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ORIGINAL PAPER

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Contribution of plant-derived carbon to soil microbial biomass dynamics in a paddy rice microcosm

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Abstract An understanding of the microbial biomass dynamics in rice paddies is essential for managing their nutrient and C cycling. Our objectives were to determine whether the seasonal dynamics of microbial biomass C (MBC) was related to the release of organic substance from rice roots. MBC and the dissolved organic C (DOC) in soil solutions were measured over a growing period of rice plants in a pot experiment. The ^{13}C pulse labelling (through supplying rice plants with $^{13}CO_2$ for 6 h) was performed at different growth stages of rice to estimate the contribution of photosynthesized C to MBC. DOC concentrations increased with plant growth, reflecting the release of soluble root exudates from rice roots. MBC declined in the early period, and then rapidly increased from the maximum tillering stage to the heading stage of rice. During this period of increase, MBC was positively correlated to the DOC concentration and root biomass. About 0.15–0.94% (mean 0.54%) of photosynthesized ^{13}C was incorporated into MBC immediately after pulse labelling, and 0.18–0.75% (mean 0.41%) still remained at the end of the season. The estimated total contribution of photosynthates to MBC amounted to 91 mg C plant^{-1}, corresponding to 28% of total MBC at the end of the season or a 100% increase in MBC over the growing season. The results suggest that MBC dynamics in rice soil are largely controlled by organic substances released from rice roots.

Keywords Rice soil · Microbial biomass · Photosynthesis · Pulse labelling

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Introduction

Microbial processes play key roles in nutrient and C cycling in rice soils (Conrad 1996; Kimura 2000). The growth and activity of microorganisms are likely limited by C availability in soils (Smith and Paul 1990). Previous research showed that the incorporation of plant residues and organic manures significantly increased microbial biomass in rice soils in both pot (Azmal et al. 1996; Witt et al. 2000) and field experiments (Bhardwaj and Datt 1995; Yoshikawa and Inubushi 1995; Chakrabarti et al. 2000; Kushwaha et al. 2000). Besides the application of organic matter, the release of photosynthesized C from plant roots (known as rhizodeposition) provides an important C source for biological activity in soils (Curl and Truelove 1986; Lynch and Whipps 1990). The rhizodeposition occurs continuously in the form of root exudates, mucilage, sloughed-off cells and litter within the growing season of plants. Of these substances, soluble root exudates are readily available for microorganisms (Curl and Truelove 1986). The influence of plant growth on microbial dynamics, however, is complex and poorly understood in rice soils. Hoque et al. (2001) and Inubushi et al. (2001) found that microbial biomass C (MBC) increased with plant growth and with an increase in the air CO_2 concentration. On the other hand, Witt et al. (2000) reported that MBC decreased with plant growth and there was no difference between planted and unplanted soils. Reichardt et al. (1997) observed a decline of total microbial biomass but an increase in anaerobic populations toward the maturation stage of rice. Ghoshal and Singh (1995) and Bai et al. (2000) reported that microbial biomass substantially decreased during the early growing period and gradually increased during the late growing period of rice.

Upland crop experiments using isotopic C techniques revealed that the incorporation of the assimilated C into microbial biomass was rapid (Rattray et al. 1995; Kuzyakov et al. 2001) and significant (Merckx et al. 1985; Liljeroth et al. 1990; Martin and Merckx 1992; Van Ginkel et al. 2000), indicating that the growth and

activity of soil microbes are closely related to the photosynthesis in the aboveground parts. CH_4 is produced through anaerobic decomposition of organic matters in rice soils. Rapid transformation of photosynthesized C to CH_4 was also reported (Minoda and Kimura 1994, 1996; Dannenberg and Conrad 1999) and the seasonal pattern of CH_4 emissions appeared to be largely governed by organic substances released from rice roots (Neue et al. 1997; Lu et al. 2000a, 2000b; Wassmann and Aulakh 2000). Rice plants provide not only an energy source but also a nutrient source to soil microorganisms. Inubushi and Watanabe (1996) postulated that microbial N was replenished by N contained in root exudates and decomposing root debris. We hypothesized that the dynamics of microbial biomass in rice soil, especially of facultative and anaerobic populations, were significantly influenced by plant growth.

