



# Rapid response of soil microbial communities from conventional, low input, and organic farming systems to a wet/dry cycle

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## Abstract

Soil microbial communities may be strongly influenced by agricultural practices which change the soil environment. One such practice is the use of organic amendments and cover crops which increase carbon availability to microorganisms. Another is irrigation which, in California's hot, rain-free growing season, can cause severe wet/dry cycles. We investigated (i) long-term differences in amounts of organic inputs using soils from organic, low input, and conventional farming systems, and (ii) differences in severity of soil drying following irrigation, using soil from two depths, 0–3 and 3–15 cm. All soils were air-dried and re-wetted, and we measured short-term changes in microbial biomass carbon (MBC), dissolved organic carbon (DOC), respiration, and phospholipid ester-linked fatty acid (PLFA) composition before and for 27 h after re-wetting. Respiration rates were fit to a two-first-order-component model. Carbon respired from the more slowly utilized C pool of the two-component model, MBC, and DOC increased with increasing amounts of organic inputs, and PLFA composition of the organic and conventional soils clearly differed in their mole percentages of numerous fatty acids when analyzed by principal components analysis and redundancy analysis. Despite these differences, the response of microbial communities in the three farming systems to soil drying and re-wetting was similar. For example, the relative increase in MBC following soil re-wetting did not differ among the farming system soils. In contrast, the relative increase in MBC after re-wetting was greater, and the respiratory response to soil re-wetting was more rapid in the surface (0–3 cm) than deeper (3–15 cm) layer. Higher ratios of cyclopropyl fatty acids to their precursors suggested greater stress to bacteria in the deep than surface layer, and these ratios declined more rapidly after re-wetting in the deep than surface layer. This study suggested that adaptation to wet/dry cycles by surface microorganisms had occurred during the 3-month growing season, leading to changes in both microbial process rates and community composition. © 1999 Published by Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

Agricultural practices strongly affect the soil environment and thus are likely to disturb soil microbial communities. Changes in microbial community composition may, in turn, influence soil processes (Schimel, 1995). Because microbial activity is central to C and N

cycling in soil, disturbances may alter retention of C and N in soil and N availability to plants.

Some of the disturbance effects are of the order of hours or days, a shorter time frame than usually considered in agricultural studies of microbial processes and communities. For example, incorporation of cover crops into agricultural soils can produce rapid fluctuations (lasting one to several days) in microbial biomass (MB) and inorganic N (Wyland et al., 1995, 1996). Microbial community composition may also respond rapidly to disturbance. Phospholipid fatty

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acid (PLFA) composition of a sediment microbial community shifted substantially during the first 12 h after sieving (Findlay et al., 1990).

Increases in MB often occur following increased amounts of organic inputs. Short term increases occur for days to months after organic amendments are applied (Ocio et al., 1991; Wyland et al., 1995; 1996; Gunapala and Scow, 1998). Higher stable amounts of MB may accumulate after several years of increased organic inputs (Schnürer et al., 1985; Collins et al., 1992; Scow et al., 1994; Gunapala and Scow, 1998).

The rates of microbial processes associated with heterotrophic metabolism often increase when soils receive higher organic inputs. In many studies, N mineralization rates were higher following long-term increases in organic amendments (Bonde et al., 1988; Fraser et al., 1988; Wander et al., 1994; Gunapala and Scow, 1998). Gunapala and Scow (1998) found higher rates of potential activity (arginine ammonification and glucose-induced respiration) in soils under organic farm management, receiving cover crops and manure, compared to conventional soils which did not receive these amendments, and Wander et al. (1996) found differences in  $^{13}\text{C}$  acetate metabolism in soils under organic or conventional management.

Expressing rates of microbial processes on a per unit biomass basis may help to determine whether the change in a process rate is due to the presence of a larger population capable of carrying out the process, or due to metabolic or species composition differences between microbial communities. For example, Anderson and Domsch (1990) found a higher ratio of respiration to MB in soils under long-term monoculture than in those under long-term crop rotations. They suggested that the increased C use efficiency by microbial communities in the crop rotation soils could have been due to a shift in microbial community composition.

Amounts or types of organic inputs to soils can influence microbial community composition as measured by analysis of microbial lipids. Phospholipid ester-linked fatty acids (PLFAs) are major constituents of the cell membranes of all eubacteria and eukaryotes, and these compounds are rapidly degraded following microbial death (Vestal and White, 1989; White et al., 1996). The large variety of PLFAs present in living organisms and extracted from soil may provide a unique fingerprint of the viable microbial community of a given soil, at a given time. Certain PLFAs are limited to specific groups of organisms and appear promising in their use as biomarkers for these organism groups (Vestal and White, 1989; White et al., 1996). Differences in the PLFA composition of microbial communities have been observed in farming systems which receive different amounts of organic inputs (Zelles et al., 1992, 1994, 1995; Bossio and Scow, 1998;

Bossio et al., 1998), and changes in PLFA composition can be distinguished following specific management practices over a cropping season (Bossio et al., 1998).

The environmental conditions to which a soil has been exposed may also affect microbial biomass, function and community composition. During irrigation cycles in mid-summer in California, surface soil (approximately 0–3 cm depth) dries to a nearly air-dry condition and reaches higher temperatures than the deeper soil layer which experiences much lower fluctuations in water content and temperature (Lundquist, unpub. data). In soils exposed to different temperature conditions in the laboratory, changes in both microbial respiration kinetics and PLFA composition were found (Zogg et al., 1997). Soil drying is stressful to soil microorganisms because as water content decreases, the diffusion of nutrients is retarded which creates starvation conditions for bacteria. Also as water potential decreases, soil microorganisms divert energy to production of compatible solutes in order to avoid plasmolysis (Rosacker and Kieft, 1990). Studies have shown substantial reductions in MB as the soil dries from field capacity to air-dry (Bottner, 1985; West et al., 1992; Van Gestel et al., 1993). When soil is rapidly re-wetted, soil microorganisms may lyse as soil water potential increases (Kieft et al., 1987). Exposure of microbial communities to fluctuating moisture and temperature may lead to selection for organisms better adapted to these conditions. West et al. (1988) found greater resistance of MB to desiccation in soil from a low than soils from higher rainfall areas.

We hypothesized that there would be a faster recovery of microbial communities exposed to severe wet/dry cycles in soils receiving higher than lower amounts of organic inputs. Additionally, we hypothesized that communities exposed to more severe wet/dry cycles, as in the surface layer of soil, would recover more rapidly than communities deeper in the soil profile. We measured short-term changes in the biomass, respiration and PLFA profiles of microbial communities after re-wetting air-dried soils from conventional, low input, and organic farming systems.

## 2. Materials and methods

### 2.1. Experimental design

In July 1996, soil was sampled from the University of California at Davis Sustainable Agriculture Farming Systems (SAFS) project which was initiated in 1988 in Davis, California. The experiment is a randomized complete block design with four blocks, and individual plots are approximately 1300 m<sup>2</sup>. The soil types at the SAFS experiment are Reiff and Yolo loams, respectively coarse silty and fine-silty, mixed,

Table 1

Soil characteristics (0–15 cm) of the organic, low input, and conventional soils. Values are mean (standard error),  $n = 4$

	Organic matter (%)	pH	P ( $\mu\text{g P g}^{-1}$ soil)	C.E.C. (meq 100 $\text{g}^{-1}$ soil)
Organic	1.95 (0.03)	7.30 (0.04)	31.0 (1.9)	24.4 (0.4)
Low input	1.78 (0.01)	7.33 (0.02)	14.3 (0.6)	25.1 (0.5)
Conventional	1.42 (0.01)	7.15 (0.03)	14.0 (1.1)	24.4 (0.4)

non-acid, thermic Typic Xerorthents. Soil was sampled from three farming system treatments: conventional, which receives inorganic fertilizers and synthetic pesticides; low input, which receives a vetch cover crop and supplemental inorganic fertilizer; and organic, which receives a vetch cover crop and poultry manure as fertility sources. Average annual dry matter inputs, including non-harvested plant residues, were 13.0, 15.7 and 17.8  $\text{Mg ha}^{-1}$  in the conventional, low input and organic treatments, respectively (Scow et al., 1994; Sean Clark, personal communication). All stages of a four-year rotation, tomato/safflower/corn/wheat or grain legume, are represented for each of the three systems; however, we sampled soils under tomatoes only. Soil characteristics for each system in plots under tomatoes in 1996 are summarized in Table 1.

