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Microbial biomass in agricultural topsoils after 6 years of bare fallow

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Abstract Inherent soil properties have an influence on microbial activity. These effects were measured in a field trial at Weihenstephan with 30 agricultural and 2 vineyard soils from different sites in Bavaria which had been kept under bare fallow for 6 years. The soils represented a wide range of arable soils from a temperate climate. Unaffected by recent differences in climatic conditions or cropping managements, they were used to assess the relationship between microbial biomass C and a broad spectrum of soil physical and chemical properties (clay content 5–63%, pH 4.5–7.5, organic C 0.55–2.93%). Microbial C was measured using the substrate-induced respiration method. In addition, soil catalase activity and the abundance and biomass of earthworms were determined. Among the soil properties, microbial C was most strongly correlated with organic C ($r = 0.86$, $n = 29$). In a comparison of linear regressions between microbial biomass C and organic C for different cropping managements, the slope under bare fallow was lowest, followed by monoculture and crop rotation. The microbial : organic C ratio ranged from 1.1 to 4.3% and was significantly correlated with soil pH ($r = 0.66$). A positive relationship between microbial C and the clay content ($r = 0.66$) was significantly improved when soils with more than 25% clay were excluded ($r = 0.80$). Partial correlation analysis indicated that clay had a direct influence, hardly affected by an intercorrelation with organic C. Catalase activity was highly correlated with microbial C ($r = 0.95$) and, because a rapid and sensitive method of determination is available, was considered suitable for estimating relative amounts of active microbial biomass. A positive relationship between microbial C and the abundance of earthworms indicated interactions between microorganisms and mesofauna.

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Introduction

Soil microorganisms are of great importance for soil ecosystems because they affect plant-available nutrients and soil structural stability (Paul and Clark 1989). Numerous methods that have recently become available have increased interest in soil microbial biomass estimates (Jenkinson 1988). Physiological and biochemical methods are used most frequently, although the various methods have their particular limitations and the significance of microbial biomass values is often undefined (Alef 1993). The $CHCl_3$ fumigation–incubation method (Jenkinson and Powlson 1976) determines the size of the total microbial biomass, while the substrate-induced respiration method (Anderson and Domsch 1978) estimates its active component (Wardle and Parkinson 1991; Hassink 1993). Soil enzyme activities have been considered an indirect measure of soil microbial activity (Beck 1984; Ladd 1985). As a cellbound oxidoreductase, catalase (E.C.1.11.1.6) is a characteristic enzyme for nearly all aerobic and facultative anaerobic microorganisms and its activity is, for the most part, ascribed to metabolically active cells (Beck 1971). Strong correlations between soil catalase activity and microbial biomass estimates have been found by various authors (Frankenberger and Dick 1983; Beck 1984; Gehlen and Schröder 1989).

The size and activity of the microorganic population depend on soil organic matter quantity, quality, and distribution and have been related to soil texture (Amato and Ladd 1992; Kaiser et al. 1992), to soil pH (Gehlen and Schröder 1989), to climatic conditions (Insam et al. 1989), and to different agricultural practices (Beck 1984; Anderson and Domsch 1989). The ratio of microbial biomass C to total organic C has proved a sensitive indicator of changes in soil organic matter due to changing management conditions (Anderson and Domsch 1986, 1989; Sparling 1992).

Earthworms usually improve microbial performance, as reported in many studies (reviewed by Lee 1985). Earthworm gut passage can stimulate microbial activity and possibly increase microbial numbers (Daniel and Anderson 1992). Vice versa, soil microorganisms are a significant food for earthworms. In addition to the mutual and complex relationships between earthworms and microorganisms, co-dependences with soil properties may exist.

The complex interactions between climate, soil, and land use make it difficult to recognize and measure the different effects on microorganisms. The problem in recognizing the effect of a single factor like pH is further aggravated by close correlations among climatic and soil properties. Therefore, the influence of climate and land use was held constant in this study in order to isolate the soil effects. Soils with contrasting properties were selected to cover almost the whole range of arable soils in a temperate climate. Correlations between different soil properties were minimized as far as possible in the selection of soils. This allowed us to measure the effect of individual soil properties on selected biological parameters with minimal bias.

