.

The experiment consisted of the following treatments: (1) soil without plants (analyzed for total CO_2 and $\delta^{13}C$-CO_2); (2) planted soil without ^{14}C labeling under (2a) normal, (2b) prolonged and (2c) strongly prolonged darkness period (analyzed for total CO_2 and $\delta^{13}C$-CO_2); (3) soil with plants labeled with ^{14}C under (3a) normal, (3b) prolonged and (3c) strongly prolonged darkness period (analyzed for total CO_2 and ^{14}C-CO_2). All treatments were conducted with 4 replicates, which resulted in 8 replicates for the measurements of total CO_2 and 4 replicates for ^{14}C and $\delta^{13}C$ analysis. The data are presented as means of four or eight replicates ± standard deviation (SD). The t-test ($\alpha \leq 5\%$) was used to indicate the significance of differences between treatments.

Results

Total CO_2 efflux from soil

Total CO_2 efflux from planted soil was affected by the manipulation of light and dark periods (Figure 1). At the beginning of the monitoring period, when the light/dark condition was the same (12/12 h day/night) for all treatments, the amounts of below-ground CO_2 efflux were also similar for all three planted treatments. One day without light led to a decrease of

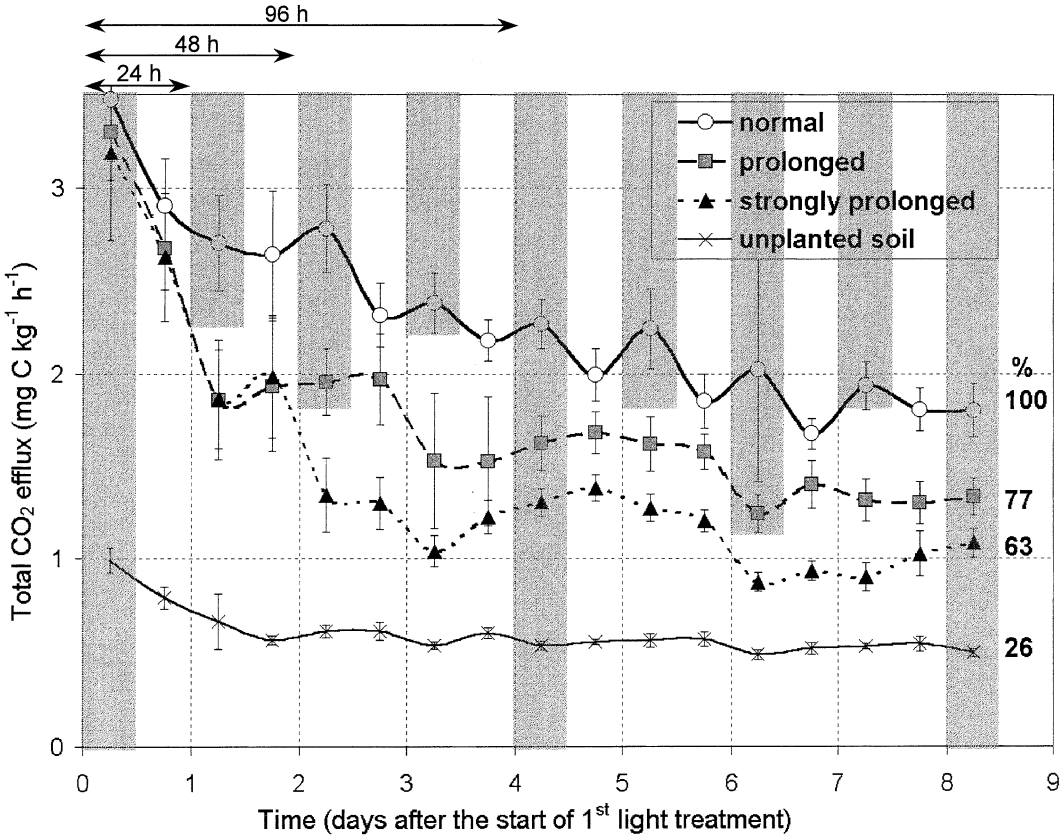

Figure 1. Total CO_2 efflux from the soil (± SD, n = 8) 14 days after germination of maize under different light regimes (○ normal night, 12 h; ▩ prolonged night, 36 h; ▲ strongly prolonged night, 84 h) and from a bare soil (×). The light phases for the normal, prolonged and strongly prolonged night phases are shown as descending gray columns at the top.

below-ground CO_2 efflux of about 31% compared to the soil–plant system with normal (12/12 h) day/night period. This difference increased during d 2 and d 3 of the strongly prolonged darkness treatment. During d 4 when light was resumed for 12 h for all treatments, the total below-ground CO_2 efflux of the prolonged darkness treatment increased for about one day, but was not as high as the CO_2 efflux rate from the treatment with a normal day/night period. After 8 days with light treatments, the intensity of CO_2 efflux amounted to 74% and 60% of the normal light treatment for the prolonged and strongly prolonged night treatment, respectively.

The average total CO_2 efflux from the soil–plant system with a normal day/night period was 2.3 ± 0.14 mg C kg^{-1} h^{-1} during the 8-d observation period (= 100%; Figure 1). During the same period, CO_2 efflux from the soil–plant system decreased to 1.76 ± 0.09 mg C kg^{-1} h^{-1} under the prolonged darkness treatment (= 77%), and 1.45 ± 0.08 mg C kg^{-1} h^{-1} under the treatment of strongly prolonged darkness (=63%; Figure 1). These results indicated that total below-ground CO_2 efflux was closely coupled with above-ground photosynthesis.