Thirty 2 cm dia soil cores (0–15 cm) were collected from locations halfway between the tomato plants and the edge of the raised tomato beds throughout each plot. The soils were separated into 0–3 and 3–15 cm layers. After thorough mixing, the soil samples were air-dried with frequent turning in a greenhouse at 20–30°C. Drying was completed in 3 d, and soils were stored at 25°C for 2–3 weeks before initiation of the experiment.

Soil water content was determined on the air-dry soils. Each soil sample was spread out in a thin layer and water was applied evenly to bring the soils to 0.24  $\text{g H}_2\text{O g}^{-1}$  soil, or approximately  $-0.03$  MPa, based on moisture retention curves using a pressure-plate apparatus. The soil samples were gently mixed and divided into three portions, and each 200 g portion was placed in a separate 250 ml Mason jar and incubated at 25°C. The jars were opened every 8 h to maintain aerobic conditions. One day prior to water addition, and at 3, 8 and 27 h after water addition, soil gravimetric water content, and duplicate measurements of MBC and DOC (methods below) were determined on one set of jars. Soil was also frozen at  $-36^\circ\text{C}$  for duplicate PLFA analysis.

A Micro-Oxymax closed system respirometer (Columbus, Columbus, OH) was used to measure respiration following re-wetting of the air-dry soil. Fifty grams of air-dry soil were placed into 250 ml test chambers, sufficient water was added to bring the soils to 0.24  $\text{g H}_2\text{O g}^{-1}$  soil, the soils were gently mixed,

and the chambers were attached to the respirometer. The  $\text{CO}_2$  concentration in the headspace was sampled at 45 min intervals. The first  $\text{CO}_2$  production rate could not be calculated until the interval between 0.75 and 1.5 h after wetting because two sample points were needed to calculate the  $\text{CO}_2$  production rate. The respirometer was set to replace the chamber air with ambient air if the  $\text{CO}_2$  concentration changed by more than 0.5% from the original concentration, but this did not happen during the 27 h measurements. The ratio of respiration to MBC was calculated by using the double exponential model (described below) for each soil sample to calculate the respiration rate at 3, 8 and 27 h, and dividing by MBC measured at that time.

## 2.2. Laboratory analyses

Soil characteristics were measured by the University of California Division of Agriculture and Natural Resources laboratory on 0–15 cm samples taken on 20 September, 1997. Organic matter was measured by combustion, pH was measured in a saturated paste, cation exchange capacity was measured according to Janitzky (1986), and phosphorous was measured according to Olsen et al. (1954).

MBC was measured by the fumigation extraction method (Vance et al., 1987; Sparling and West, 1988; Tate et al., 1988). Twenty-five grams of soil were extracted immediately after sampling by shaking for 30 min with 60 ml of 0.5 M  $\text{K}_2\text{SO}_4$ , and another 25 g soil were fumigated for 24 h with ethanol-free chloroform ( $\text{CHCl}_3$ ). The  $\text{CHCl}_3$  was removed and the soils were extracted as above. Carbon released by  $\text{CHCl}_3$  fumigation is reported with no conversion to total MBC. DOC was extracted with deionized water according to Burford and Bremner (1975). Organic C in the MBC and DOC extracts was analyzed using a Shimadzu TOC 5050 (Shimadzu, Columbia, MD). Only a subset of the soil samples were analyzed for PLFA. Two field replications of both depths of the organic and conventional farming systems were measured at three sample times: on air-dry soil, and 3 and 27 h after re-wetting. Duplicate 8 g dry weight subsamples were extracted for PLFA analysis according to Bossio and Scow (1998). Gas chromatography

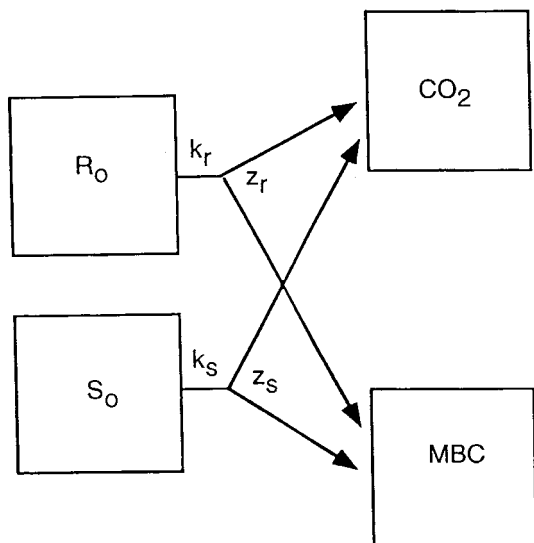


Fig. 1. Conceptual model for two-component and simplified two-component models.  $R_0$  and  $S_0$  represent the amount of organic C present in the rapidly and slowly utilized pools, respectively,  $k_r$  and  $k_s$ , the rate constants for the rapid and slow pools, respectively, and  $z_r$  and  $z_s$ , the fraction of organic C in the respective rapid or slow pool mineralized to  $\text{CO}_2$ , while the fraction  $1-z_r$  or  $1-z_s$  is partitioned to MBC.

conditions were identical to those in Bossio and Scow (1998), and individual PLFAs were identified using bacterial fatty acid standards and MIDI peak identification software (MIDI, Newark, Delaware). The nomenclature used for fatty acids was according to Bossio and Scow (1998).

### 2.3. Statistical analyses

Respiration rates following soil re-wetting were biphasic with an initial period of rapid rate decline followed by a phase of more gradual rate decline. Three models were used to analyze the data; a single-component first-order model (Stanford and Smith, 1972), a model with one linear and one first-order component, and a model with two first-order components (Bonde and Rosswall, 1987). The model fits were compared based on an  $F$ -test and the distribution of the residuals (Robinson, 1985). The two-first-order-component model, which provided the best fit, is described here. A conceptual diagram of the two-first-order-component model is shown in Fig. 1, and the model has the differential form

$$\frac{dP}{dt} = k_r z_r R_0 e^{-k_r t} + k_s z_s S_0 e^{-k_s t}$$

where  $P$  is  $\mu\text{g CO}_2\text{-C g}^{-1}$  soil,  $t$  is hours  $R_0$  and  $S_0$  are the rapidly and slowly utilized C pools ( $\mu\text{g C g}^{-1}$  soil), respectively,  $k_r$  and  $k_s$  are the first-order rate constants

for the rapidly and slowly used pools ( $\text{h}^{-1}$ ), respectively, and  $z_r$  and  $z_s$  are the fractional conversion of the C pools to  $\text{CO}_2\text{-C}$  (i.e.  $\text{CO}_2\text{-C}$  produced/unit of pool C used). Because the fractional conversion of the C pools could not be determined, the terms  $z_r$  and  $R_0$  were combined to  $R$ , and  $z_s$  and  $S_0$  to  $S$ . Therefore,  $R$  and  $S$  represent the amount of the C pools converted to  $\text{CO}_2\text{-C}$  in an equation of the form:

$$\frac{dP}{dt} = Rk_r e^{-k_r t} + Sk_s e^{-k_s t}$$

This model is similar to those used in other studies (Stanford and Smith, 1972; Bonde and Rosswall, 1987; MacDonald et al., 1995) which did not take into account that only a fraction of organic matter is converted to mineralized product.