Materials and methods

Soils and experimental design

In the autumn of 1984, topsoil from 30 agricultural sites and 2 vineyards in Bavaria was brought to Weihenstephan and filled to a depth of 20–30 cm on the B horizon of a sandy brown earth in field plots of 8 m × 1 m. The soils were selected to cover a wide range of soil properties under agricultural use. For 6 years they had been kept under bare fallow to reduce differences caused by former agricultural use. Weeds had been controlled by infrequent herbicide applications (atrazine, methylchlorphenoxyacetic acid, glyphosate) and regular tillage with horticultural tools (spade, hoe, rake) to imitate ploughing in autumn and seedbed preparation in spring (Martin 1988).

Soil sampling and storage

In spring 1991, 12 cores (4.5 cm diameter) were taken from each plot, pooled, and sieved (<2 mm). The sampling depth was only 5 cm because aggregate stability close to the soil surface was also determined. Field-moist subsamples were stored frozen (−18 °C) in polyethylene bags for 6 months until the microbial biomass was measured, or stored for 3 days at 4 °C before catalase activity was analyzed. According to Beck (1986), these storage conditions have a minimal effect on microbial C or enzyme activity. Texture, pH, and organic C were determined on air-dried samples.

Texture, pH, and organic C

Particle size distribution was determined by sieving (sand and silt fractions >20 µm) and by the pipette method (silt and clay fractions <20 µm) following dispersion with 25 m*M* $Na_4P_2O_7$ and ultrasonic treatment. The pH was measured in 1:2.5 (vol.:vol.) soil: 10 m*M* $CaCl_2$ suspension with a glass electrode. The organic C was determined by dry combustion using an induction furnace (CSA 302, Leybold-Heraeus, Germany) and, if necessary, was corrected for carbonate C as described by Rabenhorst (1988).

Microbial biomass C

The substrate-induced respiration method (Anderson and Domsch 1978) was used for soil microbial biomass measurement. The frozen soil samples were gently thawed over 3 days at 4 °C, equilibrated to room temperature (22 °C) for at least 24 h, and moistened to 45% water-holding capacity. Fresh soil (50 g) was amended with 200 mg glucose and the CO_2 production rate was measured hourly using an automated infrared gas analyser system (Heinemeyer et al. 1989). The original proportionality factor (40.04 ml $CO_2\,h^{-1}$ 100 g $soil^{-1}$) of Anderson and Domsch (1978) was used to compute microbial C from the CO_2 released. A constant factor implies that the microbial population of the soils investigated has a similar composition (active: dormant, bacterial: fungal ratio) to that of the 12 soils of Anderson and Domsch (1978). This may not be the case (Alef 1993) and is the reason why some authors have proposed other calibration equations (Wardle and Parkinson 1991; Kaiser et al. 1992). Therefore any comparison of the present microbial C values with those of other investigations has to be evaluated critically.

Catalase activity

The catalase activity was determined as described by Beck (1971). Fresh soil (10 g) was suspended in 200-ml Erlenmeyer flasks with 20 ml phosphate buffer (0.2 *M*, pH 6.8) and connected to a manometrical measuring device. A 3% H_2O_2 solution (10 ml) was added and the volume (ml) of O_2 released within 3 min (V_t) was measured. Parallel estimates were carried out with NaN_3 (0.1 *M*) as a catalase-specific inhibitor (V_{inh}) to separate real enzymatic activity from abiotic background activity. Relative catalase activity was calculated as $100\,(V_t - V_{inh})/(V_{Mn}DM)$, where V_{Mn} (ml) is the maximum amount of O_2 which could be decomposed in the H_2O_2 solution using MnO_2 instead of soil and DM is soil dry matter ($g\,g^{-1}$).

Earthworm abundance and biomass

Earthworms were collected by hand-sorting after digging out one soil block (0.34 m^2 to Ap depth) from each plot. Sampling was carried out in autumn and spring, each after a few days of rainfall so that most earthworms were in active stages. The earthworms were weighed after 24 h of storage (darkness, ice-cooled water) to allow their guts to empty. Means of the two sampling dates were used for statistical analysis and both parameters, abundance (m^{-2}) and biomass ($g\,m^{-2}$), were related to soil surface.

All parameters, except those of the earthworms, were measured in duplicate and expressed on an oven-dry soil basis (24 h at 105 °C). Other soil properties, such as clay mineralogy, Fe and Mn oxides, and nutrient status, were also determined, but are not reported because they did not contribute to explanations of microbial properties.