Compared to planted treatments, CO_2 efflux from unplanted soil was only 0.60 ± 0.03 mg C kg^{-1} h^{-1}, and was stable during the whole observation period (Figure 1). CO_2 efflux from unplanted soil was 26% of the rate from the normal light treatment at the end of the observation period.

Total CO_2 efflux intensity under the planted treatment with the normal day/night period showed clear diurnal dynamics (Figure 1), becoming higher during each light phase. The CO_2 efflux from both treatments with prolonged darkness showed no diurnal dynamics. The CO_2 efflux from the soil without plants has no diurnal changes.

Components of CO_2 efflux

Based on the ^{13}C natural abundance method (Cheng, 1996), total CO_2 efflux was separated into root-derived and SOM-derived CO_2. The $\delta^{13}C$ value of SOM-derived CO_2 (from bare soil) was $-24.45 \pm 0.57‰$ (SD). The $\delta^{13}C$ value of maize shoots and roots was $-13.21 \pm 0.33‰$ and $-14.10 \pm 0.39‰$, respectively.

Total and recently assimilated C in root-derived CO_2

Root-derived CO_2 effluxes varied between 88% and 33% of total CO_2 efflux (Figure 2), the highest for the normal day/night treatment, and the lowest for the strongly prolonged night treatment. The high plant density and the small soil volume used in our experiment could cause the high contribution of maize plants to the total CO_2 efflux from the soil. During the whole experimental period, the cumulative root-derived CO_2 efflux was 82.2%, 68.1% and 55.6% of the total soil CO_2 efflux for normal, prolonged and strongly prolonged night treatments, respectively. This root-derived CO_2 efflux included root respiration *per se* and microbial respiration from decomposing exudates, sloughed root cells and other rhizodeposits. The use of two tracer methods in one experiment allowed us to trace both the total and the recently assimilated C in root-derived CO_2. Natural ^{13}C abundance was used for tracing C assimilated by plants during the whole growth period. ^{14}C pulse labeling was used to trace recently assimilated C. The first ^{14}C pulse was used to monitor how different dark periods after the labeling affect below-ground respiration of recently assimilated C. The second ^{14}C pulse was used to investigate how different day/night periods before labeling influence recently assimilated C in root-derived CO_2.

The absence of light for one day decreased the percentage contribution of root-derived CO_2 to the total CO_2 efflux from soil (Figure 2). A greater reduction in the contribution of root-derived CO_2 to the total CO_2 efflux from soil occurred during the second day without light. The light-on event on day 4 led to an increase of root-derived CO_2 of the strongly prolonged night treatment. The differences between the light treatments are especially clear during the second half of the experiment, when the recent assimilates in plants with prolonged nights are exhausted.

The rates of root-derived CO_2 efflux from soil (Figure 3) were calculated using the percentage contribution of the root-derived CO_2 to total CO_2 efflux from soil (Figure 2) and the total CO_2 efflux (Figure 1). The effect of light treatments on the root-derived CO_2 efflux was more apparent after the separation of SOM-derived CO_2 from the total efflux. One day without light decreased the root-derived CO_2 efflux by approximately 35%. The second day without light decreased the root-derived CO_2 efflux by an additional 29%, and the third day by 7% more (Figure 3). These values show an exponential decrease of root-derived CO_2 in the absence of light. Similar exponential decrease of recently assimilated C in root-derived CO_2 was observed by means of ^{14}C pulse labeling (see below).

The light-on event on day 4 resulted in a strong increase of root-derived CO_2 efflux from the strongly prolonged night treatment, even though the increase was not high enough to reach the amount of the root-derived CO_2 from the prolonged night treatment. This increase of root-derived CO_2 after the light-on event from the strongly prolonged night treatment lasted for about 24 h. The CO_2 efflux intensity subsequently decreased. After eight days of different light treatments, the root-derived CO_2 efflux from the prolonged night treatment was 61% of that from the normal day/night treatment, and the strongly prolonged night treatment root derived CO_2 efflux was only 32% of that from the normal day/night treatment.

Respiration of recently assimilated C (^{14}C) in the rhizosphere differed from that of the total C assimilated by the plants. During the first half of the observation period no significant differences between the light treatments in the respiration intensity of recently assimilated C were observed (Figure 4). All three curves of $^{14}CO_2$ efflux showed a similar exponential decrease during 4 d after assimilation. Similar dynamics were observed in other studies (Nguyen et al., 1999; Kuzyakov et al., 1999) and are typical for $^{14}CO_2$ efflux from soil after ^{14}C pulse labeling. However, the light treatments strongly differed after the second ^{14}C pulse. The greatest intensity of $^{14}CO_2$ efflux was observed for prolonged night treatment. On average, the root-derived CO_2 from the plants with normal day/night utilized 14.4% of recently assimilated C, and 20.1% from the plants with prolonged day/night treatment. This clearly indicated that the shaded plants used more recently assimilated C for rhizosphere processes (root respiration and exudation) as compared to the plants with normal day/night period.