We used the differential rather than integral form of the model because the integral form requires cumulative data which can lead to accumulation of errors (Hess and Schmidt, 1995). For each sample, measured respiration rates and the midpoint between respiration sample times were fit to the models using the method of Marquardt in the SAS statistical software package (SAS Institute, 1988). For each parameter of the two-first-order-component model, differences due to farming system or soil depth in the respiration kinetics parameters were determined using a two-way analysis of variance.

For each farming system X depth combination, analysis of variance was used to analyze differences in MBC or DOC over time (i.e. air-dry, and 3, 8 and 27 h after water addition). In almost all cases, the air-dry MBC and DOC contents were significantly different ( $P < 0.05$ ) from the moist samples, and the moist samples showed no significant differences. Therefore, the moist samples were averaged for each farming system X depth combination. Two-way analysis of variance was used to compare MBC and DOC in moist or dry soils and to compare the absolute and relative changes in MBC between air-dry soils and 3 h after re-wetting. Simple correlations between the respiration kinetics parameters and measurements of MBC and DOC in dry or moist soil, and the difference between MBC and DOC contents in moist and dry soil, were also determined.

PLFA composition of microbial communities was analyzed with CANOCO software (Microcomputer, Ithaca, NY) using principal components analysis (PCA) and redundancy analysis (RDA). Using PCA it may be possible to infer that environmental effects are influencing the samples based on the order of soil samples on the first several principal components (ter Braak, 1987; ter Braak and Prentice, 1988). RDA allows direct comparison of the multivariate data and environmental variables because axes (similar to princi-

Table 2

Possible constituent fatty acids of three MIDI-identified peaks (sums), and ratios of fatty acids used in data analysis. Abbreviations for the ratios are given in parentheses

Name	Definition
Sum A	13:0 3OH, iso15:2 (with two different unknown locations for unsaturation)
Sum B	18:2 $\omega$ 6,9, a18:0
Sum C	18:1 $\omega$ 7c, 18:1 $\omega$ 9t, 18:1 $\omega$ 12t
Cyclopropyl 17:0/precursor (cyclo17:pre)	cyclo17:0/16:1 $\omega$ 7c
Cyclopropyl 19:0/precursor (cyclo19:pre)	cyclo19:0/sum C
Total monounsaturated/total saturated (monounsatur:satur.)	(16:1 $\omega$ 5c + 16:1 $\omega$ 7c + 16:1 $\omega$ 11c + 17:1 $\omega$ 9c + sumC + 18:1 $\omega$ 9c)/(15:0 + 16:0 + 17:0 + 18:0 + 20:0)

pal components) are constrained to be a linear combination of environmental variables. In RDA it is also possible to use classes, or nominal variables, for example, organic or conventional treatments, as environmental variables (Jongman et al., 1987). CANOCO also includes a Monte Carlo permutation which enables testing of the significance of environmental variables on PLFA composition. The techniques of PCA and RDA are explained in detail in ter Braak (1987) and ter Braak and Prentice (1988). We chose these analytical methods because they have been effective in investigating the effects of environmental variables on community composition in recent studies of soil (Bossio and Scow, 1998; Bossio et al., 1998) and other communities (Verdonschot and ter Braak, 1994; Qinghong and Bråkenhielm, 1995; Van Wijngaarden et al., 1995).

Response data in the RDA and PCA analyses were PLFA mole% based on 28 MIDI-identified peaks found in all of the samples. Conducting PCA with an additional 10 identified PLFAs which had values of zero for up to 50% of the soil samples, indicated little difference in the distribution of the common set of 28 regardless of whether or not the additional PLFAs were included. The smaller set of 28 peaks were used for the analysis because the additional 10 combined made up less than 2% of total PLFA, and may not have been reliably detected. To calculate mole% of each fatty acid, nmoles of each fatty acid were divided by total nmoles in the 28 fatty acids and multiplied by 100. The groups sum A, sum B, and sum C refer to MIDI-identified peaks that may contain two or more PLFAs (Table 2). Also included in Table 2 are three ratios of PLFAs which were used in the PCA and RDA analyses. In the ratio cyclopropyl 19:0/precursor, sum C is used in the place of the precursor. Sum C is potentially composed of 18:1 $\omega$ 7c, which is the precursor to cyclopropyl 19:0, and of 18:1 $\omega$ 9t, and 18:1 $\omega$ 12t. Because *trans* double bonds are less common in sediment samples than are *cis* double bonds (Gillan et al., 1981; Guckert et al., 1986), we assumed that sum C would be largely composed of 18:1 $\omega$ 7c.

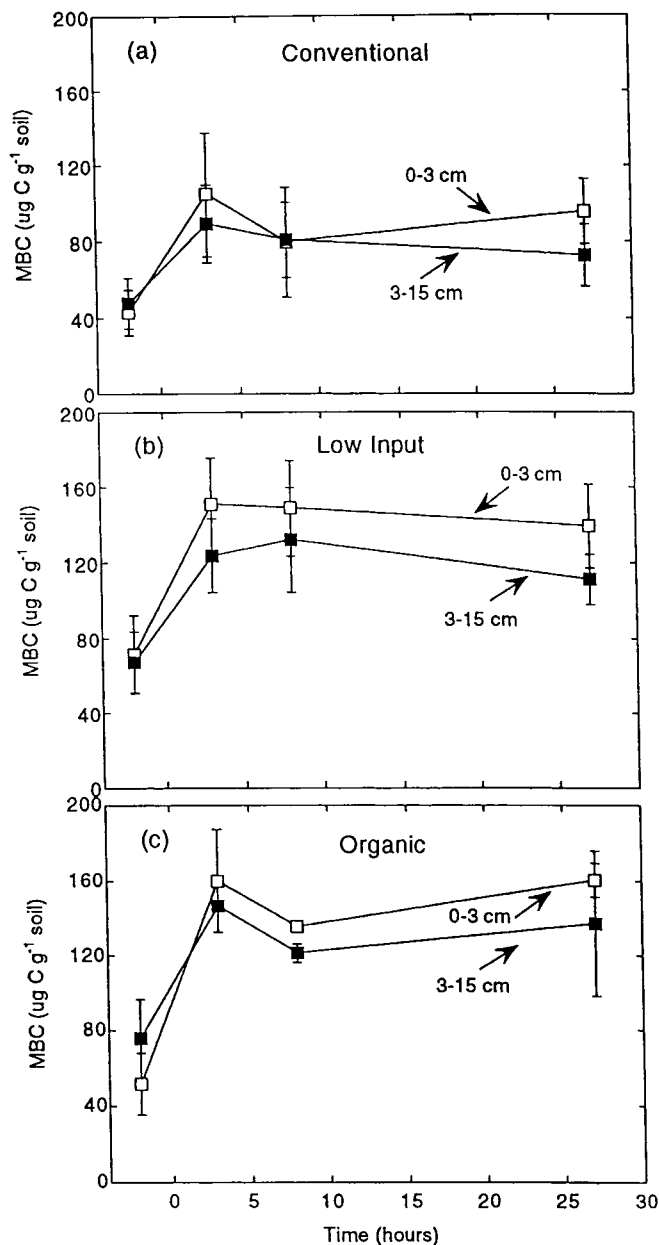


Fig. 2. Microbial biomass C in air-dry soil (prior to time 0), and in soil from 3 to 27 h after re-wetting for three farming system soils: (a) conventional, (b) low input, and (c) organic.