In the present study, MBC and the dissolved organic C (DOC) were monitored over a growing season of rice in a pot experiment to investigate their relationship with the release of organic substance from rice roots. ^{13}C pulse chase labelling was used to estimate the contribution of photosynthesized C to MBC dynamics.

Materials and methods

Soil preparation and rice growth

A yellow soil (Oxiaquic Dystrochrepts) was collected from the plough layer (0–15 cm) of a rice field at Aichi-ken Anjo Research and Extension Centre, Central, Japan (34°48′N, 137°30′E). The moist soil (water content of 16.7%) was passed through a 4-mm sieve and thoroughly mixed. The soil sample had the following characteristics: pH of 6.3 (1:1, soil/water ratio), CEC of 14.4 cmol kg^{-1}, organic C content of 12.5 g kg^{-1}, total N content of 1.1 g kg^{-1}, clay content of 23%.

Soil was basally fertilized with $(NH_4)_2SO_4$, calcium superphosphate and KCI at the rates of 0.1 g N kg^{-1} soil, 0.1 g P_2O_5 kg^{-1} soil, and 0.1 g K_2O kg^{-1} soil, respectively. One kilogram of each soil sample (equivalent to 833 g oven-dry soil) was filled into 1-l pots and submerged with deionized water. Two 35-day-old rice seedlings (*Oryza sativa* L. cv. Aoino-Kaze) were transplanted into each pot on 13 June 2000, just 1 day after the submergence of soil. Soil was irrigated regularly with deionized water maintaining a 3- to 5-cm water layer above the soil surface throughout the growing period. The plants were grown outdoors; $(NH_4)_2SO_4$ was topdressed on 12 and 29 July, 6 and 13 August at a rate of 0.1 g N kg^{-1} soil, respectively. The total applied N (basal and topdressing) was 0.5 g pot^{-1}, corresponding to 150 kg N ha^{-1}. Insects and weeds were manually controlled to avoid yield loss. Enough pots were prepared for the following: six pots (three planted pots and three unplanted pots) were used for DOC measurement; nine pots were used as controls for MBC measurement without ^{13}C labelling; and 48 pots were used for MBC measurement with ^{13}C labelling.

Measurement of DOC

DOC was determined 12 times from planted soil and 5 times from unplanted soil following the procedure of Lu et al. (2000a). One week after rice was transplanted, a rhizon sampler (Eijkelkamp, Giesbeek, The Netherlands) used to collect soil solutions was vertically inserted into soils at a depth of 5–10 cm. At sampling, a calibrated 10-ml vacutainer was connected to the rhizon sampler through a rubber septum. After 5 ml soil solution was sucked in, the vacutainer was detached from the rhizon sampler and taken to the laboratory. Soil solutions were filtered through a 0.45-µm filter and acidified to pH<3.0 with 10% HCl. DOC contents in solution samples were determined using a total C analyser (TOC-500; Shimadzu, Japan).

^{13}C labelling and MBC measurements

$^{13}CO_2$ labelling of rice plants was performed 7 times, on 4 and 19 July, 4, 21 and 29 August, and 4 and 20 September, respectively, covering the complete growth period of rice. At each labelling date, plants were transferred to an artificially lit growth chamber (area 100×60 cm^2, height 100 cm) with the pot surface covered by a black plastic sheet to avoid algal photosynthesis in flood water and to enable rice shoot exposure to $^{13}CO_2$. Since $^{13}CO_2$ diffusion into water was negligible under the neutral conditions of the flood water (pH 6.0–7.0), no specific precaution was taken to ensure the isolation of the shoots from the roots. $^{13}CO_2$ gas inside the chamber was generated through a reaction between $Ba^{13}CO_3$ (99 atom % ^{13}C) and lactic acid. The mean $^{13}CO_2$ concentrations were 180–270 ppm, corresponding to 24–57% of total CO_2 concentrations in the chamber.

