

# Temperature and Moisture Effects on Microbial Biomass and Soil Organic Matter Mineralization

Denis Curtin\*

Michael H. Beare

Guillermo Hernandez-Ramirez

New Zealand Institute for Plant & Food  
Research Limited  
Private Bag 4704  
Christchurch, New Zealand

Concern over climate change has stimulated interest in the temperature and moisture dependence of soil organic matter decomposition. In particular, there has been intense debate in relation to the factors that determine the temperature dependence of C mineralization. We examined temperature and moisture responses of C and N mineralization in an 85-d laboratory incubation (factorial combination of four temperatures [5, 12, 18, 25°C] and five moisture treatments [matric potential from -5 to -1200 kPa]) using three agriculturally important New Zealand soils (soils with a history of pasture, arable, or vegetable cropping). Mineralization was linearly related to gravimetric moisture content, except in the high-C pasture soil where O<sub>2</sub> supply apparently limited mineralization at high (25°C) temperature-moisture combinations. Temperature responses were adequately described by a Q<sub>10</sub> function (Q<sub>10</sub> values for C mineralization ranged 1.9–2.8). The pool of mineralizable C, estimated using a first-order kinetic model, increased as temperature and moisture increased, whereas the rate constant did not show a consistent trend with either temperature or moisture. Part of the C mineralized during the incubation was from the microbial biomass (post-incubation biomass C decreased by an average of 0.22–0.31 mg kg<sup>-1</sup> for each 1 mg kg<sup>-1</sup> CO<sub>2</sub>-C evolved). Microbial biomass C (MBC) was particularly sensitive to temperature (post-incubation biomass C decreased 18–35% between 5–25°C). The decline in MBC between 5 and 12°C represented an average of 40% of the C mineralization increase in that temperature interval. Between 18 and 25°C, the decline in MBC was equivalent to only 20% (on average) of the C mineralized in that temperature interval. High Q<sub>10</sub> values reported in laboratory incubations at low temperature may be partly due to mineralization of microbial C.

**Abbreviations:** DOM, dissolved organic matter; MBC, microbial biomass carbon; SOM, soil organic matter.

Soil organic matter (SOM) plays a key role in the global C and N cycles. Soils contain more than twice as much C as the atmosphere and three times the amount stored in living plants (Schlesinger, 1997). Key factors determining the levels of SOM are inputs of plant and animal residues and losses via decomposition. Decomposition (mineralization) of SOM is microbially mediated, with the rate of mineralization being strongly dependent on temperature and soil moisture. Stanford and his coworkers (Stanford and Smith, 1972; Stanford and Epstein, 1974; Stanford et al., 1973) advanced the concept of a potentially mineralizable pool of organic matter and a related mineralization rate constant to characterize the temporal pattern of N mineralization. There is wide acceptance that each soil has a fixed quantity of mineralizable N (and C), which can be experimentally determined using incubation assays (Campbell et al., 1993; Motavalli et al., 1994). In theory, potentially mineralizable C is the amount of C that will mineralize in infinite time. In practice, it is estimated by incubating soil under optimal conditions

Soil Sci. Soc. Am. J. 76:2055–2067

doi:10.2136/sssaj2012.0011

Received 6 Jan 2012.

\*Corresponding author (denis.curtin@plantandfood.co.nz).

© Soil Science Society of America, 5585 Guilford Rd., Madison WI 53711 USA

All rights reserved. No part of this periodical may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopying, recording, or any information storage and retrieval system, without permission in writing from the publisher. Permission for printing and for reprinting the material contained herein has been obtained by the publisher.

and measuring the C mineralized (i.e., CO<sub>2</sub>-C produced) as a function of time. Potentially mineralizable C is typically calculated using a first-order kinetic model:

$$C_{\min} = C_o [1 - \exp(-kt)] \quad [1]$$

where  $C_{\min}$  is the cumulative C mineralized in time  $t$ ,  $C_o$  is the potentially mineralizable C, and  $k$  is the mineralization rate constant. The value of  $k$  is considered to be temperature and moisture dependent (Campbell et al., 1993). At 35°C, Stanford and Smith (1972) estimated the value of  $k$  for N mineralization to be  $0.054 \pm 0.009 \text{ wk}^{-1}$  at a matric potential of  $-80 \text{ kPa}$ .

Since its introduction, this mineralization model has been widely used by soil scientists (Benedetti and Sebastiani, 1996; Campbell et al., 1984; Curtin et al., 1998; Deans et al., 1986); however, recent studies, including work undertaken to understand the temperature dependence of SOM decomposition, have raised questions concerning the validity of the model. For example, Zak et al. (1999) concluded from studies with forest soils that the concept of a fixed pool of mineralizable organic matter and a temperature-dependent rate constant is not valid. Their results suggested that the rate constant did not increase systematically with temperature (or moisture content); however, the pool size increased between 5 and 25°C.

When microorganisms are presented with a substrate, they normally multiply rapidly until the substrate is nearly exhausted and then their numbers decline (Joergensen et al., 1990); thus, mineralization would be expected to exhibit an initial rapid phase followed by a much slower phase as the substrate is depleted. Laboratory incubation data invariably show, however, that soil C and N mineralization proceeds at a steady rate, which decreases only slowly with time (Benedetti and Sebastiani, 1996). Joergensen et al. (1990) concluded that organic matter is made available (released to microorganisms) gradually by a temperature-sensitive process. They further concluded that this regulatory process is unlikely to be biological but did not speculate on what might prevent the soil microbial biomass from multiplying and rapidly utilizing the pool of potentially mineralizable organic matter.

Organic substrates must be in dissolved form to be transported to microorganisms and transferred across microbial membranes (Marschner and Kalbitz, 2003). Thus, factors that affect the solubility and transport of organic matter may influence the rate of mineralization. Dissolved organic matter (DOM) is central to the recently proposed "regulatory gate hypothesis," which holds that soil microorganisms can use only the "exceedingly small trickle" of DOM delivered to them via diffusion in the soil solution (Kemmitt et al., 2008). This hypothesis was offered to explain the observation that the rate of organic matter mineralization is independent of the size, composition, and activity of the microbial biomass. If the hypothesis is correct, it follows that mineralization can be increased by opening the "regulatory gate" to allow more organic matter to pass into solution so that it can diffuse to the microbial cells. Kemmitt et al. (2008) considered that the flux of DOM is abiotically regulated but the mechanisms

were not identified. Increasing the temperature can increase organic matter solubility (Chantigny et al., 2010) and affect the activity of extracellular enzymes that convert large DOM molecules to forms that can be assimilated by the microbial biomass (Allison et al., 2010). Soil moisture content may influence mineralization through effects on the amount of substrate delivered to the microbial biomass by diffusion.

Concern over the impact of increasing global temperature and climate changes on soil C stocks has stimulated interest in the mechanisms whereby temperature and moisture affect C (and N) mineralization. In this context, it is important to reevaluate the concepts embodied in the classical Stanford and Smith model (i.e., the role of temperature and moisture implicit in the rate constant) in light of emerging evidence that temperature and moisture effects on mineralization are at least partly related to their impact on substrate availability (an indirect effect). To do this, we determined first-order rate constants and substrate pool size across a wide range of temperatures and moisture contents in soils with contrasting management histories. The overall objective was to assess whether the data support the conventional assumption of a fixed pool of substrate and a temperature- and moisture-dependent rate constant or, if not, suggest an alternative model. Although the size of the microbial biomass may be a sensitive indicator of the balance between substrate supply and demand (Allison et al., 2010; Joergensen et al., 1990) information on the response of the soil biomass to temperature and moisture is sparse. Therefore, we also investigated the effects of temperature and moisture on the microbial biomass as a key determinant of the mineralization response.