Table 3  
Microbial biomass C and dissolved organic C concentrations in dry or moist soil (average of three sample times), and absolute or relative changes in MBC or DOC from air-dry to 3 h after re-wetting. Values are mean (standard error),  $n = 3$ . \*, \*\*, \*\*\*, \*\*\*\* Indicate significance at  $P \leq 0.05$ , 0.01, and 0.001 levels, respectively. Different letters indicate differences in farming system mean for a given column

	MBC ( $\mu\text{g C g}^{-1}$ soil)			DOC ( $\mu\text{g C g}^{-1}$ soil)		
	MBC <sub>dry</sub>	MBC <sub>3h</sub> -MBC <sub>dry</sub>	MBC <sub>3h</sub> -MBC <sub>dry</sub> /MBC <sub>dry</sub>	DOC <sub>dry</sub>	DOC <sub>dry</sub> -DOC <sub>3h</sub>	DOC <sub>dry</sub> -DOC <sub>3h</sub> /DOC <sub>dry</sub>
Conventional						
0-3 cm	43.0 (6.0) b	93.4 (7.3) c	61.8 (17.3) b	89.3 (6.9) b	38.8 (4.0)	0.43 (0.02)
3-15 cm	47.9 (6.7)	81.0 (5.2)	41.5 (16.1)	57.5 (3.4)	26.0 (5.9)	0.44 (0.08)
Low Input						
0-3 cm	71.5 (10.6) a	146.4 (11.8) b	79.4 (15.5) ab	73.5 (9.3) b	34.7 (9.6)	0.45 (0.09)
3-15 cm	67.4 (8.2)	122.5 (9.2)	56.5 (10.2)	66.9 (2.3)	33.8 (3.2)	0.50 (0.03)
Organic						
0-3 cm	51.7 (8.1) a	152.1 (4.2) a	108.3 (20.9) a	94.4 (9.8) a	25.5 (10.3)	0.27 (0.11)
3-15 cm	75.7 (10.5)	135.1 (9.2)	70.8 (16.2)	96.9 (4.6)	38.5 (7.9)	0.39 (0.07)
Farming system						
Depth	NS	****	NS	*	NS	NS
System X Depth	NS	NS	NS	NS	NS	NS

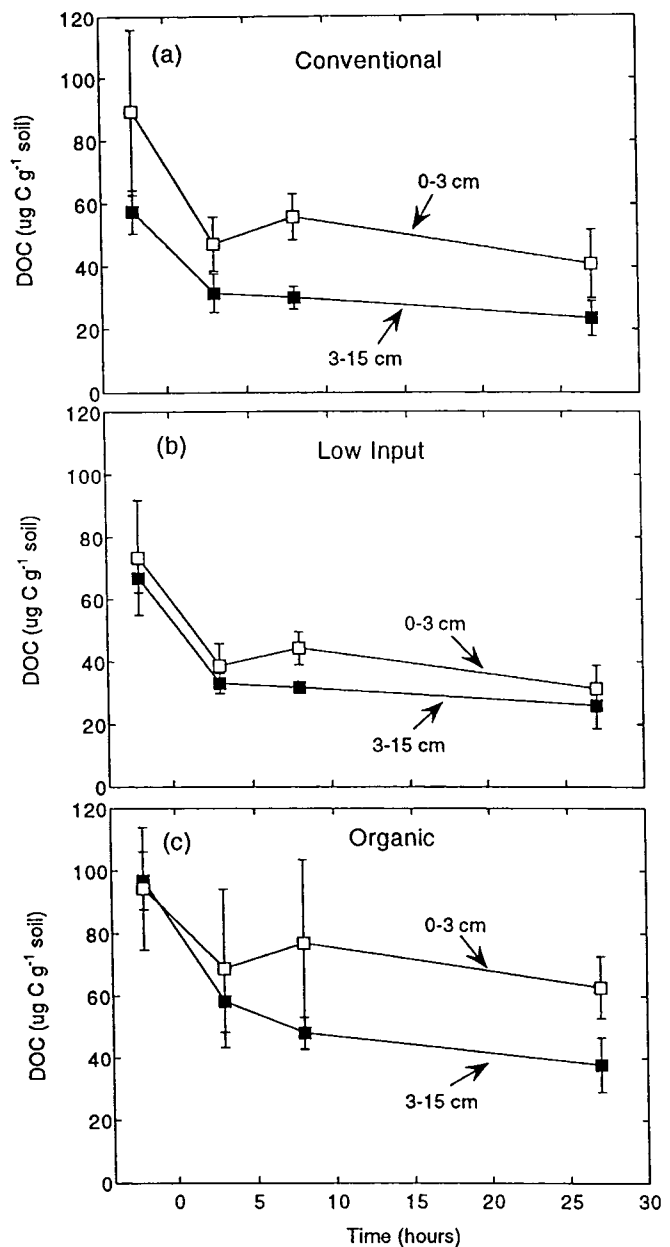


Fig. 3. Dissolved organic C in air-dry soil (prior to time 0), and in soil from 3 to 27 h after re-wetting for three farming system soils: (a) conventional, (b) low input, and (c) organic.

### 3. Results

#### 3.1. Microbial biomass C and dissolved organic C

Microbial biomass C was approximately two-fold higher in all of the soils 3 h after re-wetting of air-dry soils (Fig. 2). The total increase in MBC during this period ( $\text{MBC}_{3\text{h}} - \text{MBC}_{\text{dry}}$ ) was greater in the organic than conventional soil, but the relative increase ( $(\text{MBC}_{3\text{h}} - \text{MBC}_{\text{air-dry}}) / \text{MBC}_{\text{air-dry}}$ ) did not differ among the three farming system soils (Table 3). Both total and relative increases in MBC were greater in the sur-

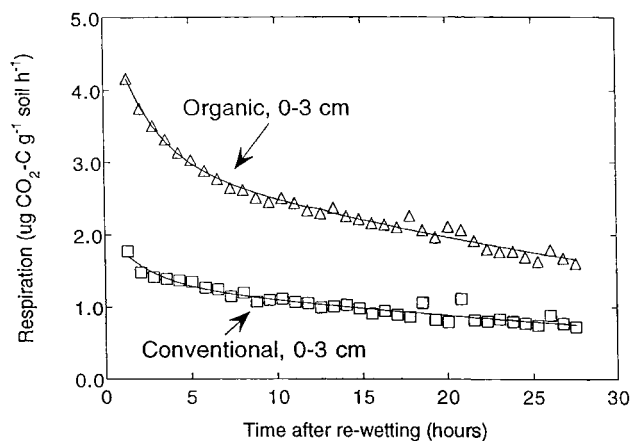


Fig. 4. Comparison of respiration kinetics following re-wetting of air-dry soil in one organic 0–3 cm and one conventional 0–3 cm sample.

face than deeper soil layer. MBC contents remained stable in moist soils from 3 to 27 h after irrigation (Fig. 2), as indicated by analysis of variance over time for each farming system X depth combination (data not shown).

Differences in MBC contents among farming systems and between soil layers were more pronounced in moist than air-dry soils. MBC was highest in the organic, followed by low input and conventional farming systems, based on average MBC contents from the three moist soil samples (Fig. 2, Table 3). In dry soil, MBC in the organic and low input soils was not significantly different. MBC was higher at 0–3 than 3–15 cm in moist soil, but did not differ between layers in dry soil.