Plants were labelled for 6 h (0900–1500 hours) under the following growth conditions: light 30 klux, temperature 30°C and relative humidity 80–90%. After labelling, plants were returned outdoors.

The destructive samplings were conducted immediately after labelling (day 0) and at the end of growing season (10 October), with triplicate pots for each sampling. Sampling at day 0 was used to determine the initial incorporation of photosynthates into MBC and sampling at harvest was used to estimate the net incorporation of photosynthates into MBC over a growing season of rice. Four additional samplings (3, 7, 14, and 23 days after labelling) were conducted for soil labelled on 29 August to investigate the dynamics of the incorporated ^{13}C in MBC over time. Shoots were clipped along the root base, and soil and roots were separated by shaking gently in 1.5 l distilled water for 15 min. For sampling at day 0, shoots, roots and soil were immediately separated after labelling. Soil suspensions were sieved through a 2-mm sieve and centrifuged at 13,000 *g* for 15 min to remove fine roots and organic debris. Plants and soils from non-labelled controls were sampled on 17 July, 30 August and 15 October, respectively.

The moist soil samples obtained after centrifugation were immediately analysed for MBC and biomass-^{13}C using a fumigation-extraction method (Vance et al. 1987). Three subsamples of 16 g soil (oven-dry equivalent 10–11 g) were weighed into 100-ml beakers, and fumigated for 24 h at 25°C in a vacuum desiccator containing 50 ml of $CHCl_3$. Both fumigated and unfumigated soil samples were extracted with 0.25 M K_2SO_4 (soil to solution ratio of 1:5). The extracts were filtered through a 0.45-µm glass fibre filter and acidified to pH<3.0. Soluble organic C in extracts was determined using a total C analyser (TOC-500; Shimadzu). MBC was calculated as the difference in soluble organic C between fumigated and unfumigated soil extracts using a k_c factor of 0.45 to account for the non-extractable microbial biomass (Witt et al. 2000). After measurement of soluble organic C in fumigated and unfumigated soil extracts, 20 ml of each extract was dried on a hot plate (~80°C) and finely ground to a powder. The stable C isotope ratio of each powder sample was measured using an isotope ratio mass spectrometer (Delta^{PLUS}; Finnigan NIAT, Bremen) coupled with an elemental analyser (NC 2500; ThermoQuest Italia, Milan) by an interface (ConFlo III; Finnigan MAT). The natural abundance of heavy isotopes was expressed as parts per thousand relative to the international standard Pee-Dee Belemnite (PDB) using delta units (δ). Atomic ^{13}C% of fumigated and unfumigated soil extracts was calculated as:

$$\text{Atom } {}^{13}\text{C}\% = \left\{\left(\delta^{13}\text{C} + 1000\right) \times R_{\text{PBD}}\right\} / \left\{\left(\delta^{13}\text{C} + 1000\right) \times R_{\text{PBD}} + 1\right\} \times 100 \quad (1)$$

where R_{PDB} was the $^{13}C/^{12}C$ ratio of the standard PDB (=0.012372) and $\delta^{13}C$ was the ^{13}C natural abundance of each soil extract. The ^{13}C incorporated into microbial biomass (^{13}C-MBC)

was estimated as the difference in ^{13}C between fumigated and unfumigated soil extracts after the deduction of natural ^{13}C in unlabelled samples:

$$^{13}C\text{–MBC} = [\{(\text{atom}^{13}C\%)_{FM,labelled} - (\text{atom}^{13}C\%)_{FM,unlabelled}\} \times C_{FM} - \{(\text{atom}^{13}C\%)_{UFM,labelled} - (\text{atom}^{13}C\%)_{UFM,unlabelled}\} \times C_{UFM}] + 0.45 \quad (2)$$

where FM indicated the fumigated soil extract and UFM indicated the unfumigated soil extract; C_{FM} and C_{UFM} indicated the total C contents of the fumigated soil extract and unfumigated soil extract, respectively.