## MATERIALS AND METHODS

Three agriculturally important soils from Canterbury, New Zealand, were sampled (0–15 cm): (i) a silt-loam (Typic Dystruptept) under long-term ryegrass (*Lolium perenne* L.)–white clover (*Trifolium repens* L.) pasture (sampled at Methven, 43°38' S, 171°38' E); (ii) a clay loam (Mollis Endoaquept) under intensive arable cropping (e.g., wheat [*Triticum aestivum* L.], barley [*Hordeum vulgare* L.], pea [*Pisum sativum* L.]) (sampled at Doylstow, 43°44' S, 172°21' E); and (iii) a sandy loam (Typic Haplustept) under long-term vegetable (e.g., potato [*Solanum tuberosum* L.], onion [*Allium cepa* L.]) production (sampled at Lincoln, 43°38' S, 172°29' E). These soils are subsequently referred to as the *pasture*, *arable*, and *vegetable* soils (Table 1). The pasture and arable soils were sampled on commercial farms and the vegetable soil on the research farm of the New Zealand Institute for Plant & Food Research Limited.

After collection, the soils were sieved (<6 mm) and slowly dried on a glasshouse bench with frequent turning to reduce the moisture content to below the lowest level to be used in the incubation experiment (we avoided complete air drying of the soil to minimize the flush of mineralization that occurs after wetting dry soil [Cabrera, 1993]). Moisture contents measured after glasshouse drying were 11, 16, and 8% for the pasture, ar-

able, and vegetable soils, respectively; the corresponding matric potentials were estimated to be  $-2000$ ,  $-3300$ , and  $-1300$  kPa.

Subsamples of soil (200 g of oven-dry equivalent) were weighed into 1-L incubation jars (fitted with air-tight lids), and the moisture content was adjusted to the required values using a mist of distilled water. There were five moisture treatments; the treatment moisture contents and the corresponding matric potentials are shown in Table 2. The highest matric potential was  $-5$  kPa, which is commonly considered the optimum for mineralization (Campbell et al., 1993), and the lowest potential ranged from  $-700$  to  $-1200$  kPa, depending on the soil. The relationship between gravimetric moisture content and matric potential was established for each soil by measuring water retention at  $-5$ ,  $-30$ ,  $-100$ ,  $-900$ , and  $-1500$  kPa using tension tables ( $-5$  kPa) and pressure plates ( $-30$  to  $-1500$  kPa). After moisture adjustment, the jars were transferred to incubators set at  $5$ ,  $12$ ,  $18$ , or  $25^{\circ}\text{C}$ . The experimental treatments covered the range of temperature and moisture potential experienced in our region. For example, the long-term mean soil temperature (measured at 10 cm) at the Lincoln site ranges from  $4^{\circ}\text{C}$  in July to  $18^{\circ}\text{C}$  in January, although the daily average topsoil temperature can range from  $0$  to  $>25^{\circ}\text{C}$ . During winter, soils wet up to field capacity and, under dryland cropping, the water potential can fall below  $-1500$  kPa in late summer.

Each temperature-moisture combination was replicated three times. The soils were allowed to equilibrate under the different temperature and moisture conditions for 14 d before commencing mineralization measurements. Carbon mineralization

**Table 1. Selected properties of experimental soils.**

Property†	Pasture soil	Arable soil	Vegetable soil
Total C, g kg <sup>-1</sup>	40.8	32.5	21.2
Total N, g kg <sup>-1</sup>	3.8	3.2	1.7
Mineralizable N, mg kg <sup>-1</sup>	135	61	40
pH	5.4	5.7	5.6
Sand, $>50\text{ }\mu\text{m}$ , %	18	5	42
Silt, $2\text{--}50\text{ }\mu\text{m}$ , %	69	63	43
Clay, $<2\text{ }\mu\text{m}$ , %	12	32	15
Microbial biomass C, mg kg <sup>-1</sup>	749	883	286
Microbial biomass N, mg kg <sup>-1</sup>	78	82	33

† Total C and N were determined using a LECO C/N analyzer; mineralizable N was determined by the method of Keeney and Bremner (1966); soil pH was measured in a 1:2.5 soil/water suspension using a glass electrode; texture was measured by standard sieving and sedimentation methods.

was measured by trapping evolved  $\text{CO}_2$  in beakers of NaOH (in the case of the  $5$  and  $12^{\circ}\text{C}$  treatments, the beakers contained  $10\text{ mL}$  of  $0.5\text{ mol L}^{-1}$  NaOH; for the other temperatures, we used  $10\text{ mL}$  of  $1\text{ mol L}^{-1}$  NaOH). Trapped  $\text{CO}_2$  was determined by back-titration with a standard solution of HCl. Measurements of  $\text{CO}_2$  production were made on Days 7, 14, 21, 28, 35, 49, 56, 70, and 85 in the case of the  $5$ ,  $12$ , and  $18^{\circ}\text{C}$  treatments, with additional measurements on Days 42 and 63 for the  $25^{\circ}\text{C}$  treatment. Soil moisture was monitored by periodically weighing the jars and adding distilled water to compensate for evaporative losses (losses were minimal). Incubator temperatures were monitored throughout the experiment. Mean recorded temperatures

**Table 2. Effect of temperature and gravimetric moisture content on the total (cumulative) C and N mineralized in an 85-d incubation for pasture, arable, and vegetable soils.**

Moisture content %	C mineralized				N mineralized			
	5°C	12°C	18°C	25°C	5°C	12°C	18°C	25°C
<u>Pasture soil</u>								
16 (-720)†	153	273	588	944	20	33	67	123
22 (-220)	207	408	806	1588	27	37	88	170
28 (-65)	269	507	811	1873	35	50	83	195
34 (-20)	300	564	951	1414	49	68	111	174
41 (-5)	346	642	1018	1266	52	89	129	162
LSD 0.05		35				4		
<u>Arable soil</u>								
20 (-1180)	116	169	279	555	8	13	20	39
25 (-320)	136	248	357	715	9	14	22	40
30 (-90)	177	305	450	827	10	16	26	60
35 (-25)	222	405	638	1102	14	22	41	86
41 (-5)	280	493	837	1165	19	33	71	111
LSD 0.05		30				2		
<u>Vegetable soil</u>								
10 (-700)	64	130	217	351	3	7	22	31
14 (-200)	95	163	279	502	7	12	28	47
18 (-60)	120	212	387	559	12	21	42	53
22 (-20)	152	283	444	660	14	25	49	60
26 (-5)	179	320	504	672	18	35	59	67
LSD 0.05		16				2		

† Values in parentheses indicate matric potential (kPa).

(with standard deviations in parentheses) based on observations at 15-min intervals were: 5.2 (0.51), 11.8 (0.37), 17.9 (0.07), and 25.2°C (0.39).

Net N mineralized during the incubation period was determined as the difference between post- and pre-incubation mineral N ( $\text{NH}_4^+$  plus  $\text{NO}_3^-$ -N). Mineral N ( $\text{NO}_3^-$  and  $\text{NH}_4^+$ -N) was extracted in 2 mol L<sup>-1</sup> KCl and determined by standard colorimetric procedures (Keeney and Nelson, 1982) using an autoanalyzer (Astoria-Pacific Rapid Flow Analyzer 300).