Dissolved organic C was approximately 30–50% higher in air-dry than moist soils, and DOC concentrations declined by 3 h after re-wetting (Fig. 3). DOC concentrations were stable in moist soils with the

exception that DOC was higher in the organic 3–15 cm depth at 3 h than at 27 h after re-wetting. Absolute and relative changes in DOC from air-dry soil to 3 h after re-wetting were the same among the farming systems and two soil layers (Table 3). In both air-dry and moist soil, DOC was higher in the organic than low input and conventional soils. DOC was also higher in the surface than deeper layer, and this effect was more pronounced in moist than dry soil (Fig. 3, Table 3).

### 3.2. Respiration kinetics

Large differences were observed in respiration kinetics among the farming system treatments. Respiration data and the fit of the two-first-order-component model are shown for the 0–3 cm layer of one organic and one conventional soil (Fig. 4). This model provided a significantly better fit ( $P < 0.05$ ) than the single first-order component or one first-order, one linear-component models. Carbon mineralized from the slowly and rapidly utilized pools,  $S$  and  $R$ , and rate constants,  $k_s$  and  $k_r$ , always followed the order: organic > low input > conventional, except for  $k_s$  which was greater in the low input than the organic surface layer (Table 4). Despite the consistency of this ranking, however, only C mineralized from the slower pool,  $S$ , was significantly higher in organic than in the low input and conventional soils. Respiration following soil re-wetting was higher in the surface than deeper layer, as indicated by higher rate constants and larger  $S$ . There were larger differences in parameters between soil layers than among the farming system soils. The two rate constants,  $k_s$  and  $k_r$ , were greater and  $S$  was smaller in the surface than deeper layer.

Relationships between MBC and DOC and the amount of mineralizable C from slowly and rapidly utilized C pools,  $S$  and  $R$ , and their respective rate

Table 4

Parameters from two component model of respiration kinetics.  $S$  and  $R$  represent the amount of mineralizable C from, and  $k_s$  and  $k_r$  the rate constants for the slowly and rapidly utilized pools, respectively. Values are mean (standard error)  $n = 4$ . \*, \*\*, \*\*\* Indicate significance at  $P < 0.05$ , 0.01, and 0.001 levels, respectively. Different letters indicate differences in farming system mean for a given parameter for both depths combined

	$S$ ( $\mu\text{g C g}^{-1}$ soil)	$k_s$ ( $\text{h}^{-1}$ )	$R$ ( $\mu\text{g C g}^{-1}$ soil)	$k_r$ ( $\text{h}^{-1}$ )
Conventional				
0–3 cm	63.1 (4.1) b	0.0208 (0.0018)	2.89 (1.17)	0.576 (0.175)
3–15 cm	129.4 (29.1)	0.0092 (0.0019)	3.79 (0.26)	0.304 (0.017)
Low input				
0–3 cm	89.5 (12.9) b	0.0231 (0.0023)	3.87 (0.23)	0.605 (0.194)
3–15 cm	157.2 (14.6)	0.0114 (0.0009)	3.93 (0.56)	0.438 (0.033)
Organic				
0–3 cm	148.6 (13.0) a	0.0209 (0.0013)	4.14 (0.29)	0.718 (0.137)
3–15 cm	187.4 (10.6)	0.0144 (0.0004)	5.46 (0.88)	0.517 (0.089)
Farming system	**	NS	NS	NS
Depth	***	***	NS	*
System X Depth	NS	NS	NS	NS

Table 5

Correlations of respiration kinetics parameters with MBC and DOC measured in dry soil, moist soil (average of three samples), and the difference between moist and dry soil. Data from three farming systems and two soil layers used,  $n = 24$ . See Table 4 for description of parameters. Values are simple correlation (probability  $|r|=0$ )

Respiration kinetics Parameters	Correlations					
	MBC ( $\mu\text{g C g}^{-1}$ soil)			DOC ( $\mu\text{g C g}^{-1}$ soil)		
	Dry soil	Moist soil	Moist–dry	Dry soil	Moist soil	Moist–dry
$S$	NS	NS	NS	NS	NS	NS
$k_s$	NS	0.431 (0.040)	NS	NS	0.489 (0.018)	NS
$R$	NS	NS	NS	0.471 (0.027)	NS	NS
$k_r$	NS	0.624 (0.002)	0.624 (0.002)	NS	NS	NS

constants,  $k_s$  and  $k_r$ , were investigated. The rapidly used C pool,  $R$ , appeared to be related to DOC since a significant positive correlation was found between  $R$  and DOC in dry soil; however, there were no significant correlations between  $S$  and MBC or DOC. Both rate constants,  $k_s$  and  $k_r$ , were positively related to MBC in moist soil as was  $k_s$  to DOC in moist soil (Table 5). Scatter diagrams between the rate constants and MBC revealed a higher  $k_s$  for a given amount of MBC in the surface compared to deeper layer (data not shown).

The ratio of respiration to MBC was significantly higher in the organic than low input and conventional soils at 3, 8 and 27 h after re-wetting (Table 6). This ratio was higher in the deeper layer than the surface layer and the effect was significant at both 3 and 27 h after irrigation.

Table 6

Ratio of respiration to MBC at 3, 8 and 27 h after re-wetting dry soil. \*, \*\*, \*\*\* Indicate significance at  $P < 0.05$ , 0.01, and 0.001 levels, respectively. Different letters indicate differences in farming system mean for a given column

	Respiration:MBC ( $\mu\text{g C g}^{-1}$ soil $\text{h}^{-1}$ ; $\mu\text{g C g}^{-1}$ soil)		
	3 h	8 h	27 h
Conventional			
0–3 cm	0.043 (0.009)	0.048 (0.012)	0.025 (0.003)
3–15 cm	0.053 (0.008) b	0.042 (0.006) b	0.034 (0.003) b
Low input			
0–3 cm	0.046 (0.004)	0.035 (0.003)	0.023 (0.001)
3–15 cm	0.055 (0.006) b	0.039 (0.005) b	0.035 (0.002) b
Organic			
0–3 cm	0.063 (0.004)	0.058 (0.003)	0.033 (0.001)
3–15 cm	0.068 (0.006) a	0.061 (0.004) a	0.042 (0.006) a
Farming system	***	**	*
Depth	*	NS	**
System X Depth	NS	NS	NS

### 3.3. PLFA composition

Microbial communities were compared on the basis of their PLFAs. Principal components analysis clearly separated organic and conventional soils along the first principal component (PC), and surface and deep soils along the second PC (data not shown). Samples clustered by sample time, but with substantial overlap between times on the third PC (data not shown). The first, second and third PCs accounted for 37, 34 and 12% of the total variation in PLFAs, respectively. An RDA was carried out to test the hypothesis that farming system, depth and time were significantly related to PLFA composition. The first axis was constrained to the nominal variable of farming system, the second to the nominal variable of soil layer and the third to time since re-wetting. This ordination accounted for 36% of the total variation on the first axis, 32% on the second and 7% on the third (Fig. 5). Monte Carlo permutation tests to investigate the significance of the environmental variables on PLFA composition gave significance levels of  $P = 0.001$ ,  $P = 0.001$ , and  $P = 0.122$  for farming system (conventional or organic), depth (surface or deep), and time, respectively.

PLFAs with a high score on an RDA axis are strongly related to the axis and to the environmental variable defining the axis (ter Braak, 1987), and the majority of PLFAs had high scores ( $>0.50$ ) on either the first or second RDA axis. PLFAs enriched in the conventional soil included 10Me 17:0, 10Me 18:0, and 10Me 16:0, and 17:0 cyclo, and 16:1 $\omega$ 5c, and 20:2 $\omega$ 6, nine were enriched in the organic soil. The ratio of monunsat:sat. fatty acids was positively related to both the organic and surface soils. Many monounsaturated fatty acids, 17:1 $\omega$ 9c, 18:1 $\omega$ 9c, sumC, and 16:1 $\omega$ 7c, were abundant in the surface soil. In the deeper layer, the fatty acid 19:0 cyclo and the ratios of cyclo17:pre and cyclo19:pre were high.