Shoots and roots were dried at 80°C for 72 h. The total organic C contents of the plant samples were analysed by a NC analyser (Sumigraph NC-800; Sumica, Japan). The $\delta^{13}C$ values were determined as described above. Total ^{13}C assimilation in shoots and roots were calculated as the difference in ^{13}C contents between labelled and unlabelled plants.

The experiment was carried out with three replicates and was arranged in a completely randomized design. The data were subjected to ANOVA. Duncan's multiple range test was used to evaluate the age effects.

Results

Plant growth

Rice plants reached the maximum tillering stage (14.2±0.8 tillers plant^{-1}) on 12 July [29 days after transplanting (DAT)]. Aboveground biomass increased continuously with plant growth (Fig. 1a), and reached 40.9±0.5 g (dry weight) pot^{-1} at the end of the growing season. Root biomass increased until the rice heading stage (73 DAT) (Fig. 1b). The shoot/root ratio increased greatly during the late growing periods (Fig. 1c), illustrating the change in photosynthate partitioning between the aboveground and the belowground parts of plants. The grain yield was 15.5±0.3 g grains (dry weight) pot^{-1} at the end of the growing season.

Seasonal dynamics of DOC

The seasonal dynamics of DOC differed significantly between planted soils and unplanted soils (Fig. 2). In planted soils, DOC concentrations increased with plant growth, ranging from 16.7 to 170 mg C l^{-1} throughout the period. The rapid increase started at 34 DAT (5 days after maximal tillering) and the maximal concentration was reached at 73 DAT (rice heading). DOC concentrations then decreased gradually toward the end of the season. In unplanted soils, however, DOC concentrations did not show significant fluctuations, being 37.8±1.2 mg C l^{-1} throughout the experimental period. The mean DOC concentrations were 3 times higher in planted soils than in unplanted soils. During the period from maximum tillering to heading of rice, the DOC concentration was positively correlated to the root biomass of rice plants (n=4, r^2=0.98, P<0.01).

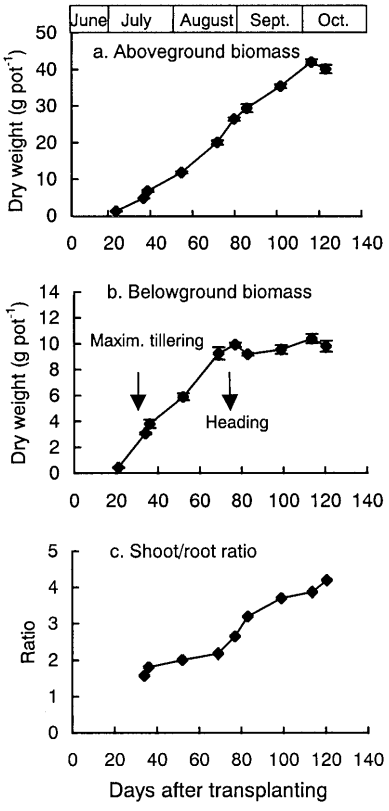

Fig. 1a–c Growth parameters of rice plants in a pot experiment. *Bars* represent SEs. *Arrows* denote the growth stages of rice plants. *Sept.* September, *Oct.* October

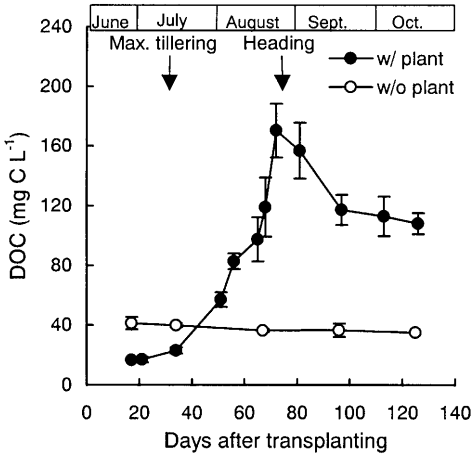

Fig. 2 Dissolved organic C (*DOC*) in rice-planted (*w/ plant*) and non-planted (*w/o plant*) soils. *Bars* represent SEs. *Arrows* denote the growth stage of rice plants. For other abbreviations, see Fig. 1