The lengths of the night period affected not only the amount of $^{14}CO_2$ evolved, but also $^{14}CO_2$ efflux dynamics after the second pulse (Figure 4). The

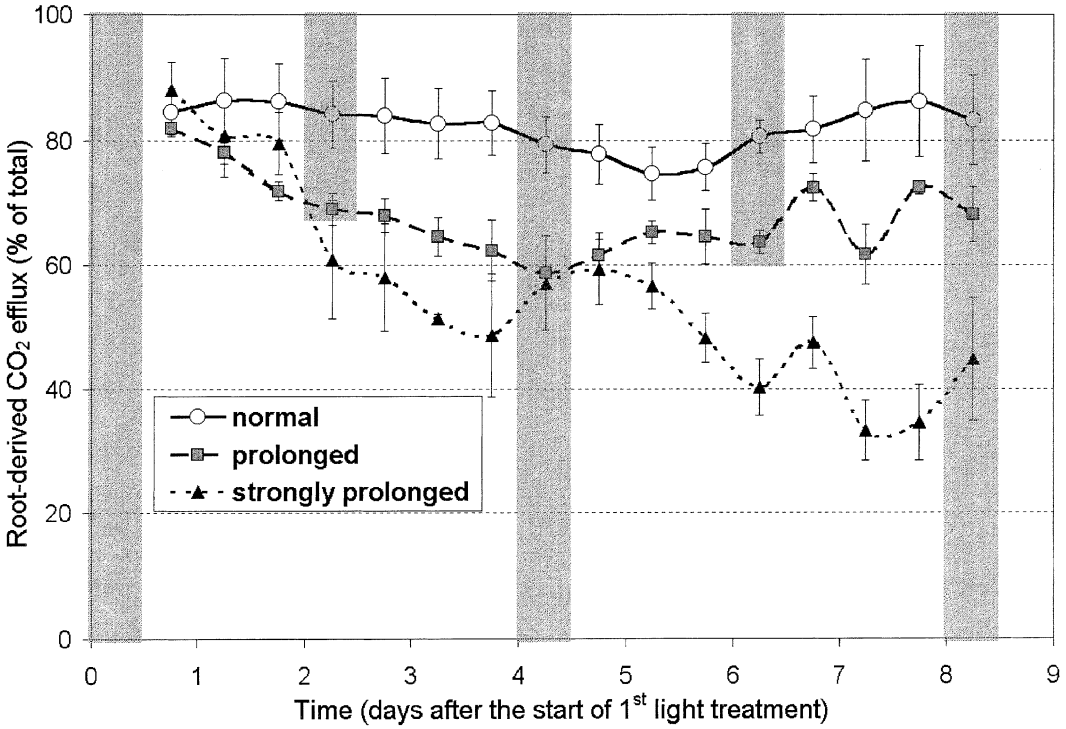

Figure 2. Percentage of root-derived and SOM-derived CO_2 efflux (± SD, n = 4) from soil with maize under different light regimes. The difference from 100% corresponds to SOM-derived CO_2 efflux. The light phases are shown as descending gray columns. The light phases for the control = normal day/night (12/12 h) phases are not shown (comp. Figure 1).

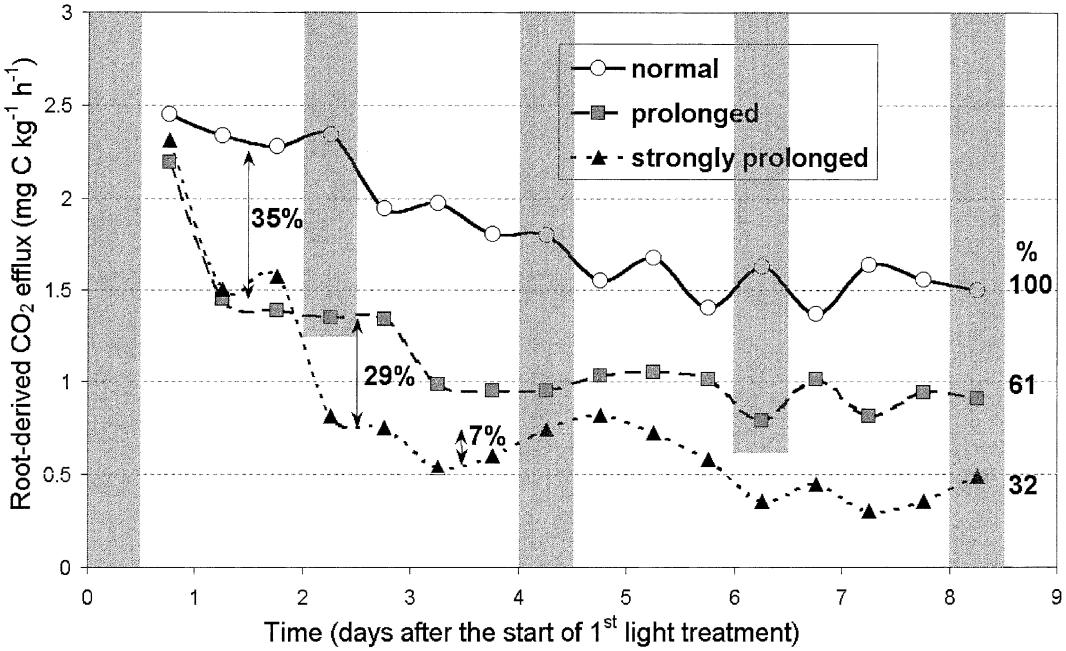

Figure 3. Root-derived CO_2 efflux (± SD, n = 4) from soil with maize under different light regimes. The light phases are shown as descending gray columns. The light phases for the control = normal day/night (12/12 h) phases are not shown (comp. Figure 1).