In the ordination of the first two axes of the RDA,

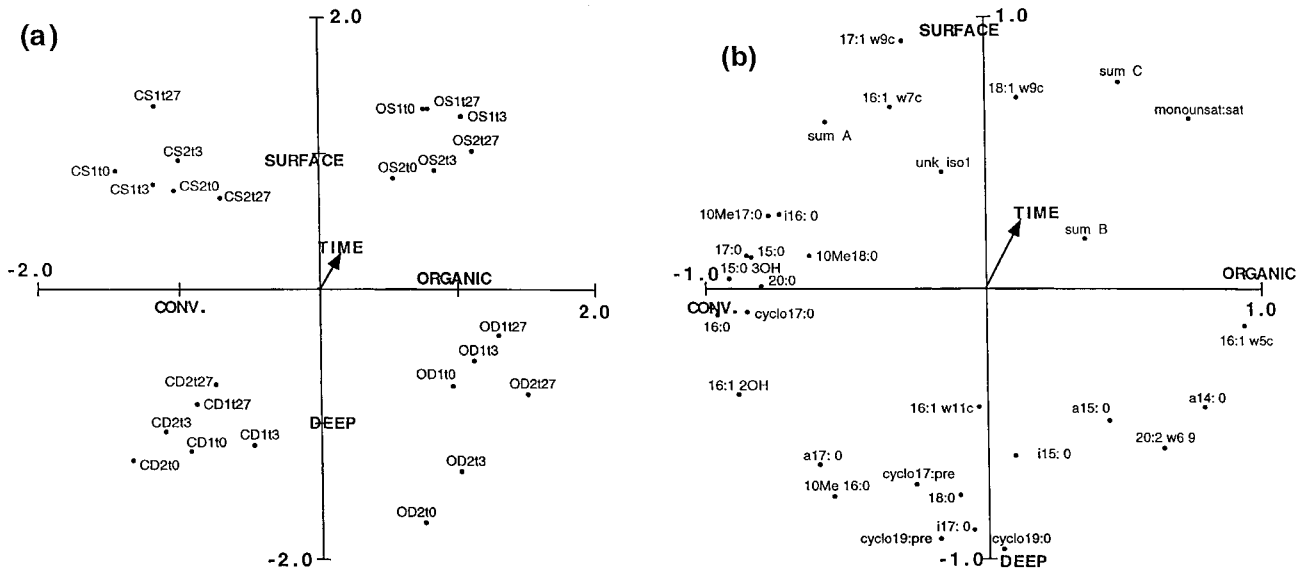


Fig. 5. Ordination of the soil samples (a) and PLFAs (b) from and RDA with the first axis constrained to farming system, and the second to soil layer. The first (horizontal) axis accounts for 36% of the variation, and the second for 32%. Soil samples in (a) are designated by O or C for organic or conventional, then S or D for surface or deeper layer, then 1 or 2 for field block 1 or 2, then *t*0 indicating air-dry soil, *t*3 indicating 3 h after re-wetting, and *t*27, indicating 27 h after re-wetting.

the samples from the deeper layer generally ran from lower left to upper right with time (Fig. 5(a)), while this pattern was less consistent for the surface layer. To better discern the effects of time, the two layers were analyzed separately with the first axis constrained to farming system and the second to time. Farming system had a highly significant effect ( $P < 0.001$ ) on PLFA distribution in both layers. Time after re-wetting had no significant effect ( $P = 0.33$ ) on community changes in the surface soil, but was significant at

$P = 0.066$  in the deeper layer. RDA ordinations show more clear separation of the samples by time in the deep than surface layer (Fig. 6).

To compare the PLFAs important in separating the samples by time after re-wetting in the surface and deep layers, those PLFAs with scores higher than 0.5 units for the RDA axis constrained to time in either the surface or deep layer are listed in Table 7. All of these PLFAs had higher scores in the deep than surface layer, indicating a higher correlation between the

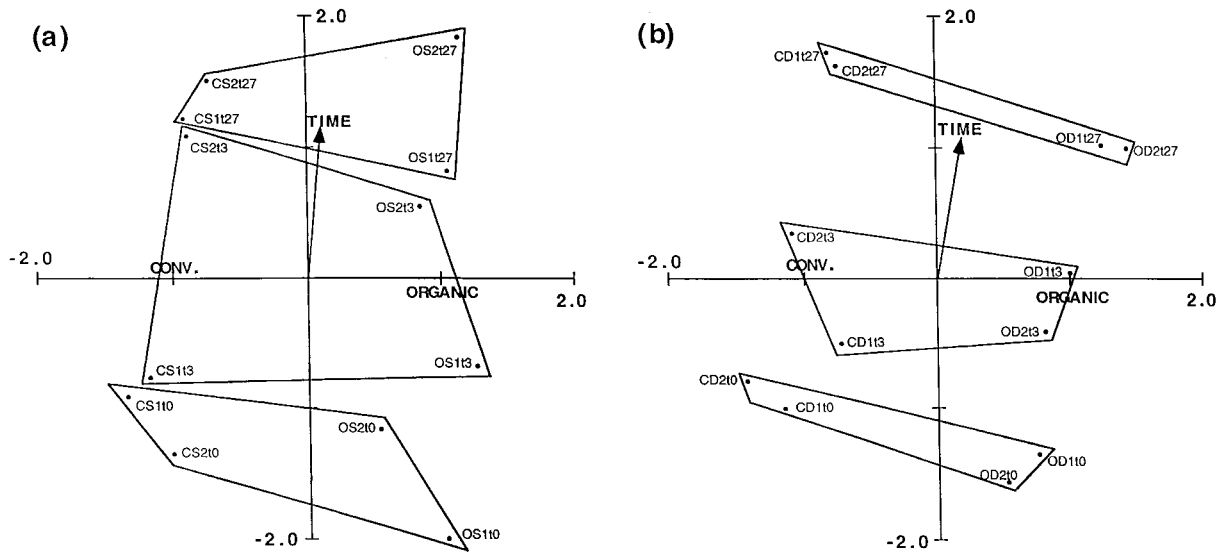


Fig. 6. Ordination of the soil samples for RDAs carried out on surface (a) or deep (b) soils alone. The first (horizontal) axis is constrained to organic or conventional and the second to time. The horizontal axes in both (a) and (b) accounted for 49% of the variation, and the second axis accounted for 10% of the variation in (a) and for 19% in (b).

Table 7

PLFA scores which were greater than 0.5 on the RDA axis constrained to time from RDAs carried out on the surface or deep layers separately

PLFA	Surface layer (0–3 cm)	Deep layer (3–15 cm)
i15:0	0.577	0.876
16:1 $\omega$ 7c	0.610	0.717
iso17:1 $\omega$ unknown	0.712	0.911
Sum B	-0.518	-0.564
18:1 $\omega$ 9c	-0.438	-0.666
18:0	-0.511	-0.576
cyclo19:0	-0.500	-0.788
cyclo17:pre	-0.258	-0.827
cyclo19:pre	-0.458	-0.509

PLFAs and time in the deep layer. In addition, three PLFAs or ratios, 18:1 $\omega$ 9c, cyclo17:pre, and cyclo19:pre, had scores higher than 0.5 in the deep but not the surface layer.