The contribution of photosynthates to dynamics of microbial biomass

MBC decreased from 233±2.3 mg C kg^{-1} soil at the start of experiment to 169±5.3 mg C kg^{-1} soil on 17 July (34 DAT). After maximum tillering of rice, MBC sharply increased and reached its maximum at the heading stage

of rice; it remained at this higher level until the end of the growing season (Fig. 3). The mean MBC during the period from rice heading to harvest (312±4.9 mg C kg^{-1} soil) was 85% higher than the lowest value on 17 July and 34% higher than the value at the start of experiment. From maximum tillering to heading of rice, MBC was positively correlated to DOC concentration (n=4, r^2=0.99, P<0.01) and root biomass (n=4, r^2=1.00, P<0.01).

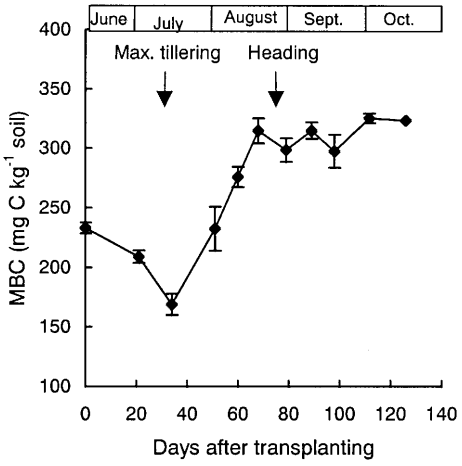

Fig. 3 Microbial biomass C (*MBC*) in a rice soil. *Bars* represent SEs. *Arrows* denote the growth stage of rice plants. *Max.* Maximum; for other abbreviations, see Fig. 1

The $\delta^{13}C$ values (‰) of fumigated and unfumigated soil extracts without ^{13}C labelling were similar and did not change over time, being –25.89±0.1‰ for fumigated extracts and –26.23±0.11‰ for unfumigated extracts, respectively (Fig. 4). $^{13}CO_2$ labelling of rice plants caused remarkable increases in $\delta^{13}C$ values of fumigated soil extracts. The increases were more significant for the samples labelled on 19 July, 4, 21 and 29 August than for those labelled on 4 and 20 September. The increases at day 0 indicated that the assimilated ^{13}C was released into soil and utilized by soil microorganisms rapidly. The $\delta^{13}C$ values of unfumigated soil extracts at day 0 also increased but to a lesser extent compared with those of fumigated soil extracts.

The amounts of ^{13}C in MBC, calculated from the difference between the fumigated and unfumigated soil extracts, ranged from 10 to 121 µg ^{13}C pot^{-1} at day 0 (Table 1). The amounts recovered at the end of the growing season were 16–81 µg ^{13}C pot^{-1}. To allow the comparison among various ages of rice, ^{13}C in MBC was expressed as percentage of total assimilated ^{13}C (≈total ^{13}C in shoots and roots at day 0). The percentages at day 0 increased with plant growth and reached their maximal value on 4 August (Table 1). From 29 August to 4 Sep-