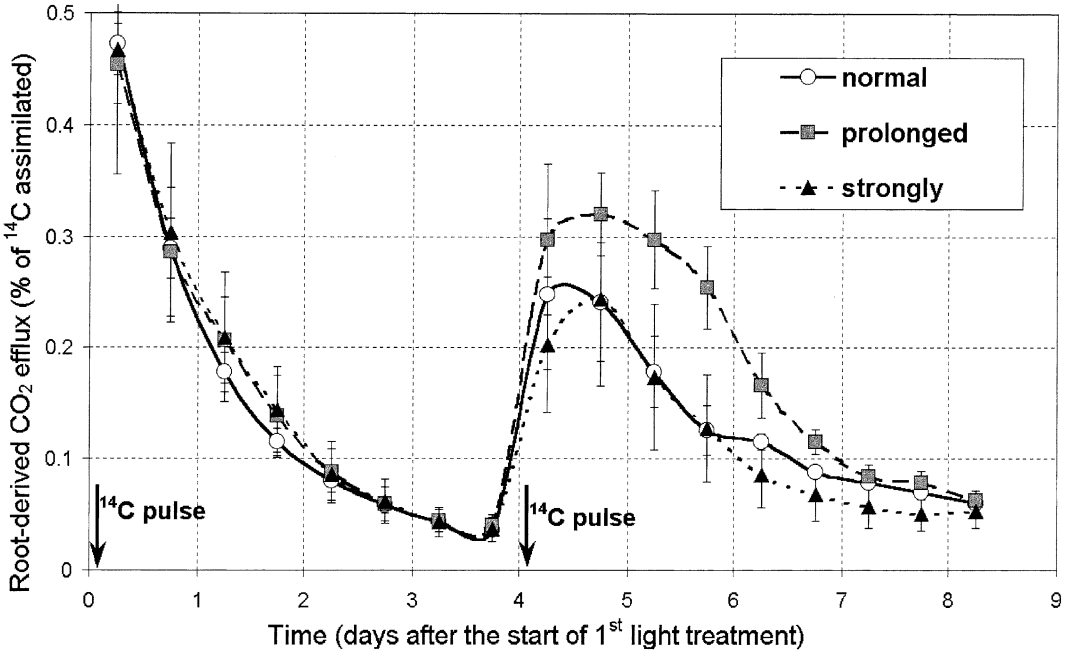

Figure 4. Root-derived CO_2 efflux from recently assimilated C measured with two ^{14}C pulse labelings of the shoots under different light regimes ○ normal night, 12 h; ▩ prolonged night, 36 h; ▲ strongly prolonged night, 84 h (n = 4).

greatest rate of $^{14}CO_2$ efflux for plants with normal day/night period was observed at the first measurement point after each labeling (after about 6 h). For the plants with prolonged and strongly prolonged day/night period, the greatest rate of $^{14}CO_2$ efflux was observed by the second measurement after the labeling (after about 20 h), indicating a slower transport of assimilates to belowground by shaded plants compared to non-shaded plants. This effect was more clearly for the strongly prolonged darkness treatment (Figure 4). Therefore, shading of plants also delayed the response of rhizosphere processes to the change of above-ground photosynthesis.

SOM-derived CO_2 and rhizosphere priming effect

SOM-derived CO_2 efflux varied between 12% and 67% of total CO_2 efflux from the rooted soil depending on the light treatment (Figure 2; Table 1). On average, the SOM-derived CO_2 efflux was 17.8%, 31.9% and 44.4% of the total soil CO_2 efflux from the normal day/night, prolonged and strongly prolonged day/night treatments, respectively (Table 1). Therefore, the root-derived CO_2 was the predominant component in the total CO_2 efflux from planted soils.

SOM-derived CO_2 efflux in the experiment could be divided into three distinctive periods. During the first two days the SOM-derived CO_2 from planted soil was much lower than that from the unplanted soil. Between day 3 and day 6 the SOM-derived CO_2 efflux from the soil with reduced photosynthesis was similar to that of the unplanted soil. After day 6 there were significant differences in the SOM-derived CO_2 from the soil of all four treatments and the treatments can be arranged from the highest to the lowest in the following order: strongly prolonged night time > unplanted soil > prolonged night time > normal day/night period (Figure 5).

During the observation period, the average SOM-derived CO_2 flux from the unplanted soil was 0.57 mg C kg^{-1} h^{-1}, 0.53 for the treatment with plants under strongly prolonged night time, 0.50 for the treatment with plants under prolonged night time, and 0.39 for the treatment with plants under normal day/night period (Table 1). These values correspond to CO_2 efflux approximately 45, 42, 40 and 31 kg C ha^{-1} d^{-1} (calculated for 30 cm soil layer and 1.1 g cm^{-3} soil density).

This result indicated that the cultivation of maize under normal day/night period reduced the SOM-derived CO_2 by about one third compared to the unplanted soil (Table 1). Such retardation of SOM decomposition intensity in the presence of actively growing roots has been frequently referred to as a negative rhizosphere priming effect. Rhizosphere priming