Microbial biomass C was determined before and after incubation using the chloroform extraction method (48-h fumigation, 1-h extraction with 0.5 mol L<sup>-1</sup>  $\text{K}_2\text{SO}_4$ ) as described by Horwath and Paul (1994). Carbon in the  $\text{K}_2\text{SO}_4$  extracts was determined using a Shimadzu TOC-5000A Total Organic Carbon Analyzer. Microbial biomass C was estimated assuming an extraction efficiency factor of 0.38 (Vance et al., 1987).

Treatment means were compared by analysis of variance performed separately for each soil using GenStat (GenStat Committee, 2005). Significant differences among treatment means were assessed by least significance difference (LSD) tests. Mineralizable C and the rate constant were calculated using Eq. [1]. Relationships between variables were evaluated using regression analysis and correlations.

We used the van't Hoff equation to describe the temperature dependence of mineralization:

$$y = D \exp(bt) \quad [2]$$

where  $y$  is the amount of C mineralized in 85 d (mg C kg<sup>-1</sup>),  $t$  is temperature (°C),  $D$  is the intercept (mineralization at 0°C), and  $b$  is a constant. The  $Q_{10}$  value, the factor by which mineralization increases for a 10°C increase in temperature, was calculated from

**Table 3. Moisture response of C mineralization at different temperatures estimated from linear regressions between C mineralized in 85 d ( $y$ , mg C kg<sup>-1</sup>) and gravimetric moisture content ( $x$ , % moisture) in pasture, arable, and vegetable soils.**

Soil	Temperature	Regression equation	R <sup>2</sup>	Moisture response
Pasture	5	$y = 7.7x + 38$	0.99	0.031
	12	$y = 14.4x + 74$	0.97	0.057
	18	$y = 16.1x + 379$	0.92	0.065
	25	NLT†		ND‡
Arable	5	$y = 8.1x - 59$	0.99	0.04
	12	$y = 15.5x - 143$	0.99	0.07
	18	$y = 29.6x - 352$	0.96	0.14
	25	$y = 30.7x - 56$	0.96	0.15
Vegetable	5	$y = 7.2x - 8$	0.999	0.05
	12	$y = 12.5x - 2$	0.99	0.08
	18	$y = 18.2x + 40$	0.99	0.11
	25	$y = 20.0x + 189$	0.93	0.12

† NL, nonlinear relation between moisture content and mineralization.

‡ ND, not determined.

$$Q_{10} = \exp(10b) \quad [3]$$

## RESULTS AND DISCUSSION

### Soil Properties

The soils used in this study represented a range of organic matter levels that were a product of their management histories (long-term pastoral, arable, and vegetable cropping) and textural classes. Total SOM decreased in the order pasture > arable > vegetable (Table 1). This trend is mainly a reflection of the amounts of organic matter returned to the soil in plant residues and excreta (most under grazed pastures, least under intensive vegetable cropping) (Haynes and Tregurtha, 1999); however, the low organic matter level in the vegetable soil may be partly due to its high sand content. The pasture soil had substantially more anaerobically mineralizable N, based on the method of Keeney and Bremner (1966), than the other two soils. Microbial biomass did not follow the same trend as total organic matter because the heavy-textured arable soil was higher in MBC than the pasture soil; these soils had 2.6 to 3.1 times as much MBC as the vegetable soil (Table 1). Texture effects on microbial biomass have been observed by Hassink (1994), who showed that the proportions of soil C and N in the biomass were higher in fine- than in coarse-textured soils. Soils were mineralogically similar (dominated by micaceous clays) and had pHs in the narrow range of 5.4 to 5.7.

### Carbon Mineralization

Overall, C mineralization was highest in the pasture soil and least in the vegetable soil (Table 2). Total C mineralized in the 85-d incubation averaged 746, 474, and 315 mg C kg<sup>-1</sup> for the pasture, arable, and vegetable soils, respectively. Analysis of variance of C mineralization data obtained after selected incubation periods (14, 28, and 85 d) showed that, for each soil, cumulative C mineralization was influenced ( $P < 0.001$ ) by temperature and moisture (data for the 85-d incubation shown in Table 2); however, temperature had a relatively larger effect than moisture content for all three soils. There was also a significant ( $P < 0.001$ ) temperature  $\times$  moisture interaction; temperature responses were generally greater at higher moisture content and moisture responses usually increased as temperature increased (Table 3; Fig. 1). Mineralized C was linearly related to gravimetric moisture content except for the pasture soil at the highest incubation temperature (25°C), where it peaked at 28% moisture (matric potential of -65 kPa) and declined substantially at higher moisture contents (Fig. 1). Linear relationships between mineralized C (or N) and soil water content have been reported in several previous studies (Orchard and Cook, 1983; Stanford and Epstein, 1974).

Except in the pasture soil at the highest temperature, small reductions in water potential below -5 kPa (i.e., from -5 to -20 or -25 kPa) resulted in relatively large reductions in C mineralization (Table 2). For example, in the case of the vegetable soil, there was an average decrease in C mineralization (85 d) of 13% when the matric potential decreased from -5 to -20 kPa, suggesting

that mineralization is very sensitive to soil moisture. On the other hand, substantial mineralization occurred at the lowest matric potentials that were imposed in the study. At  $-1200$  kPa (close to the wilting point), C mineralization (85 d) in the arable soil ranged from 32 to 48% (depending on temperature) of that measured at  $-5$  kPa. The relatively high rates of mineralization observed close to the wilting point confirm that soil microorganisms are more tolerant of moisture stress than plants. Therefore, the reduction in mineralization caused by a small moisture decrease in wet soil (matric potential decrease from  $-5$  to  $-20$  or  $-25$  kPa) was probably not a direct effect of moisture stress on the microbial biomass but possibly an indirect effect due to a decrease in substrate supply owing to a reduction in the diffusion of DOM as the moisture content decreased (Schjønning et al., 2003). The decline in mineralization at high moisture content ( $>28\%$ ) in the pasture soil at  $25^{\circ}\text{C}$  was probably because  $\text{O}_2$  diffusion was insufficient to meet the large demand associated with the rapid rate of mineralization in this high-C soil (Linn and Doran, 1984; Skopp et al., 1990).

The response of C mineralization to soil moisture, assessed from the linear relationship between C mineralized in 85 d and the gravimetric moisture content (Table 3), increased between  $5$  and  $25^{\circ}\text{C}$  in the arable and vegetable soils, although there was relatively little difference between the  $18$  and  $25^{\circ}\text{C}$  treatments. For these soils, the moisture response at  $25^{\circ}\text{C}$  was 2.4 to 3.8 times that at  $5^{\circ}\text{C}$ . In the case of the pasture soil, the moisture response also increased between  $5$  and  $18^{\circ}\text{C}$ . As explained above,

mineralization was not linearly related to soil moisture at  $25^{\circ}\text{C}$  and, therefore, data for this treatment were not included when evaluating the moisture response.