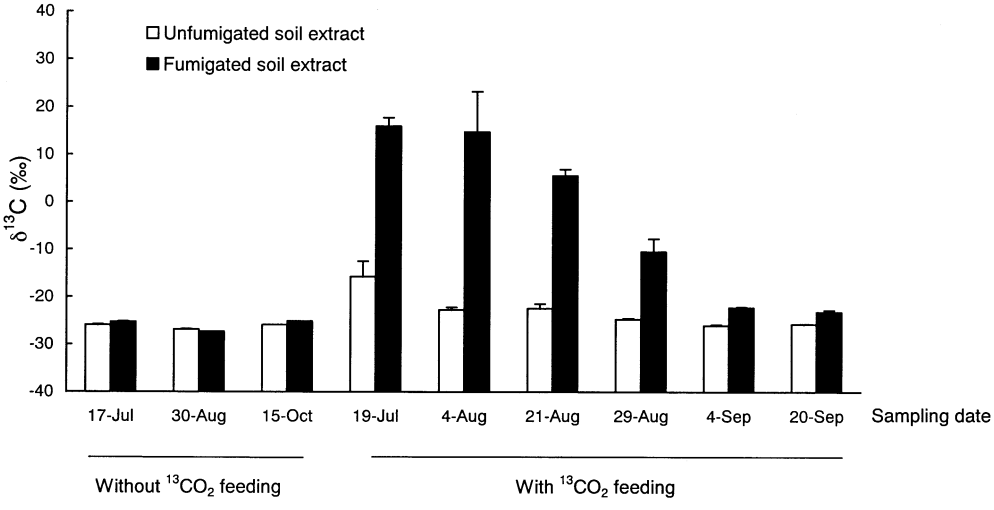

Fig. 4 $\delta^{13}C$ (‰) of fumigated and unfumigated soil extracts of soil samples from pots with and without $^{13}CO_2$ labelling of rice plants. Soil samples were collected immediately at the end of 6-h labelling. *Bars* represent SEs. *Jul* July, *Aug* August, *Sep* September, *Oct* October

Table 1 ^{13}C recovered in plant and soil biomass after 6-h labelling of rice plants under a $^{13}CO_2$-enriched atmosphere. *DAT* Days after transplanting, *ND* not determined

Labelling	DAT	Plant ^{13}C (mg pot^{-1})	Microbial biomass			
			^{13}C (µg pot^{-1})		% Of plant ^{13}C[a]	
			Day 0[b]	Harvest[c]	Day 0	Harvest
4 July	21	5.16	ND	25.9	ND	0.50 ab
19 July	36	15.46	119.6	81.2	0.78 ab	0.53 ab
4 August	51	11.61	111.3	80.8	0.94 a	0.75 a
21 August	68	19.68	120.9	66.7	0.63 b	0.34 bc
29 August	76	11.57	57.3	33.9	0.59 b	0.35 bc
4 September	83	16.54	28.9	30.5	0.17 c	0.18 c
20 September	99	6.74	9.8	15.8	0.15 c	0.23 c

[a] Data in the *same column* followed by the *same letter* are not significantly different at P<0.05
[b] Day 0: plant and soil were sampled immediately after the end of 6-h labelling
[c] All plants were harvested at the end of the growing season (10 October 2000)

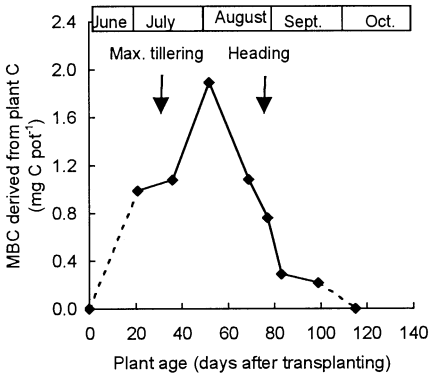

Fig. 5 Contribution of photosynthesized C to soil microbial biomass (*MBC*) over a growing season of rice. The contribution was estimated by multiplying the microbial biomass ^{13}C as percentages of plant ^{13}C (Table 1) and the rates of plant growth. The contributions at the time of transplanting and at final harvest were assumed to be zero as indicated by the *dashed lines*. *Arrows* denote the growth stages of rice. For other abbreviations, see Fig. 1