Results and discussion

Soil properties

The 32 soils represented a wide range of soil types (Alfisols, Spodosols, Inceptisols, Mollisols), derived from different parent material (loess, moraine, triassic sediments, gneiss) under different climatic conditions (500–1100 mm rainfall, 6.0–9.0 °C mean annual temperature) and therefore exhibit a broad range of soil properties (Table 1). Clay contents ranged from 5 to 63%, silt from 8 to 80%, sand from 2 to 86%, and pH from 4.5 to

Table 1 Physical, chemical, and (micro-)biological properties of the soils (sorted according to microbial C). Catalase activity is shown in relative units

Soil no.	Clay (%)	Silt (%)	Sand (%)	pH	Organic C (%)	Microbial C (μg C g^{-1} soil)	Ratio microbial to organic C (%)	Catalase activity	Earthworms	
									Number (m^{-2})	Biomass (gm^{-2})
8	8	12	81	4.5	0.62	84	1.35	1.9	19	6.0
15	11	31	58	5.0	0.61	123	2.02	2.9	52	18.5
14	6	8	86	6.0	0.55	127	2.31	2.4	37	10.7
7	10	21	69	5.6	0.79	135	1.71	2.4	28	12.3
31[a]	31	45	24	7.4	0.67	149	2.22	3.2	12	3.4
13	8	10	82	5.7	1.61	175	1.09	4.4	30	8.0
25	5	9	86	5.1	1.59	183	1.15	4.4	33	10.6
1	20	78	2	7.0	0.78	201	2.57	4.0	74	16.9
22	16	33	51	5.0	1.50	215	1.43	5.5	62	12.8
24	21	36	43	6.6	0.95	216	2.27	5.8	36	8.4
5	12	27	61	7.1	0.84	230	2.74	4.8	146	26.8
16	15	37	48	6.3	1.00	233	2.33	4.3	86	21.7
21	22	40	38	5.8	1.16	248	2.14	5.9	77	27.1
12	17	79	4	6.5	0.94	250	2.66	4.9	221	29.3
19	24	33	43	6.0	0.98	254	2.60	5.7	113	25.1
32[a]	38	50	12	7.4	1.04	260	2.50	7.1	12	2.3
23	16	29	55	6.6	1.76	275	1.56	6.5	54	14.0
9	22	64	14	5.6	1.11	277	2.50	7.7	97	17.2
18	25	49	25	5.1	1.64	287	1.75	6.0	68	23.9
11	37	52	12	5.6	1.82	288	1.58	8.5	169	45.1
2	34	64	2	6.6	0.84	291	3.47	5.1	43	6.2
20	25	49	25	6.3	1.26	337	2.67	7.2	64	9.0
4	25	62	13	7.4	0.88	351	3.99	7.5	88	22.6
6	23	60	18	5.7	1.54	359	2.33	9.1	174	39.4
17	21	58	22	6.8	1.37	365	2.67	8.8	92	21.8
10	22	16	63	6.9	1.44	386	2.68	8.5	235	29.4
27	63	33	4	7.4	1.43	407	2.84	12.8	21	4.0
3	24	67	9	7.5	0.98	423	4.32	10.2	110	24.0
28	36	19	45	7.3	1.48	430	2.91	12.3	107	17.4
26	45	38	17	6.9	1.90	436	2.30	13.4	143	18.5
30	36	43	21	7.0	2.90	531	1.83	13.3	274	26.9
29	31	39	30	7.1	2.93	548	1.87	14.0	156	18.6

[a] Vineyard soils (all others agricultural soils)

7.5. Organic C ranged between 0.55 and 1.90%, as typical for agricultural soils. Two moraine soils had almost 3% organic C. Among the soil properties that were significant for further interpretation, clay was positively correlated with pH ($r = 0.56$, $P < 0.001$) and less significantly with organic C ($r = 0.37$, $P < 0.05$), while no correlation was found between organic C and pH ($r = 0.12$, $P > 0.05$).

Microbial C in relation to organic C

The soils showed large differences in microbial C in spite of identical climatic and management conditions over the previous 6 years. The lowest value, 84 μg microbial C g^{-1} soil, was very low for an arable soil, while 284 μg g^{-1} soil as the average and 548 μg g^{-1} soil as the maximum agree with measurements made by other authors using the substrate-induced respiration method (Anderson and Domsch 1989; Gehlen and Schröder 1989; Insam et al. 1989; Kaiser et al. 1992).