Differences among the soils in the mineralization vs. soil moisture relationship may be partly due to large differences in their water-holding capacities associated with differences in texture and organic matter content. This issue may be avoided by relating mineralization to relative water content (RWC) rather than to actual water content ( $\text{MC}_{\text{a}}$ ) (Paul et al., 2003). Relative water content is expressed as the available water content relative to the total available range, which is defined in terms of an upper (e.g.,  $-5$  kPa,  $\text{MC}_{-5}$ ) and lower ( $-1500$  kPa,  $\text{MC}_{-1500}$ ) limit:

$$\text{RWC} = \frac{\text{MC}_{\text{a}} - \text{MC}_{-1500}}{\text{MC}_{-5} - \text{MC}_{-1500}}$$

To relate C mineralization to RWC, we normalized mineralization by expressing the values obtained at each moisture content as a fraction of the mineralization measured at  $-5$  kPa. At  $5$  and  $12^{\circ}\text{C}$ , a single regression adequately described ( $R^2 = 0.97$ ,  $P < 0.001$  for both temperatures) the relationship between relative mineralization and relative water content for all three soils (Fig. 2). At  $18^{\circ}\text{C}$ , a single regression gave an acceptable fit ( $R^2 = 0.94$ ,  $P < 0.001$ ) for the arable and vegetable soils, but the pasture soil was less responsive to RWC. At  $25^{\circ}\text{C}$ , relative mineralization was again linearly related to RWC in the arable and vegetable soils. Except for the pasture soil at  $18^{\circ}\text{C}$ , the regressions be-

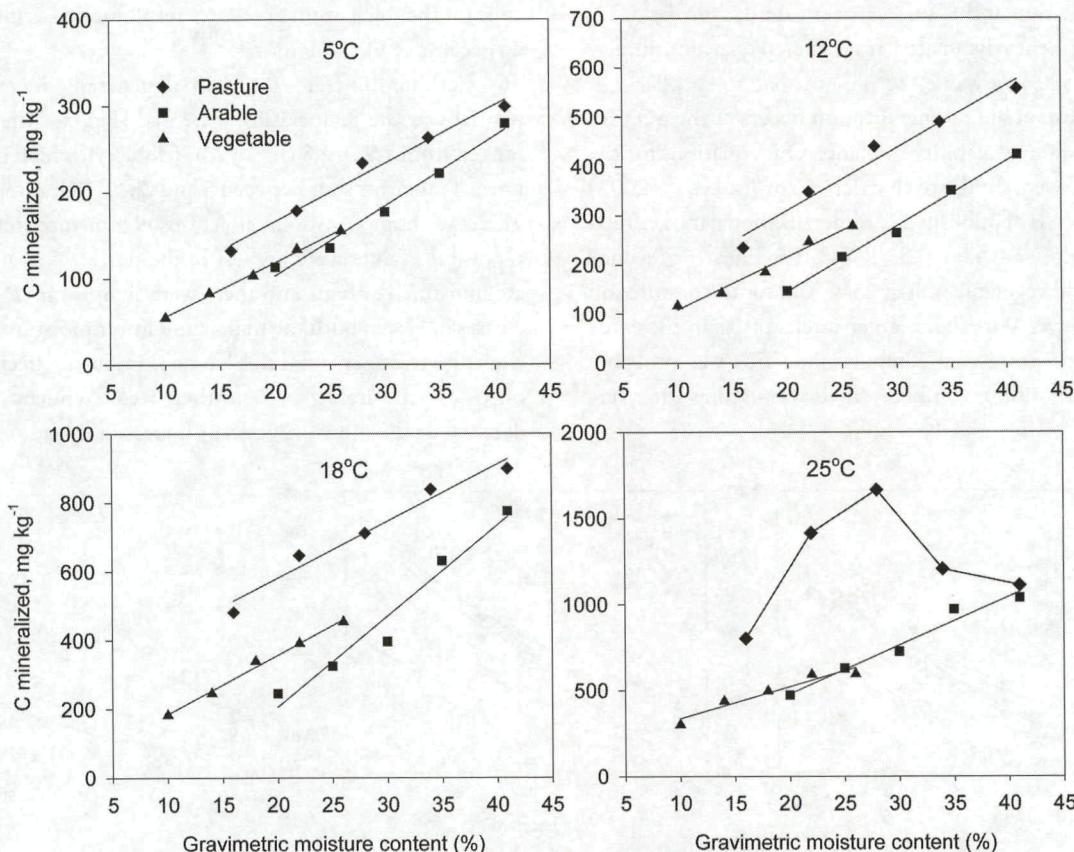
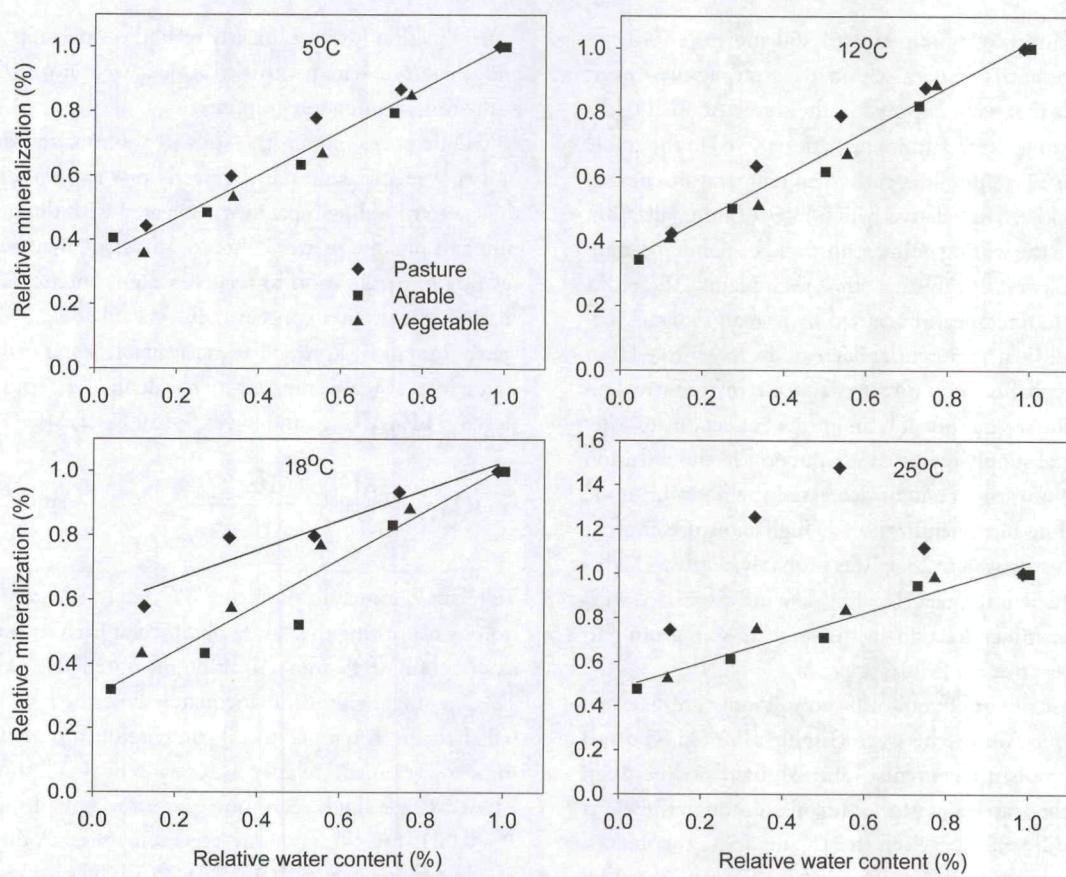


Fig. 1. Relationship between soil moisture content and C mineralized in 85 d for pasture, arable and vegetable soils incubated at 5, 12, 18, and  $25^{\circ}\text{C}$ .