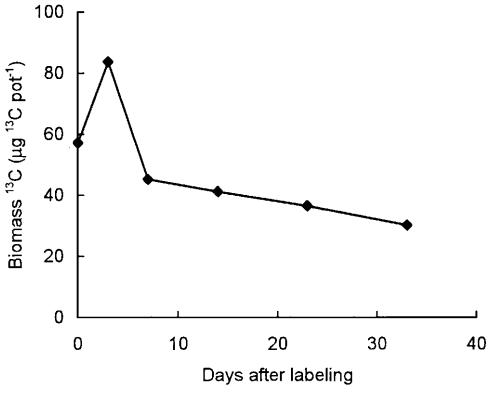

Fig. 6 Temporal change in ^{13}C of microbial biomass. Rice plants were labelled on 29 August for 6 h and soil was sampled 6 times within 35 days after labelling

tember (within 7 days), there was a significant decrease in percentages of ^{13}C in MBC. The percentages at the end of the season, except those due to labelling in September, were lower than the values at day 0 (Table 1).

The ^{13}C incorporation into MBC was extrapolated to give the total photosynthesized C. This was done by multiplying the percentages of assimilated ^{13}C in the microbial biomass and the rates of plant growth. The percentages at the end of the growing season were used to estimate the net contribution of photosynthates to MBC after a growing season of rice. The estimated contribution of photosynthates to MBC showed a more significant difference among various growth stages of rice (Fig. 5) than the ^{13}C percentage itself. This was because the plants with greater growth rates also showed greater ^{13}C incorporation into MBC. Assuming zero contribution at the time of transplanting and at the time of harvest, the overall contribution of photosynthates to microbial biomass was estimated to be 91 mg C pot^{-1}, corresponding to 28% of total MBC at the end of the season or 100% of MBC increase over the growing season.

Turnover of C in microbial biomass

The ^{13}C-MBC levels decreased at the end of growing season compared with those at day 0 (Table 1). To observe the ^{13}C dynamics in MBC, ^{13}C-MBC in soil samples labelled on 29 August was monitored 6 times after labelling. The labelling was carried out at the period when the plants started to shift from the vegetative stage to the reproductive stage. We assumed that the dynamics of ^{13}C labelled at this time represented an average over the growing season. The ^{13}C-MBC increased immediately after labelling and showed a peak at day 3, followed by a sharp decrease between days 3 and 7 and a gradual decline afterwards (Fig. 6).

Discussion

DOC in the planted soil showed a rapid increase between the maximum tillering and heading stage of rice and a gradual decrease toward the end of growing season. Organic manure was not applied to soil in this experiment. The increase in DOC in the planted soils largely resulted from the release of soluble root exudates. The seasonal pattern of DOC was consistent with previous reports by Lu et al. (2000a, 2000b) that the DOC pool in root zone soil was significantly enriched by organic C released from rice roots. The increase in DOC with plant growth illustrated the increase in C substrates, which were readily available for microorganisms.

MBC decreased at first and then significantly increased during the period of maximum tillering and heading of rice. The decrease in MBC during the early period was likely due to the change in the microbial community structure after soil flooding. The analysis of the phospholipid fatty acid composition revealed that facultative and obligate anaerobic populations increased at the expense of aerobic populations after prolonged submergence of rice soil (Reichardt et al. 1997; Bai et al. 2000). During the first month of our experiment, the aerobic populations probably decreased while those of anaerobes had not yet developed. Consequently, total MBC decreased. The seasonal pattern of MBC in this experiment differed from that reported by Witt et al. (2000) who found that MBC decreased with plant growth. In their study, however, a larger soil sample was used for the production of a relatively small plant biomass. The plant effects were expected to be less significant in their study. Ghoshal and Singh (1995) and Bai et al. (2000) observed a substantial decrease in MBC during the early periods and a slight increase during the late periods of rice growth. Ghoshal and Singh (1995) suggested that plant competition for nutrition resources depressed microbial growth during the early periods. This effect seemed not to occur in our experiment because the rapid increase in MBC was concomitant with the rapid growth of plant roots (Figs. lb, 3).