As expected, soil organic C showed the strongest relationship to microbial C (Fig. 1 a). Three soils (nos. 13, 22, and 25) were excluded from the regression because they were comparably high in organic C but had relatively low microbial C contents. All three were coarse-textured soils with a low pH, therefore providing relatively poor conditions for soil microorganisms (few microhabitats, large temperature and moisture fluctuations, especially in the upper 5 cm) and possibly having a more resistant type of organic C. In a decomposition experiment Amato and Ladd (1992) found greater amounts of residual organic C (percentage of C input) in acidic soils than in neutral to alkaline soils. A relative enrichment of less decomposable organic material in soils with high organic C (Gehlen and Schröder 1989) could be the reason for the subproportional increase in microbial C with increasing organic C (particularly in the two moraine soils nos. 29 and 30). This supports the findings by Anderson and Domsch (1989) that linearity between microbial and organic C seems to be limited only up to 2.5% organic C.

In the present study a stepwise multiple regression including all 32 soils with pH as second variable accounted for 77% of the variance in microbial C (microbial C = −313 + 136.0 organic C + 66.6 pH; $n = 32$; $R^2 = 0.772$). The pH interaction is demonstrated in Fig. 1 a, where positive deviations from the regression line are

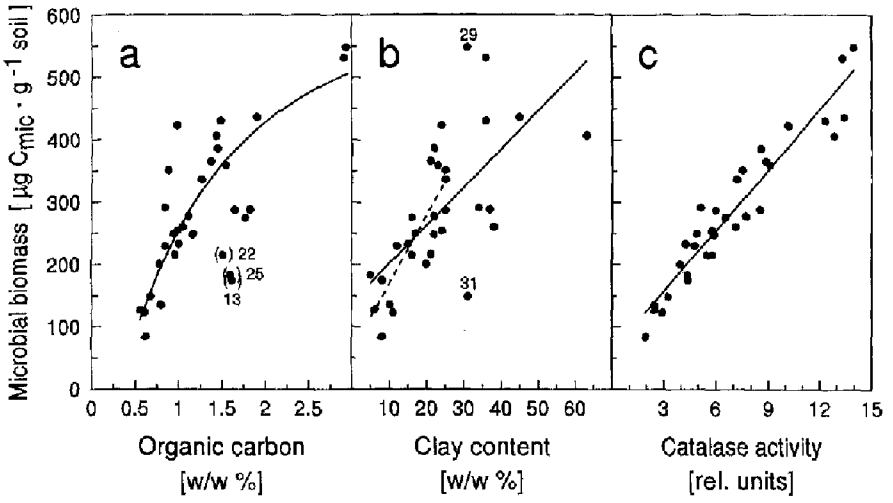

Fig. 1a–c Relationship between microbial biomass C (C_{mic}, assessed by substrate-induced respiration) and organic C (**a**), clay content (**b**), and catalase activity (**c**). Organic carbon: $C_{mic} = 717 \times (0.36^{1/C_{org}})$, $n = 29$, $r^2 = 0.745$, $P < 0.001$; Clay content: $C_{mic} = 140 + 6.1$ clay, $n = 32$, $r^2 = 0.430$, $P < 0.001$ (all soils); $C_{mic} = 61 + 10.9$ clay, $n = 23$, $r^2 = 0.643$, $P < 0.001$ (clay < 25%); Catalase activity: $C_{mic} = 61 + 32$ CAT, $n = 32$, $r^2 = 0.910$, $P < 0.001$ (where CAT is catalase activity in relative units)

caused by alkaline soils and negative deviations by the more acidic soils. Apart from a more general pH influence on microbial reactions, the positive relationship between microbial C and pH for equal levels of organic C again points to differences in organic matter quality.

Comparing 134 different agricultural soils under various long-term cropping systems, Anderson and Domsch (1986, 1989) also found strong linear correlations between microbial and organic C. The regression lines differed in slope, being higher for soils that had been given organic matter amendments (other than crop residues) than for unamended soils and higher for crop rotation than for monoculture systems (Fig. 2, lines 1–3). Anderson and Domsch (1989) assumed that the higher microbial : organic C ratio for green manure treatments is a result of a temporarily higher level of labile organic matter. Without organic matter amendments the more heterogeneous organic residues derived from crop rotation systems compared to the more uniform residues from monoculture could be the reason for a more efficient organic matter use and a therefore higher microbial : organic C ratio. In the present study, under bare fallow, without any kind of organic residues or rhizodeposits, but with decreasing, probably more stable organic C sources, the efficiency of microbial C metabolism should be even lower, a conclusion supported by the lowest slope of the four regressions (Fig. 2, line 4).