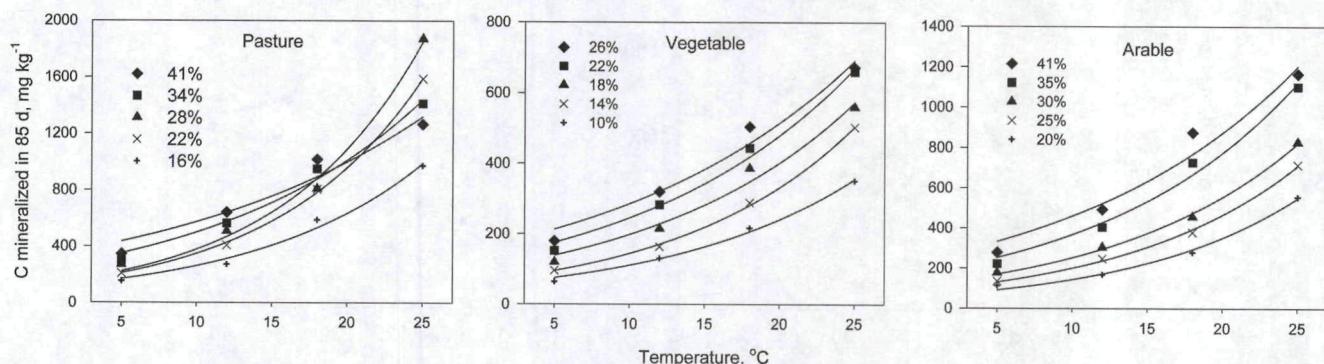


**Fig. 2.** Relationship between relative water content (available water as a proportion of total available water range) and normalized C mineralization values (C mineralized as a fraction of that at the highest moisture content) for pasture, arable, and vegetable soils incubated for 85 d at 5, 12, 18, and 25°C.

tween mineralization and RWC were very similar for the 5, 12, and 18°C treatments. Estimated from these equations, mineralization at -1500 kPa was 29 to 33% of that at -5 kPa, confirming that substantial C mineralization occurs at the putative lower limit of water availability to plants. Our equations for the 5 to 18°C range were similar to that derived by Paul et al. (2003) based on an analysis of published N mineralization data, i.e., relative mineralization = 0.42 + 0.83 RWC. The linear regressions for the arable and vegetable soils at 25°C and for the pasture soil at 18°C have lower slopes and larger intercepts than those for other temperature-moisture combinations. This was probably because mineralization at -5 kPa, which was used as the refer-

ence for the calculation of relative respiration, was underestimated because of O<sub>2</sub> limitation.

Carbon mineralized in 85 d generally increased exponentially as the temperature increased (Fig. 3). The  $Q_{10}$  values ranged from 1.9 to 2.8 (mean 2.3) (Table 4), which is within the normal range for soils between 5 and 25°C (Kirschbaum, 1995). There was not a consistent effect of soil moisture content on the  $Q_{10}$  value. Values were highest in the pasture soil at intermediate moisture contents and there were significant ( $P < 0.05$ ) decreases in  $Q_{10}$  in both the higher and lower moisture treatments. Moisture treatments did not have a significant effect ( $P > 0.05$ ) on  $Q_{10}$  in the arable soil, and there was a tendency for  $Q_{10}$  to decrease as the moisture content increased in the vegetable soil.



**Fig. 3.** Carbon mineralized in an 85-d incubation vs. temperature for pasture, arable, and vegetable soils at different moisture contents. Solid lines are  $Q_{10}$  fits.

Because  $Q_{10}$  values may be influenced by substrate depletion in long-term incubations (Kirschbaum, 1995), we also calculated  $Q_{10}$  values for the initial 14 d of incubation. These  $Q_{10}$  values tended to be slightly lower than those estimated for the entire 85 d (mean 2.2 vs. 2.3). There was no consistent relationship between  $Q_{10}$  values for the first 14 d and soil moisture.

Although the  $Q_{10}$  values did not show a consistent response to soil moisture, it is clear from the results presented above (Table 3) that the effect of temperature on C mineralization (measured as the *absolute* increase in C mineralized between 5 and 25°C) became greater as moisture content increased (provided O<sub>2</sub> was not limiting). The van't Hoff equation (Eq. [2]) relating mineralization to temperature has two variables:  $D$ , which provides an estimate of mineralization at a base temperature (0°C), and  $b$ , which is used to calculate the  $Q_{10}$  value. The  $D$  value increased systematically as moisture content increased (Table 4), but, as will be apparent from the above discussion of  $Q_{10}$ , the  $b$  value did not change consistently with moisture ( $b$  values not shown). Thus, the absolute size of the temperature response was greater when moisture constraints were eliminated mainly because the  $D$  value was higher. In evaluating the temperature responses of mineralization, it is important to distinguish between *relative* responses, which are commonly assessed using a  $Q_{10}$  value, and *absolute* responses, which take both the  $D$  and  $b$  terms in Eq. [2] into account. To illustrate, the vegetable soil had a higher  $Q_{10}$  value at the 10% than at the 26% moisture level (2.4 and 2.0, respectively), yet the increase in C mineralization (85 d) between 5 and 25°C was much greater in the soil incubated at the higher moisture content (492 vs. 288 mg C kg<sup>-1</sup>).

## Pool Size and Rate Constants for Carbon Mineralization

Using nonlinear regression, we fitted cumulative C mineralization vs. time data for each temperature–moisture combination to the first-order kinetic model (Eq. [1]) to estimate potentially mineralizable C and the mineralization rate constant (model fits for the vegetable soil shown in Fig. 4). At temperatures of 5, 12, and 18°C, the model fit was generally very good ( $R^2 > 0.98$ ), but the fit was less satisfactory at 25°C and therefore  $C_0$  and  $k$  values are not presented for this treatment (Table 5). Also, model fit was unsatisfactory for the two lowest moisture levels in the pasture soil at 18°C. The mineralizable C pool size tended to increase in response to temperature and moisture increases (Table 5). There was not a consistent effect of temperature or moisture on the rate constant. Although these results run counter to conventional thinking that soils have a fixed pool of mineralizable C that is independent of incubation temperature and moisture (Campbell et al., 1984; Stanford and Smith, 1972), they are in agreement with MacDonald et al. (1995) and Zak et al. (1999), who reported that the mineralizable C pool size was temperature dependent in forest soils in Michigan. Zak et al. (1999) hypothesized that the effects of temperature and moisture on the mineralizable C pool size could be a reflection of the influence

**Table 4. Effect of moisture content on  $Q_{10}$  values for C mineralized in 85 d and in the first 14 d of incubation and on two other measures of the temperature response:  $D$  values estimated from the van't Hoff equation (Eq. [2]) and the difference between C mineralized at 5 and 25°C ( $\Delta C$  mineralized).**

Soil	Moisture content	$Q_{10}$		$D$ 0–85 d	$\Delta C$ mineralized mg kg <sup>-1</sup>	
		0–85 d	0–14 d		0–85 d	0–14 d
Pasture	%				mg kg <sup>-1</sup>	
	16 (-720)†	2.56	2.12	95	790	113
	22 (-220)	2.80	2.39	123	1381	228
	28 (-65)	2.60	2.26	161	1604	241
	34 (-20)	2.20	2.04	213	1113	218
	41 (-5)	1.93	1.99	272	920	211
Arable	LSD 0.05	0.14	0.12	13	154	28
	20 (-1180)	2.22	2.00	71	439	75
	25 (-320)	2.27	1.97	90	579	93
	30 (-90)	2.15	2.04	121	650	135
	35 (-25)	2.26	2.14	152	880	174
	41 (-5)	2.08	2.45	204	885	280
Vegetable	LSD 0.05	0.17	0.22	11	129	21
	10 (-700)	2.35	2.34	44	288	58
	14 (-200)	2.32	2.17	63	407	83
	18 (-60)	2.21	2.22	84	440	100
	22 (-20)	2.09	2.07	112	508	115
	26 (-5)	1.95	2.06	137	492	119
	LSD 0.05	0.27	0.34	18	75	24

† Values in parentheses indicate matric potential (kPa).

of these variables on the flux of organic substrates to microbial cells via diffusion.