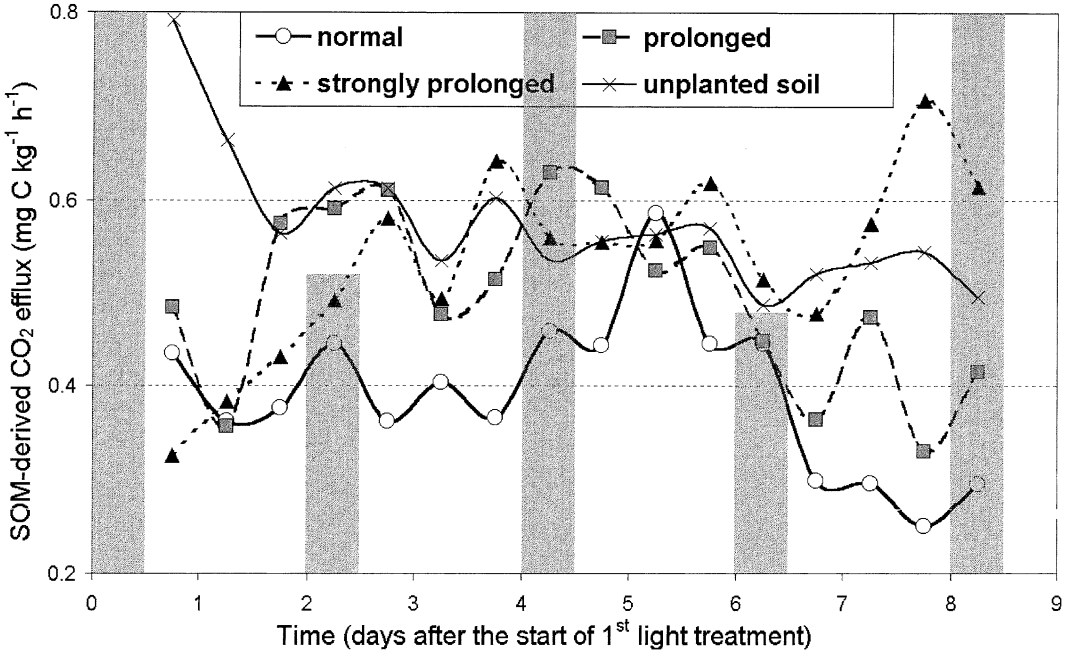

Figure 5. SOM-derived CO_2 efflux from unplanted soil and soil planted with maize under different light regimes. The light phases are shown as raised gray columns. The light phases for the control = normal day/night (12/12 h) phases are not shown (comp. Figure 1) (n = 4).

effect induced by plants with normal day/night period was consistently negative during the whole observation period (Figure 6). Strong reduction of photosynthesis changed this negative priming effect and it became zero later. Seven days of strong reduction in photosynthesis led to the increased SOM decomposition – positive priming effect. After 8 d of light treatments, the priming effect was greatest for strongly reduced photosynthesis, and smallest for the plants with normal day/night period.

Discussion

Total CO_2 efflux from planted soil and CO_2 partitioning

Our results showed that the root-derived CO_2 was the dominant component in the total CO_2 efflux from the planted soil (Figure 7). This may vary depending on root development and the C content of the soil used. The root-derived CO_2 was, on average, 82% and 56% of the total soil efflux for plants with normal day/night and strongly prolonged night, respectively (Figure 1 and Table 1). However, these percentages should not be compared directly with values from any field experiment because of the limited soil volume and the high plant density used in our growth chamber experiment. Similar results (root-derived CO_2 = 75%) were also found in our previous experiment with wheat grown on a Haplic Chernozem with C_t = 2.3% (Kuzyakov and Cheng, 2001). Both results indicate that root-derived CO_2 should be separated from SOM-derived CO_2 in any study on soil C sequestration; otherwise, soil C loss would be strongly overestimated.

Compared to wheat investigated in our previous study (Kuzyakov and Cheng, 2001), maize plants have very slow growth of shoots and roots in the young development stage. The intensive biomass increase begins at the second month or later. Therefore we expect, that the contribution of root-derived CO_2 to the total CO_2 efflux from soil will strongly increase in the second and third months. However, this result cannot be directly extrapolated to the field situation because the effective soil volume and the root density in the laboratory were different than under common field conditions. In our experiment, only 1 kg of soil was used for three maize plants in each container, resulting in a plant density of approximately 600 plants m^{-2} of soil surface. Under common field conditions 10 to 12 plants m^{-2} are common. Therefore, the share of root-derived CO_2 efflux by young maize plants grown under the field conditions would be smaller than observed under laboratory conditions.

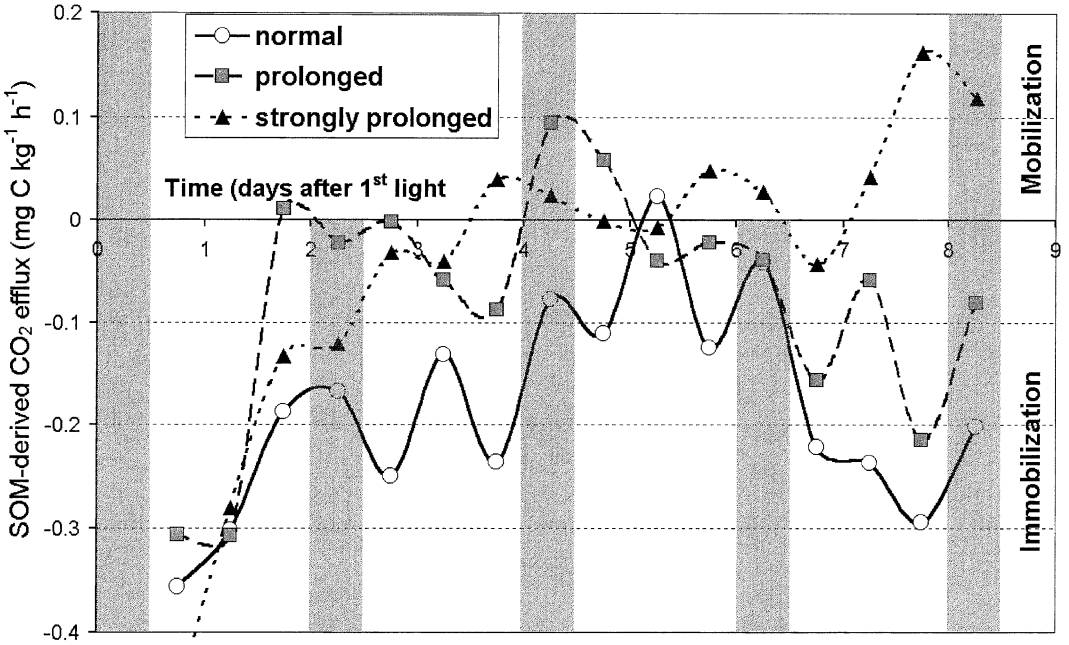

Figure 6. Dynamics of priming effect (= changes in the decomposition of SOM) induced by maize roots under different light regimes: ○ normal light, 12 h; ▩ prolonged night, 36 h; ▲ strongly prolonged hight, 84 h. The light phases are shown as descending gray columns. The light phases for the normal day/night (12/12 h) length are not shown (comp. Figure 1). (n = 4).