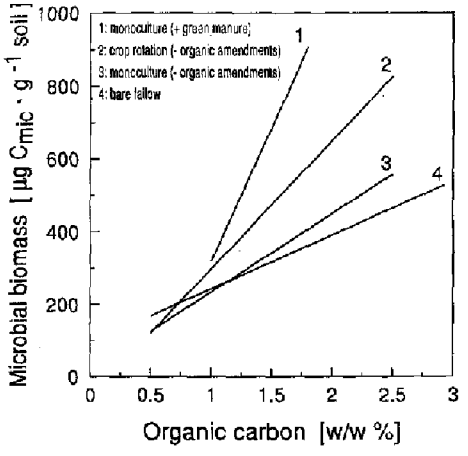

Fig. 2 Regressions between microbial biomass C (C_{mic}) and organic C (C_{org}) under bare fallow and other cropping systems. Equations: *1* $C_{mic} = -415 + 734\, C_{org}$, $n = 13$, $r = 0.89$ (Anderson and Domsch 1989); *2* $C_{mic} = -55 + 352\, C_{org}$, $n = 26$, $r = 0.98$ (Anderson and Domsch 1986); *3* $C_{mic} = 18 + 216\, C_{org}$, $n = 26$, $r = 0.96$ (Anderson and Domsch 1986); *4* $C_{mic} = 95 + 148\, C_{org}$, $n = 32$, $r = 0.73$ (present study)

The average microbial : organic C ratio in the bare fallow plots (2.3%) was similar to ratios obtained under monoculture without organic amendments (Anderson and Domsch 1986, 1989). For soils under steady-state conditions Anderson and Domsch (1986) found constant microbial : organic C ratios, while Insam et al. (1989), working with soils from contrasting climatic regions, showed the superimposing effects of the macroclimate (as calculated by a precipitation/evaporation quotient) and presented an equilibrium function between microbial and organic C. Although the bare fallow plots had been under the same climatic conditions for the last 6 years, they came from sites with different macroclimates. Together with the pronounced differences in soil physical and chemical properties, this may explain the wide range of microbial : organic C ratios (1.09–4.32%). The strongest correlation was found between the microbial : organic C ratio and the soil pH ($r = 0.66$, $n = 32$, $P < 0.001$). A similar positive relationship has also been reported by other studies. Anderson and Domsch (1993) suggested that an increasing soil pH provides more favorable environmental conditions for microbial communities and thus could explain higher microbial : organic C ratios. Further, a greater accumulation of recalcitrant organic material in acidic soils could result in a lower retention of organic C in microbial biomass (Amato and Ladd 1992). Gehlen and Schröder (1989) assumed that the overall impact of pH on soil microbial parameters was suppressed in most investigations by the dominant influence of organic C when using soils with a wide range of organic C.

Microbial C in relation to soil texture

In the present soils microbial C was negatively correlated with the sand content ($r = -0.52$, $P < 0.01$) and positively with the clay content ($r = 0.66$, $P < 0.001$, Fig. 1b). Because of a negative correlation between sand and clay ($r = -0.71$, $P < 0.001$) partial correlation coefficients were computed. Controlling alternately for both texture variables, a more indirect effect of sand and a more direct effect of clay content on microbial C was indicated ($r_{C,\,clay \times sand} = 0.48$, $P < 0.01$, and $r_{C,\,sand \times clay} = -0.11$, $P > 0.05$). The beneficial effects of clay on the performance of microorganisms have been reviewed extensively (Martin and Haider 1986; Stotzky 1986; England et al. 1993; Hassink 1993). Mechanisms proposed to explain these effects included (1) a higher proportion of refuge microsites, providing a better protection against predation, (2) increased stability and better survival of microorganisms under stress conditions such as drying, (3) respiratory stimulation, and (4) better nutrient availability. Up to a clay content of 25%, the microbial C in the bare fallow soils of the present study was correlated closely with clay ($r = 0.80$, $n = 23$), while soils higher in clay deviated more from the regression line and reduced the overall correlation. For example, the microbial biomass in one of the vineyard soils (no. 31) and one of the moraine soils (no. 29), both having a clay content of 31%, varied by a factor of 4. This was probably caused by a similar difference in organic C (0.67 vs. 2.93%) and by the rather unfavorable, blocky soil structure of the vineyard soil.