The three PLFA ratios changed with time after soil re-wetting, and the changes were generally greater in the deep than surface layer (Fig. 7). Cyclo19:pre was nearly twice as high in the deep as surface layer in air-dry soil, and this ratio decreased more rapidly following re-wetting in the deep than surface layer. Cyclo17:pre showed a similar, but less dramatic, pattern. The ratio of monounsaturated to saturated fatty acids was higher in the organic than conventional soil, and it increased slightly over time after re-wetting in all the soils.

The relationships of PLFA patterns to MBC and DOC were tested using RDA. Both were significantly related to PLFA composition of the samples ( $P = 0.008$ ), and axes constrained to MBC or DOC each explained approximately half as much of the variation in PLFA data as did farming system or soil layer (data not shown).

Total nmoles of PLFA showed a linear relationship with MBC in moist soils (3 and 27 h after re-wetting); however, the air-dry soils did not fit this relationship (Fig. 8).

## 4. Discussion

### 4.1. Respiration kinetics following re-wetting of air-dry soils

The turnover rates of organic matter measured in our study were at least an order of magnitude higher than measurements from longer incubations of 13–32 weeks reported in other studies (Paustian and Bonde, 1987; MacDonald et al., 1995; Dou et al., 1996; Zogg et al., 1997). Therefore, it is likely that the respiration measured in this experiment was a very short-term re-

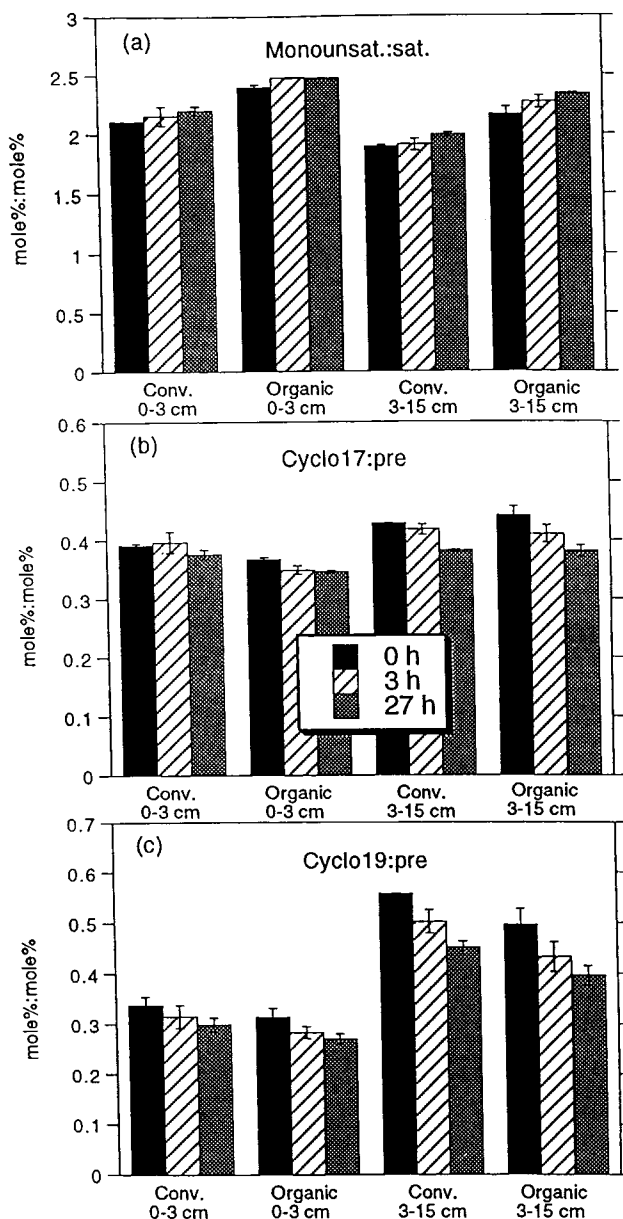


Fig. 7. Ratios of PLFAs, (a) monounsatur.:sat., (b) cyclo17:pre and (c) cyclo19:pre. Error bars are  $\pm$  one standard error ( $n = 2$ ).

sponse to air-drying and re-wetting. Based on the rate constants, the rapidly and slowly utilized C pools had half-lives of 1–2, and 30–75 h, respectively.

Carbon mineralized from the rapidly utilized pool,  $R$ , was significantly correlated with DOC in air-dry soils, even though its size was much less than the changes in DOC or MBC from air-dry to re-wet soils. This significant relationship suggests that part of the increase in DOC due to air drying was composed of very labile compounds released by soil drying and re-wetting.

Decomposition rates are controlled by the population of decomposers present (Simkins and Alexander, 1984), and so the positive correlations between the rate

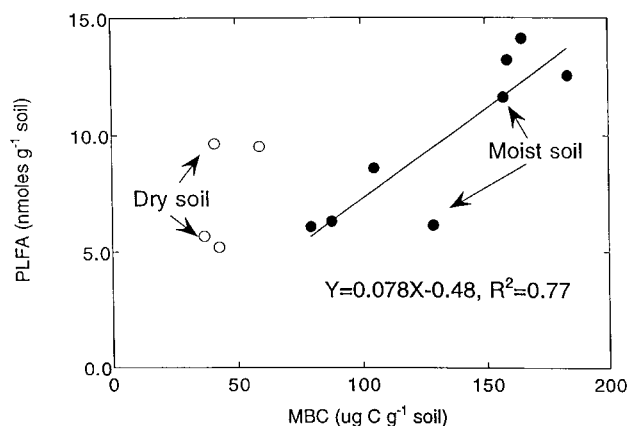


Fig. 8. Relationship between microbial biomass C measured by fumigation extraction and total nmoles of PLFAs extracted from the same samples. Open circles are air-dry samples, and closed circles are moist samples.

constants for the slowly and rapidly utilized C pools,  $k_s$  and  $k_r$ , and MBC in moist soil were not surprising. Microbial biomass C in dry soils and the rate constants were not correlated, perhaps because a large part of the microbial community which survives soil drying does not respond to soil re-wetting. A large proportion of bacteria in soil are likely to be in a 'starved' condition due to low C availability, and most bacteria are more resistant to stress when in a starved, non-growing condition, than when actively growing (Bakken, 1998).

#### 4.2. Microbial response to soil air-drying and re-wetting in farming system soils

Microbial biomass contents were higher in those farming systems receiving higher amounts of organic inputs as had been found in the SAFS project (Gunapala and Scow, 1998; Bossio et al., 1998). Differences in C availability to microorganisms in the three farming systems were also indicated by higher DOC contents, higher absolute increases in MBC following re-wetting of air-dry soil, and higher mineralizable C with increasing organic inputs.

Part of the increase in MBC after soil re-wetting observed in our study may have been due to erroneously low MBC measured on the dry soils (Sparling and West, 1989). We believe that at least some of the increase was a real effect as it coincided with rapid changes in soil DOC contents and respiration, as similar results have been found by researchers using alternative methods to measure MBC (Kieft et al., 1987; West et al., 1992; Van Gestel et al., 1993), and as the chemical composition of the organic C released by air-drying or by fumigation is similar (Christ and David, 1994).

PLFA composition clearly separated the organic

and conventional soils and the surface and deeper layers. The differences between systems and layers were much greater than the changes that followed, which was likely due to several reasons. (1) A large proportion of the microbial community is likely to be inactive (Bakken, 1998), and therefore will not respond to soil wet/dry cycles. (2) Certain changes in fatty acids such as chain lengthening, or addition of methyl branches, require synthesis of new fatty acids. This synthesis takes a longer time and greater resources than does modification of existing fatty acids (Harwood and Russell, 1984), and thus a longer period than 27 h may be necessary to observe shifts in these fatty acids. (3) Farming system differences had been in place for 8 y, and differences in the severity of wet/dry cycles had occurred for 3 months since the soil was tilled in April. The cumulative changes in microbial community composition due to these long term differences were likely to be greater than those due to one wet/dry cycle.