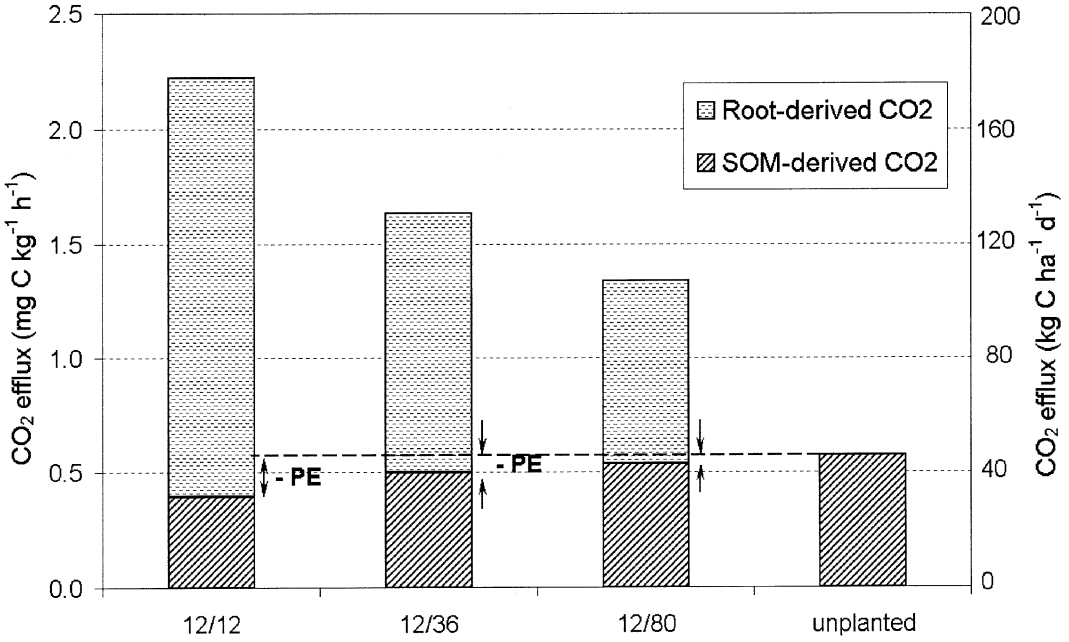

Figure 7. Average intensity of CO_2 efflux from unplanted soil and soil planted with maize under different light regimes and negative rhizosphere priming effects (-PE) induced by maize.

Table 1. Components of CO_2 efflux from unplanted soil and soil planted with maize under different light regimes

Treatment	CO_2-total		Root-derived CO_2						SOM-derived CO_2		Priming effect	
			Long + short term C (^{13}C)			Short term C (^{14}C)						
	mg C kg^{-1} h^{-1}	% of 12/12	% of total CO_2	mg C kg^{-1} h^{-1}	% of 12/12	1st% of assimilated	2nd% of assimilated	% of total CO_2	mg C kg^{-1} h^{-1}	mg C kg^{-1} h^{-1}	Change of SOM mineralization %
12/12	2.22 ± 0.14	100	82.2	1.83	100	15.3	14.4	17.8	0.39	−0.18	−31.7
12/36	1.66 ± 0.09	74.7	68.1	1.14	62.2	15.8	20.1	31.9	0.50	−0.08	−13.4
12/80	1.34 ± 0.08	60.2	55.6	0.81	44.1	17.9	14.6	44.4	0.53	−0.04	−7.19
unplanted	0.57 ± 0.03	26.1	0	0	–	0	0	100	0.57	0	0
LSD, 0.05	0.12		8.89			3.76	4.29				

Root-derived CO_2 was very sensitive to reduction of photosynthesis, and decreased significantly after 1 or 2 d without photosynthesis (Figures 2 and 3). The absence of photosynthesis for 3 d led to the decrease of root-derived CO_2 to approximately 60% of the normal lighting treatment. Further decrease of CO_2 efflux during the second strongly prolonged dark period indicated that assimilates were utilized more strongly than during the first prolonged dark period of 84 h without light (Figures 2 and 3).

Our results confirmed the proposition of Craine et al. (1999) that photosynthesis strongly controls total soil CO_2 efflux. Indirect approaches (i.e., shading and removal of above-ground biomass) were employed by Craine et al. (1999). These indirect approaches inherently involved possible confounding factors such as alterations of SOM-derived CO_2, temperature, and plant physiological responses to cutting. Those confounding factors were avoided in our study by using isotope tracers to monitor separately SOM-derived CO_2 and root-derived CO_2 without destruction. Our results clearly indicated that rhizosphere respiration is tightly coupled with plant photosynthetic activity. This tight coupling can be inferred from the results of our previous pulse-labeling studies (Cheng et al., 1993, 1994; Kuzyakov et al., 1999, 2001) which showed that photosynthates were transported to roots and metabolized by roots and rhizosphere microorganisms within a few hours after initial assimilation. Any factors that affect photosynthesis, or substrate supply to roots and rhizosphere microorganisms, are an important determinant of root-derived CO_2 efflux, and thereby, total CO_2 efflux from soils, such as irradiation, water stress, nutritional status, and herbivory activities. This strongly encourages the inclusion of photosynthesis as a crucial controlling factor for total soil CO_2 efflux in studies of C cycling in soils in addition to temperature and other abiotic factors. A similar conclusion was also reached by Högberg et al. (2001) who studied the effect of tree girdling on soil CO_2 efflux in a boreal Scots pine (*Pinus sylvestris* L.) forest. In their study, a 37% reduction of soil CO_2 efflux rate was reported five days after tree girdling, which terminated the transport of current photosynthates to the belowground system.