Higher clay contents could be accompanied by higher amounts of soil organic matter due to a reduced decomposition rate (Martin and Haider 1986) which in turn could affect the level of microbial biomass. However, in the present soils this could not be confirmed. Partial correlation coefficients hardly differed from simple correlations when controlling for clay content or organic C ($r_{C_{mic}, C_{org} \times clay} = 0.69$ vs. $r_{C_{mic}, C_{org}} = 0.73$ or $r_{C_{mic}, clay \times C_{org}} = 0.61$ vs. $r_{C_{mic}, clay} = 0.66$, for all $P < 0.001$, where C_{mic} is microbial C and C_{org} is organic C), because there was only a weak correlation between organic C and the clay content. In contrast, a positive correlation between microbial C and pH ($r = 0.57$, $P < 0.001$) was biased by the intercorrelated clay because the partial correlation showed that the effect of clay content on microbial C was more direct than that of soil pH ($r_{C_{mic}, clay \times pH} = 0.49$, $P < 0.01$ vs. $r_{C_{mic}, pH \times clay} = 0.33$, $P > 0.05$).

Microbial C in relation to catalase activity

Catalase activity was closely related to microbial C and had similar relationships with soil properties ($r_{CAT,\,C_{org}} = 0.74$; $P < 0.001$; $r_{CAT,\,clay} = 0.74$, $P < 0.001$; $r_{CAT,\,sand} = -0.49$, $P < 0.01$; $r_{CAT,\,pH} = 0.52$, $P < 0.01$, where CAT is catalase activity). As a sensitive indicator, among others, catalase activity was believed "to best predict the relative activity and mass of the microbial population" (Frankenberger and Dick 1983). Our results support this finding. In the 32 bare fallow soils a sevenfold range of microbial C coincided with a sevenfold range of catalase activity and a linear regression accounted for 91% of the variance (Fig. 1c). Other studies, by including forest or grassland soils, established this relationship for a wide range of organic C contents and for different management conditions (Beck 1984), while the present results demonstrate the validity for soils under a uniform management but with a broad spectrum of soil properties. As a simple, rapid, and particularly sensitive method, determination of catalase activity seems to be well suited for estimating relative amounts of active microbial biomass.

Microbial C in relation to earthworms

The number of earthworms was highly significantly correlated with microbial C (Fig. 3). To compare microbial C and earthworms, both were expressed per unit area of soil surface (corrected for differences in depth of Ap, stone content, and bulk density). The positive relationship between earthworms and microorganisms might be linked to their correlation with organic C. The correlation coefficient between microbial C and the number of earthworms decreased when controlling for organic C, but was still significant ($r_{C_{mic},\,number\ of\ worms \times C_{org}} = 0.41$, $P < 0.05$) and indicates the presence of a positive relationship between earthworms and microbial C.

Among the soils used in the present study two were quite deviant (Fig. 3). Soil no. 27 was the highest in clay (63%). While soil microorganisms obviously found sufficient conditions for life, earthworms avoid this soil because of a periodical O_2 deficit and a high soil strength which limits earthworm burrowing activity (Kretzschmar 1991). The second deviant soil (no. 12) was the highest in silt (79%) and had a distinctively high earthworm abundance in relation to microbial C. This soil seems to be well suited for earthworms because of its high water-holding capacity, low burrowing resistance,

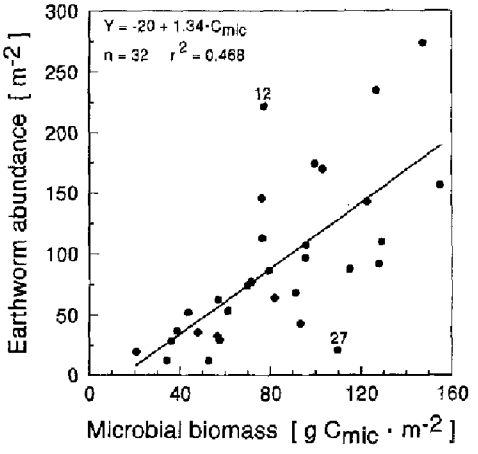

Fig. 3 Relationship between earthworm abundance and microbial biomass C (C_{mic}, assessed by substrate-induced respiration)

but high stability of burrows and a low risk of cuticle hurting. The soil appears to provide particularly good reproductive conditions, because 91% of the sampled earthworms were juvenile. When discarding these two soils the regression accounted for 63% of the variance.

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