## Nitrogen Mineralization

The effects of temperature and moisture on net N mineralization (Table 6) generally paralleled those described above for C mineralization (the correlation between C and N mineralized in 85 d was  $R^2 = 0.91$ ,  $n = 180$ ). As in the case of C, N mineralization was significantly ( $P < 0.001$ ) affected by moisture, temperature, and their interaction. As observed for C, however, the influence of temperature was stronger than that of moisture content. The van't Hoff equation adequately described the temperature response of N mineralization ( $R^2$  generally  $>0.97$ ). The  $Q_{10}$  values (Table 6) were generally similar to those for C mineralization, and they did not follow a consistent trend with moisture content. The temperature response, however, assessed as the difference between N mineralized at 25 and 5°C or as the  $D$  value in Eq. [2], increased with moisture content provided that O<sub>2</sub> was not limiting (pasture soil). In most cases, N mineralization was linearly related to gravimetric moisture content. As with C mineralization, N mineralization in the pasture soil incubated at 25°C peaked at the 28% moisture level and declined at the higher moisture contents.

Most (average 93%) of the mineralized N accumulated as NO<sub>3</sub>-N. Although nitrifiers are less tolerant of moisture stress than are ammonifiers (Paul and Clark, 1996), the proportion of NH<sub>4</sub>-N showed only modest increases as moisture content decreased (NH<sub>4</sub>-N represented an average of 11% of the miner-

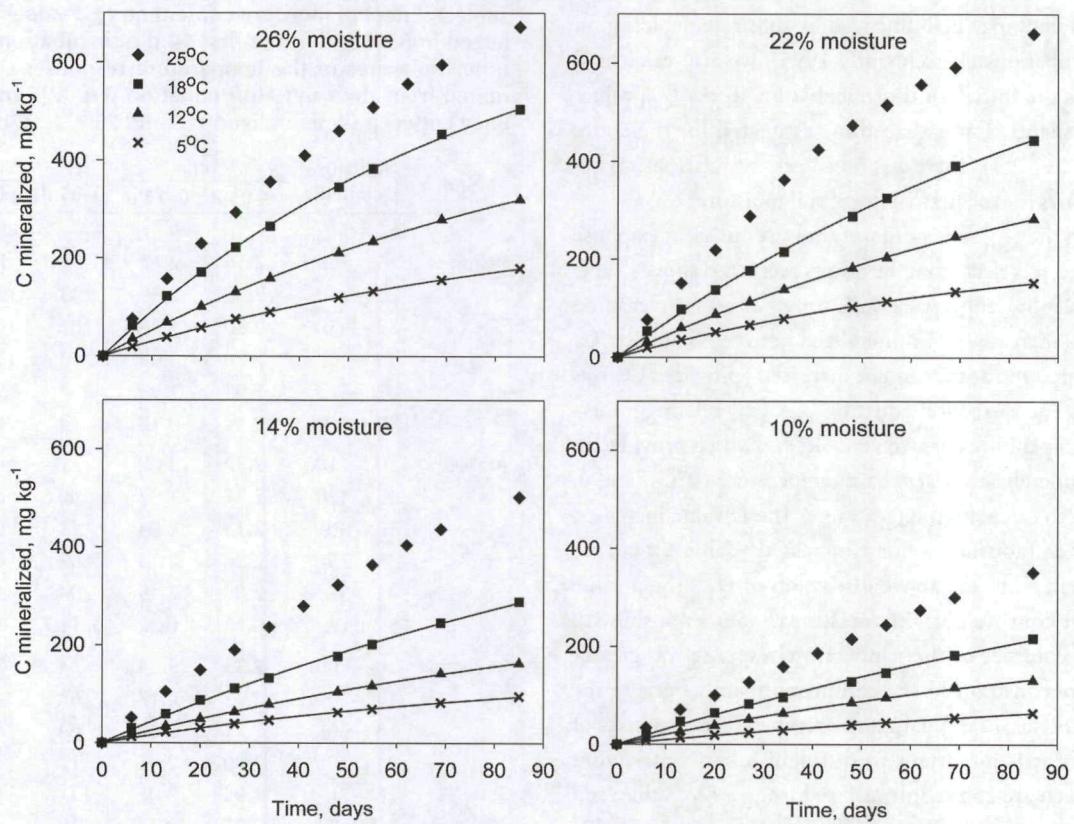


Fig. 4. Cumulative C mineralization in a vegetable soil during an 85-d incubation at different moisture contents and temperatures. Solid lines are best fits to a first-order kinetic model (Eq. [1]).

Table 5. Effect of temperature and moisture on potentially mineralizable C and the mineralization rate constant estimated using first-order kinetics (Eq. [1]) from C mineralization data obtained from an 85-d incubation.

Moisture content	Potentially mineralizable C				Rate constant			
	5°C	12°C	18°C	25°C	5°C	12°C	18°C	25°C
%	mg kg <sup>-1</sup>				d <sup>-1</sup>			
16 (-720)†	308	591	ND	ND‡	0.0082	0.0073	ND	ND
22 (-220)	388	867	ND	ND	0.0090	0.0075	ND	ND
28 (-65)	529	991	1292	ND	0.0085	0.0086	0.0116	ND
34 (-20)	488	1033	1515	ND	0.0113	0.0093	0.0116	ND
41 (-5)	713	1149	1596	ND	0.0078	0.0096	0.0119	ND
LSD 0.05	119				0.0017			
<u>Pasture</u>								
20 (-1180)	238	311	563	ND	0.0080	0.0093	0.0093	ND
25 (-320)	235	457	655	ND	0.0103	0.0093	0.0096	ND
30 (-90)	367	490	975	ND	0.0078	0.0113	0.0075	ND
35 (-25)	484	723	1275	ND	0.0081	0.0096	0.0081	ND
41 (-5)	633	1044	1566	ND	0.0069	0.0074	0.0092	ND
LSD 0.05	141				0.0031			
<u>Arable</u>								
10 (-700)	187	326	409	ND	0.0052	0.0064	0.0090	ND
14 (-200)	177	389	620	ND	0.0091	0.0067	0.0071	ND
18 (-60)	226	559	811	ND	0.0089	0.0183	0.0084	ND
22 (-20)	253	628	975	ND	0.0109	0.0073	0.0074	ND
26 (-5)	341	641	844	ND	0.0088	0.0082	0.0110	ND
LSD 0.05	169				0.0086			
<u>Vegetable</u>								
10 (-700)	187	326	409	ND	0.0052	0.0064	0.0090	ND
14 (-200)	177	389	620	ND	0.0091	0.0067	0.0071	ND
18 (-60)	226	559	811	ND	0.0089	0.0183	0.0084	ND
22 (-20)	253	628	975	ND	0.0109	0.0073	0.0074	ND
26 (-5)	341	641	844	ND	0.0088	0.0082	0.0110	ND

† Values in parentheses indicate matric potential (kPa).