Diurnal changes in CO_2 efflux

In our experiment, plants were grown at a uniform day and night temperature (25 °C). Microbial decomposition of the native soil organic matter (which is strongly

influenced by temperature) should be the same during both day and night phases, if it was not affected by rhizosphere activities. CO_2 efflux from unplanted soil was constant and independent of the day/night changes (comp. CO_2 efflux from unplanted soil, Figures 1 and 5). However, there was a clear diurnal change in the total CO_2 efflux from soil planted with maize grown under normal day/night period. In each light period, the CO_2 efflux from planted soil was higher than the 'night' values (Figures 1 and 5). In our previous study with wheat (Kuzyakov and Cheng, 2001), we proposed that there were only two reasons that might be responsible for the diurnal dynamics: 1) increased *exudation of organic substances* from roots and 2) increased *root respiration* a few h after photosynthesis began. Fast assimilation of ^{14}C by photosynthesis and the following fast transport of this C into the roots lead to the rapid appearance of recently assimilated C in the root-derived CO_2. Therefore, the intensity of root-derived CO_2 follows the diurnal dynamics of photosynthesis. However, as shown in a previous study separating root respiration and rhizomicrobial respiration in non-sterile soil planted with *Lolium*, only the exudation has distinct diurnal dynamics (Kuzyakov and Siniakina, 2001; Kuzyakov, 2002). Root respiration did not show significant differences between the day and night periods. But in this study with maize, not only the root-derived CO_2 showed a 24-h diurnal cycle (Figure 3). CO_2 originated from microbial decomposition of SOM also has a clear diurnal cycle (Figures 5 and 6). These dynamics are visually clear in the induced priming effect (Figure 6), indicating that the microbial response to exudates, which is released diurnally, is fast. This short activation of microorganisms by exudates leads to the change of SOM decomposition.

In our previous study with wheat (Kuzyakov and Cheng, 2001), the diurnal dynamics of total and root-derived CO_2 efflux from soil were also observed during 2 days without light, indicating that a memory effect on the light conditions was observed by wheat plants. In this study with maize such memory effect was not found.

Diurnal changes of CO_2 efflux rates under the field conditions have also been reported in some studies (Baldocchi et al., 1986; Kim and Verma, 1992; Oberbauer et al., 1996). In most cases the increase of soil CO_2 efflux rate in the afternoon has been attributed to increased soil temperatures. There is no doubt that a rise of soil temperature leads to an increase of CO_2 efflux, but our results also demonstrate that the diurnal pattern of root-derived CO_2 efflux and induced rhizosphere priming effects are coupled with the plant photosynthetic cycle. This indicates that the diurnal CO_2 efflux from soil is controlled by the photosynthesis cycle together with temperature changes, thereby invalidating the approach of estimating daytime soil CO_2 efflux based on night-time rates after adjustment of temperature differences only, without any consideration of photosynthetic cycles. This result also provides an explanation for the high degree of unaccounted variation in some correlation analyses (Baldocchi et al., 1986; Kim and Verma, 1992) between temperature and total soil CO_2 efflux due to the exclusion of photosynthesis-related variables. This also implies that one measurement per day is insufficient for accurate estimation of total CO_2 efflux from soil under field conditions.

Use of assimilates by maize for rhizodeposition

There were two seemingly contradicting results in terms of assimilate utilization. One result indicated that the total root-derived CO_2 efflux (^{13}C natural abundance) from planted soils with the normal day/night setting was higher than that from plants with prolonged and strongly prolonged night (Figure 1). Similar results were observed in our previous study with wheat grown in a C_4 soil (Kuzyakov and Cheng, 2001). This may be caused by the lack of new assimilates for exudation and root respiration by plants in the absence of light. But another result shows that the $^{14}CO_2$ efflux derived from recently assimilated C (^{14}C pulse labeling) was higher for the plants with prolonged night compared to that from plants with the normal day/night changes (Figure 4 and Table 1). Both results were statistically significant after the second ^{14}C pulse. These contrasting results reflect the main difference between the utilization of total assimilated C traced here with natural ^{13}C method and recently assimilated C traced with ^{14}C pulse labeling. More recent assimilates (^{14}C) are used for respiration after prolonged darkness because of the diminished C reserve, even though total root-derived CO_2 (^{13}C) declines for the prolonged night treatments due to the absence of new input of C and energy in the rhizosphere.

Compared to our previous study with wheat, maize needed longer time to respire recently assimilated C in the rhizosphere. For $^{14}CO_2$ efflux from wheat rhizosphere, much sharper peaks were observed at the 1st day after the assimilation (Kuzyakov and Cheng,

2001). This fact shows faster utilization of assimilates by wheat compared to maize. These sharp peaks in wheat allowed tracing the day/night cycles not only in the total assimilated C (^{13}C) but also in the recently assimilated C (^{14}C). Because of longer usage of assimilates by maize it was not possible to trace diurnal dynamics in recently assimilated C. This prolonged period between assimilation and $^{14}CO_2$ efflux from maize rhizosphere could be connected with longer transport of assimilates as well as with their longer usage. The other reason of minor importance could be that in the previous experiment with wheat, $^{14}CO_2$ efflux from soil was measured 4 times daily and in this experiment with maize only twice daily. Such differences in the transport and utilization of assimilates in different plants are important for investigating short-term $^{14}CO_2$ effluxes as well as rhizosphere processes (Nguyen et al., 1999; Todorovic et al., 2001).