The ratio of monunsat:sat. fatty acids has been tied to nutrient availability. In pure culture studies this ratio decreased in Gram-negative bacteria subjected to starvation conditions (Kieft et al., 1994, 1997; Guckert et al., 1986). In our study the ratio of monunsat:sat. PLFAs increased with increasing organic inputs to the soils (conventional to organic), as was observed by Bossio et al. (1998) for the SAFS soils in 1995. Similar results have been found with increasing straw inputs in a rice farming system (Bossio and Scow, 1998), and the ratio was higher in grassland or wheat soils than under potato cultivation or fallow (Zelles et al., 1992).

In the conventional soil, the fatty acids 10Me16:0, 10Me17:0 and 10Me18:0 were more abundant than in the organic soil, similar to the results of Bossio et al. (1998). The latter two fatty acids are common in actinomycetes (Kroppenstedt, 1985).

The fatty acids 20:2 $\omega$ 6,9c and 20:4 $\omega$ 6,9,12,15c have been proposed as biomarkers for protozoa (White et al., 1996). The fatty acid 20:2 $\omega$ 6,9c was enriched in both the organic and deeper soil layers, and 20:4 $\omega$ 6,9,12,15c was detected in only two of 12 conventional soil samples, but in all 12 organic soil samples. Protozoa graze on bacteria and so the larger MB in the organic than conventional soil may have supported a larger community of protozoa in the former. Because protozoa are aquatic organisms and require moist soil conditions for activity (Kuikman et al., 1991), it is not surprising that they would be more abundant in the deeper than surface layer. The abundance of these fatty acids did not change with time after re-wetting, perhaps because protozoa had not yet responded to bacterial growth. Clarholm (1989) found that growth of amoebae lagged 24 to 48 h behind an increase in bacterial biomass.

Changes in MB and microbial processes on a per

unit biomass basis were similar among the farming systems. The proportional increase in MBC from air-dry to re-wet soils was equivalent in all three soils. The rate constants for the rapidly and slowly utilized C pools,  $k_r$  and  $k_s$ , were positively related to MBC in moist soils, but this relationship did not differ among farming system soils. Only the ratio of respiration to biomass was higher in the organic than low input and conventional soils. An increased ratio of respiration to biomass as observed in the organic compared to conventional soil has been interpreted to reflect stress to the microbial community (Wardle and Ghani, 1995). This interpretation was inconsistent with the PLFA results, however. The ratios of cyclopropyl fatty acids to their precursors (indicators of stress) (Knivett and Cullen, 1965; Guckert et al., 1986; Kieft et al., 1994, 1997), were not elevated in the organic relative to conventional soil. The higher ratio of monounsaturat: saturat. fatty acids in the organic soil suggested that a more likely explanation for the higher ratios of respiration to MBC was increased C availability in the organic soil.

#### 4.3. Microbial response to soil air-drying and re-wetting by soil layer

The microbial communities in the two soil layers differed in their response to soil re-wetting. Higher relative and absolute increases in MBC occurred in the surface than deeper layer. Recovery of MBC to a higher content in moist surface soil may indicate higher C availability in the surface than deeper layer (indicated also by higher DOC levels). Greater C availability may have resulted from there being less time overall during which C could be metabolized in the surface than deeper soil.

The rate constant  $k_s$  was higher in the surface than deep layer for a given amount of MBC. This difference could reflect adaptation to fluctuating moisture conditions in surface soils. Because of the short periods with moist soil conditions during each irrigation cycle, organisms in the surface layer may have been selected for their ability to rapidly utilize available C following soil re-wetting.

Evidence for increased substrate availability and a reduced stress response in the surface relative to deeper layer was suggested by the PLFA analysis. The ratios of monounsaturat: saturat. fatty acids, were higher in the surface relative to deeper layer in our study, and the ratio of monounsaturat: saturat. fatty acids increased in all soils following re-wetting of air-dry soils, possibly due to increased accessibility of substrates in moist relative to dry soil. Bacteria rely on water films in soil for diffusion of nutrients to them and for their ability to move to locations with available substrates.

Increases in the ratio of cyclopropyl fatty acids to their precursors, also observed changing in our study,

appear to be indicators of stress in bacteria. These ratios increased under a variety of stress conditions in pure culture studies of Gram-negative bacteria including oxygen depletion, decrease in pH, high temperature and low nutrient availability (Knivett and Cullen, 1965; Guckert et al., 1986; Kieft et al., 1994, 1997). Cyclopropyl formation also occurred mainly during late logarithmic and stationary growth phases of three Gram-negative bacteria (Law et al., 1963). In our study the ratios cyclo17:pre and cyclo19:pre were initially higher and decreased more following re-wetting in the deep than surface layer, suggesting greater stress due to air drying in the deep layer and a more substantial recovery from stress.

In our study, shifts in PLFA composition following soil re-wetting may have been due both to degradation of fatty acids from organisms killed by soil drying, and to growth or physiological adjustment of living organisms following soil re-wetting. Phosphate groups in PLFAs are rapidly removed by phospholipases following cell death in moist soils and sediments (Vestal and White, 1989; White et al., 1996), and the resulting nonpolar lipid diglycerides are not extractable by the methods we used in our study. However, in dry soil, phospholipase activity may be reduced. A similar problem has been suggested when measuring MBC by the chloroform fumigation extraction method. Sparling and West (1989) have suggested that chloroform fumigation of dry soils without re-moistening leads to lower measured MBC contents because enzymes to solubilize MBC are inactive in dry soil. The combination of reduced PLFA degradation and reduced MBC solubilization may explain the discrepancy we found in the relationship between nmoles of PLFA and MBC in air-dry soils. Between 3 and 27 h after re-wetting, the relationship between MBC and total PLFAs appeared constant, suggesting that the methodological difficulties for measuring MBC and PLFA in dry soil had been alleviated in these samples. Whether the shift between air-dry soil (0 h) and 3 h after re-wetting was due to degradation of dead microbial cells, or to changes in live cells, the trends in stress indicator PLFA ratios suggested reduced stress 3 h after air-dry soils were re-wetted, and these trends continued from 3 to 27 h after re-wetting.

The greater abundance of iso- and anteiso-PLFAs in the deep than surface layer and of monounsaturated fatty acids in the surface than deep layer may have been due to the abundance of microorganisms containing those PLFAs. For example, Gram-positive bacteria have higher proportions of odd-numbered branched-chain fatty acids, and Gram-negative bacteria have higher amounts of cyclopropyl and even-numbered, saturated fatty acids (Harwood and Russell, 1984).

#### 4.4. Conclusions

The kinetics of respiration following re-wetting of air-dry soils indicated rapid use of C which may have been released and accumulated during soil drying. Respiration kinetics also suggested differences in C availability among farming systems and between soil layers. MBC and indicators of C availability were higher in farming system soils receiving larger organic inputs, and PLFA profiles clearly distinguished microbial communities in the organic and conventional soils. The functional response of all farming system soils to re-wetting of air-dry soil, however, was similar on a per unit biomass basis, and changes in PLFA composition with time after re-wetting were not markedly different between organic and conventional soils. In contrast, differences in microbial processes (per unit biomass) between the surface (0–3 cm) and deep (3–15 cm) layer were large. Microbial community composition differed between the two layers, and there were greater changes in soil PLFAs associated with stress response in the deep than surface layer following soil re-wetting. Therefore, it appears that adaptation to wet/dry cycles by surface microorganisms occurred during the 3-month growing season.

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