‡ ND, not determined.

alized N in the driest treatment compared with 5% at the highest moisture content).

#### Effect of Incubation Temperature and Moisture on Microbial Biomass Carbon

Microbial biomass C measured at the termination of the experiment decreased significantly ( $P < 0.001$ ) as the temperature of incubation increased (Table 7). There was also a significant effect of moisture content, but it was small compared with the temperature effect. In contrast to temperature, there was not a consistent trend with moisture content across soils. There was a significant temperature  $\times$  moisture interaction on microbial biomass in all three soils. While there was a relatively large temperature effect at the highest moisture content in each soil, the temperature response did not show a systematic change with moisture level. Averaged across moisture treatments, the decrease in microbial biomass in the three soils between 5 and 25°C ranged from 18 to 35%, with the heavy-textured arable soil showing the smallest proportional decrease and the pasture soil showing the greatest rela-

**Table 6. Effect of soil moisture content on  $Q_{10}$  values and on two other measures of the temperature response of N mineralization: the difference in N mineralized at 5 and 25°C ( $\Delta N$  mineralized) and D values estimated from the van't Hoff equation (Eq. [2]).**

Soil	Moisture content	$Q_{10}$	D	$\Delta N$ mineralized
				mg kg <sup>-1</sup>
Pasture	16 (-720)†	2.5	12.1	103
	22 (-220)	2.6	14.9	143
	28 (-65)	2.4	20.0	161
	34 (-20)	1.9	33.9	125
	41 (-5)	1.8	41.7	110
	LSD 0.05	0.15	3.2	13
Arable	20 (-1180)	2.3	5.3	31
	25 (-320)	2.1	6.1	31
	30 (-90)	2.4	5.9	50
	35 (-25)	2.5	8.1	72
	41 (-5)	2.5	12.1	91
	LSD 0.05	0.35	1.8	7
Vegetable	10 (-700)	3.4	1.8	28
	14 (-200)	2.7	4.0	40
	18 (-60)	2.2	8.6	41
	22 (-20)	2.1	10.3	46
	26 (-5)	1.9	14.5	49
	LSD 0.05	0.38	1.6	6

† Values in parentheses indicate matric potential (kPa).

tive decline (Fig. 5). In all soils, the decrease in microbial biomass was a linear function of incubation temperature.

There was a trend in all soils, but especially in the pasture and vegetable soils, for treatments that mineralized the least C during the 85-d incubation to have the most microbial biomass C at the termination of the experiment (Fig. 6). According to the regression equations in Fig. 6, post-incubation biomass C decreased by an average of 0.22 to 0.31 mg kg<sup>-1</sup> for each 1 mg kg<sup>-1</sup> of CO<sub>2</sub>-C evolved during the incubation. Changes in microbial C storage may be a significant factor affecting the temperature dependence of C mineralization (discussed further below). Our results are consistent with those of Alvarez et al. (1995), who reported that microbial C was inversely related to soil temperature in a field study in Argentina. In an incubation study in which a grassland soil was maintained at either 15, 25, or 35°C for 240 d, microbial C was observed to decline during incubation, with the largest drop occurring at the highest temperature (Joergensen et al., 1990). Recent results from soil warming experiments have shown a tendency for biomass to decline when the temperature was raised (Rinnan et al., 2007).

### Mineralization—Moisture and –Temperature Relations

The maximum C mineralization was observed at the highest temperature and moisture content except in the pasture soil where, at 25°C, there was a substantial reduction between 28% (-65 kPa) and 41% (-5 kPa) moisture contents. The pasture soil at 25°C exhibited the highest overall mineralization rate and thus

**Table 7. Microbial biomass C (MBC) measured after an 85-d incubation of pasture, arable, and vegetable soils at different temperatures and moisture contents.**

Moisture content	Post-incubation MBC			
	%	mg kg <sup>-1</sup>		
Pasture			<u>Pasture soil</u>	
16 (-720)†	16 (-720)†	1183	987	974
22 (-220)	22 (-220)	1244	1079	955
28 (-65)	28 (-65)	1254	1124	1097
34 (-20)	34 (-20)	1246	1108	1021
41 (-5)	41 (-5)	1256	1096	940
LSD 0.05	LSD 0.05	44		
Arable			<u>Arable soil</u>	
20 (-1180)	20 (-1180)	1123	1066	1045
25 (-320)	25 (-320)	1162	1101	1079
30 (-90)	30 (-90)	1191	1132	1043
35 (-25)	35 (-25)	1175	1135	1052
41 (-5)	41 (-5)	1166	1199	832
LSD 0.05	LSD 0.05	85		
Vegetable			<u>Vegetable soil</u>	
10 (-700)	10 (-700)	363	326	314
14 (-200)	14 (-200)	386	343	324
18 (-60)	18 (-60)	384	370	301
22 (-20)	22 (-20)	352	356	265
26 (-5)	26 (-5)	352	335	261
LSD 0.05	LSD 0.05	23		

† Values in parentheses indicate matric potential (kPa).

had the greatest O<sub>2</sub> demand. Very likely, the supply of O<sub>2</sub> was limiting due to slow O<sub>2</sub> diffusion at the higher moisture levels, as observed in previous studies (Linn and Doran, 1984). There was some evidence of minor O<sub>2</sub> deprivation in the other soils at high moisture and temperature, which may have resulted in the underestimation of  $Q_{10}$  values in the highest moisture treatments (Fig. 3). Where the O<sub>2</sub> supply was adequate, mineralization was linearly related to gravimetric moisture content (Fig. 1).

Our results confirm that, while soil microorganisms can tolerate moisture stress (mineralization at -1500 kPa was estimated to be about one-third of that at -5 kPa), even relatively small reductions in the moisture content of wet soil can significantly reduce mineralization. These apparently contradictory observations can probably be explained in terms of the influence of substrate supply on the mineralization rate. Dissolved organic matter, which may be the immediate substrate for soil microorganisms (Kemmitt et al., 2008; Marschner and Kalbitz, 2003), is transported to microbial cells by diffusion. The DOM includes large molecules (Kalbitz et al., 2003) that must presumably be broken down by extracellular enzymes before they are transported across membranes into microbial cells. Thus, slower diffusion of enzymes to substrate molecules may also contribute to lower mineralization rates in dry soil. The observed linear relationship between mineralization and moisture content may reflect the fact that solute diffusivity is a linear function of moisture content, provided that the moisture content is above the threshold at which diffusion ceases (i.e., the point at which water films on soil