Rhizosphere priming effect

Priming effects (PE) are short-term changes (in most cases increases) in decomposition rates of soil organic matter induced by input of organic and mineral substances (i.e., exudates, plant residues, fertilizers) in soil. PE have been measured in many studies after application of mineral or organic fertilizers to the soil (reviewed by Jenkinson et al., 1985; Kuzyakov et al., 2000). However, there is conflicting evidence in the literature on the effects of plant roots on soil organic matter (SOM) decomposition. Roots have been found to have both stimulatory and inhibitory effects on SOM decomposition (reviewed by Kuzyakov 2002; Cheng and Kuzyakov, 2004). Laboratory experiments have shown that when ^{14}C-labeled plant materials were decomposed in soil planted with maize, ryegrass, wheat or barley, $^{14}CO_2$ release from the soil was reduced compared to bare soil controls (Reid and Goss, 1982, 1983; Sparling et al., 1982). The authors of these reports proposed that this inhibitory effect of living roots on SOM decomposition was due to competition between the roots and the rhizosphere microflora for substrates. In contrast, a stimulatory effect of living roots on SOM decomposition has been reported in other laboratory experiments (Helal and Sauerbeck, 1986, 1989; Cheng and Coleman, 1990; Kuzyakov et al., 2001; Kuzyakov and Cheng, 2001). The stimulation of the rhizosphere microflora by exudation of easy available organic compounds was proposed as the responsible mechanisms that lead to the increased decomposition of SOM. Furthermore, another study also indicated that rhizosphere PE is dependent upon the length of exposure to living roots. In a two-year study, the presence of plant roots suppressed the decomposition of newly-incorporated ^{14}C-labeled plant material during the first 200 d but stimulated the mineralization of ^{14}C in the soil during the later stage, (200 d until 2 y) when compared to bare soil (Sallih and Bottner, 1988).

Previously, methodological differences among those studies have been assumed to be an important reason for the controversy. However, the simultaneous use of two methods estimating the contribution of SOM-derived CO_2 to the total CO_2 from planted soil (^{13}C natural abundance and ^{14}C pulse labeling) showed that both methods produce similar results (Kuzyakov and Cheng, 2001). Methodological differences were probably not as critical as it was assumed. In the study with wheat grown on a SOM-rich Chernozem, positive priming effects were observed by normal photosynthesis intensity (Kuzyakov and Cheng, 2001). The absence of photosynthesis decreased easily decomposable substrates in the rhizosphere, and also reduced the PE to SOM decomposition. Therefore, we assumed that microbial activation was the mechanism responsible for the positive PE (Helal and Sauerbeck, 1986; Sallih and Bottner, 1988; Cheng and Coleman, 1990). In this study maize was grown on Chromic Luvisol, which had less total organic C as well as much less decomposable C than Chernozems. Only negative priming effects were found for the normal day/night treatment on Luvisol. Therefore we suppose, that in the presence of maize plants, microorganisms prefer easily available root exudates instead of less decomposable SOM. Therefore the mechanism of preferential substrate utilization would be responsible for the negative priming effect observed in this study (Sparling et al., 1982; Billes et al., 1988). Results from both the present and our previous study (Kuzyakov and Cheng, 2001) suggested that the direction and the magnitude of rhizosphere priming effects strongly depends on the plant – soil pair chosen for the experiment. Not only the plant exudates but also the amount of organic substances available for microorganisms are crucial for priming effect direction. Based on a study of four plant – soil pairs, Fu and Cheng (2002) found that rhizosphere priming effects on SOM decomposition were positive at all developmental stages in a C_3 plant – 'C_4 soil' system, but the direction of the rhizosphere priming effect changed at different developmental stages in the C_4 plant – 'C_3 soil' system. However, the content of

decomposable C in both soils, responsible for the direction of rhizosphere PE, was not considered in this study. Analysis of different SOM fractions, especially the amount of easily available ones, must be included in further studies investigating rhizosphere priming effects.

Nevertheless, the physiological differences between C_3 and C_4 plants may have also an effect on rhizosphere processes due to different amounts and probably qualities 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. This leads to smaller activation of microbial biomass in the rhizosphere, which is not sufficient to increase SOM decomposition. However, this remains an hypothesis until the amounts and quality of organic substances released by roots of C_3 and C_4 plants are investigated comparatively.

Regarding the variation between plant types, the amount of roots and the type of root system may have an effect on SOM decomposition. Most experiments were conducted with plants having a fibrous root system. However, in a study using plants with different root systems, Fu and Cheng (2002) found a 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 may produce stronger PE on SOM decomposition.

Qualitative changes in root exudates by prolonged nighttime may also be important in modifying C flows in the rhizosphere and the balance of microbial mineralization and immobilization processes. As shown by Kuzyakov and Siniakina (2001) the decrease of exudation in the nighttime is much stronger than that of the root respiration. So the diurnal variation is mostly associated with exudates and not as much with root respiration. Therefore, the relative increase in SOM decomposition for the prolonged darkness treatments as compared to that of the normal night could also be connected with the shift in the exudates composition (Kuzyakoo et al., 2003).

The tight coupling of SOM decomposition with photosynthesis suggests that root exudates are the main agent responsible for the rhizosphere priming effect. Many other hypothetical mechanisms reviewed by Kuzyakou (2002) and Cheng and Kuzyakov (2004) have been proposed to be possible agents for the rhizosphere priming effect. However, root turnover (Sallih and Bottner, 1988) and breaking down of soil aggregates (Helal and Sauerbeck, 1986, 1987) by roots may not be changing quickly enough to play a significant role, because of the short duration of our experiment. Preferential utilization of easily available exudates instead of SOM is probably the most important mechanism responsible for the negative rhizosphere priming observed in this study.

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