About 0.54% of assimilated ^{13}C was recovered as MBC at day 0. The measurements of MBC at day 0 were

conducted immediately (within 1 h) after pulse labelling. Rapid incorporation of photosynthates into MBC proved that root exudates derived from recent assimilates were readily utilized by microorganisms in rice soil. Rapid allocation of photosynthates to the belowground parts and incorporation into MBC was also reported earlier for upland soils (Rattray et al. 1995; Kuzyakov et al. 2001).

The incorporation of photosynthates into MBC showed a clear seasonal pattern: it increased with plant growth and reached the maximum on August 4, followed by sharp decreases toward the maturation of plants (Table 1, Fig. 5). Apparently, the greater incorporation of photosynthates during maximum tillering to heading of rice accounted for the significant increase in MBC during this period (Fig. 3). The seasonal pattern of the photosynthate incorporation appeared to be strongly controlled by the change in physiological properties of rice plants. Root biomass increased linearly until the end of August, and thereafter plants started heading (Fig. 1). Consequently, more of the photosynthesized C was retained in the aboveground parts after August for the requirements of reproductive growth (i.e. grain filling) than in the younger plants.

The percentages of assimilated ^{13}C in MBC were 0.15–0.94% (mean 0.54%) at day 0 an 0.18–0.75% (mean 0.41%) at the end of the season. Comparable data are not available for rice soils. In upland soils, Rattray et al. (1995) reported 0.55% in *Lolium perenne*, and Kuzyakov et al. (2001) showed 0.8–3.2% in similar ryegrass materials. Using a continuous labelling method, greater values (1–5%) were obtained in wheat and maize plants (Merckx et al. 1985; Liljeroth et al. 1990; Martin and Merckx 1992; Van Ginkel et al. 2000). Our values were relatively low compared with those in upland soils. Apparently, the differences are due to different plant species, growth conditions and experimental techniques. However, the utilization efficiency of photosynthates by microbial communities is also possibly different between those inhabiting flooded soil (predominantly facultative and anaerobic populations) and those inhabiting upland soils (predominantly aerobic populations).

In the present experiment, the seasonal contribution of photosynthesized C to microbial biomass amounted to 91 mg C pot^{-1}, accounting for 28% of total MBC at the end of the season or 100% of the increase in MBC over the growing season. According to these data, complete turnover of MBC in rice soils possibly occurs after every 4 years. However, caution should be taken when extrapolating this result to field conditions, because a relatively smaller volume of soil (about one-sixth compared to field conditions) was used for plant growth in the present study. The soil in the pots was probably close to being considered rhizosphere, and consequently, the plant effects on MBC were manifest. Helal and Sauerbeck (1989) found that the rhizosphere microbial biomass increased five-fold after 30 days of maize growth in a chernozem soil whereas fewer changes were found in the bulk soil.

The dynamics of ^{13}C in MBC showed a maximal value at day 3 followed by a sharp decrease from day 3 to day 7 and a gradual decrease afterwards (Fig. 6). The ^{13}C in MBC may have had two fates: a fraction released as CO_2 through respiration, another fraction transformed to structural components of microorganisms. The fast decrease during the first week possibly indicated an initial loss of ^{13}C through microbial respiration and the slower phase indicated the C turnover through structural components of microbial cells.

In conclusion, our study demonstrated that microbial biomass decreased in the early period but markedly increased in the late period of rice growth. During the maximum tillering to the heading of rice, the increasing supply of plant-derived C, as evidenced by the increasing DOC concentrations, significantly stimulated the growth of microbial biomass. The rapid incorporation of labelled photosynthates into microbial biomass proved that photosynthates released from rice roots were readily available for microorganisms in the soil. Over a growing season of rice, the net contribution of photosynthates to MBC was estimated to be 91 mg pot^{-1} (or $plant^{-1}$), corresponding to 28% of total MBC at the end of the season and a 100% increase in MBC over the growing season. Since the microbial biomass serves as a sink and source of plant nutrients, it is essential to further investigate whether the significant seasonal variation of MBC influences nutrient uptake and growth of rice plants.

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