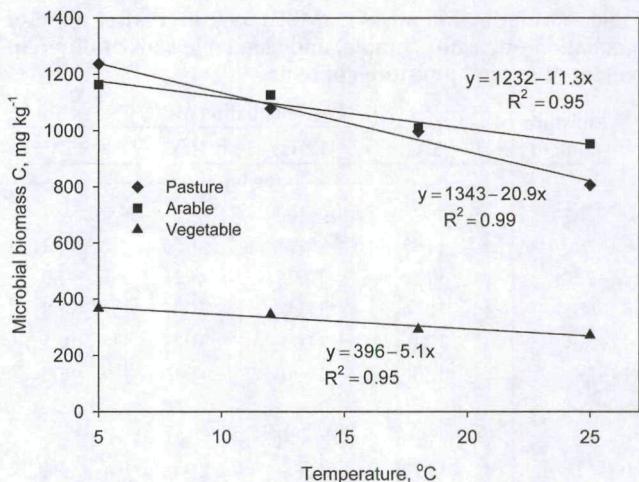


Fig. 5. Relationship between post-incubation microbial biomass and incubation temperature for the pasture, arable, and vegetable soils (biomass values are averaged across moisture treatments).

particles become discontinuous) (Schjønning et al., 2003). By restricting substrate diffusion, decreases in soil moisture content may reduce mineralization even when water availability is not directly limiting microbial activity. According to Griffin (1981), direct effects of moisture stress on soil microbes (cell dehydration) occur only at low water potentials. Stark and Firestone (1995) showed that substrate supply was the main constraint for nitrifying bacteria above  $-600$  kPa, with cell dehydration becoming a major inhibitory factor below  $-600$  kPa. They concluded that for xeric-tolerant organisms, including many fungi, substrate supply may be the primary constraint.

Our results show that the optimum matric potential for mineralization may be as high as  $-5$  kPa, provided that the O<sub>2</sub> supply is not limiting. This is considerably above the water potential for maximum crop production (as a general guideline, plant growth does not decline until a threshold of about  $-500$  kPa is reached; H. Brown, personal communication, 2010). Maintaining a high soil moisture content may thus increase respiratory C output to a greater extent than inputs of C in crop residues, leading to a decline in soil C stocks. There is evidence from a long-term trial (1949–present) that frequent irrigation may indeed adversely affect soil C (Condron et al., 2006). The trial, which is on a ryegrass–white clover pasture (sheep grazed) on the South Island of New Zealand, includes treatments receiving no irrigation (dryland, mean annual precipitation 740 mm) and irrigation applied when the topsoil gravimetric moisture content reaches either 10 or 20%. The 10 and 20% treatments received an average of 260 and 770 mm yr<sup>-1</sup> of irrigation, respectively. Irrigation at the 10% rate substantially increased pasture production, with only a small additional increase at the 20% rate. Measurements in 2001 showed no difference in total soil C (0–15-cm depth) between the dryland and the low irrigation treatment but a decrease of about 25% in the highly irrigated (20%) treatment (Condron et al., 2006). The decline in soil C when the moisture content was maintained above 20% is strong evidence that the moisture optimum for soil respiration is higher than that for plant production.

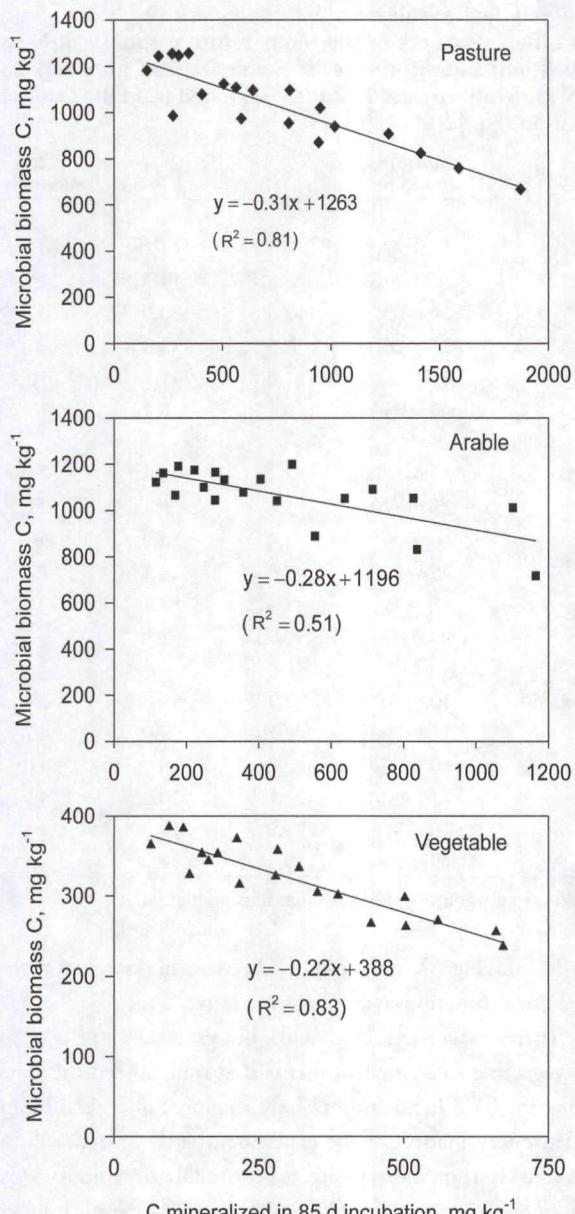


Fig. 6. Relationship between post-incubation microbial biomass and amounts of C mineralized in 85 d for pasture, arable, and vegetable soils (the data represent 20 temperature–moisture treatment combinations for each soil).

The observation that C mineralization can be significant at the lower limit of water availability to plants ( $-1500$  kPa) agrees with recent findings that the sensitivity of net cropland productivity to drought is greater than that of respiration (Schwalm et al., 2010).

Moisture-induced changes in substrate supply undoubtedly influenced the mineralization–soil moisture relationship, but it is difficult to quantitatively separate this indirect effect from the direct effect of water stress. The results in Table 5, showing that the pool of mineralizable C increased with moisture content, could be interpreted as an effect of moisture on the substrate supply. A direct effect of moisture stress would presumably manifest itself as a decrease in the mineralization rate constant,  $k$ , but there was no trend for  $k$  to decline at low moisture content. A similar effect of moisture on the mineralizable C pool size was

also observed by Zak et al. (1999), who postulated that, because fewer microorganisms are active at low potentials (bacteria are generally less tolerant of moisture stress than fungi), the pool size may effectively decrease at lower potentials. This explanation appears to be in conflict with the findings of Kemmitt et al. (2008), however, who concluded that the rate of mineralization is independent of the size of the microbial biomass.

Increases in the rate of DOM diffusion (substrate supply) may partly explain why the mineralizable C pool increased as temperature increased (Table 5). The presence of DOM in the soil solution is an essential precondition to its utilization by microorganisms (Agren and Wetterstedt, 2007; Kemmitt et al., 2008). Key steps in the mineralization process include the release of organic matter into solution, diffusion to the surface of microbial cells, and absorption into the cell (Agren and Wetterstedt, 2007).

### Mineralization Model

A conceptual model of the mineralization process, in which the release of DOM is assumed to be the rate-limiting step, is shown in Fig. 7. There is strong evidence that, once released into solution, DOM is rapidly mineralized. For example, Gregorich et al. (2003) showed that about one-third of the organic C in water extracts of soil had a turnover time of <1 d at 35°C; the remaining C was also relatively labile (turnover time of 80 d). The concentration of DOM is extremely low, although it is buffered by the solid-phase organic matter. There is some uncertainty regarding the process(es) by which organic matter is released into solution (conversion of SOM to DOM in Fig. 7). Allison et al. (2010) and Schimel and Bennett (2004) considered that this step is exclusively mediated by extracellular enzymes released by the microbial biomass. If that were the case, then a larger microbial population, producing greater quantities of enzymes, would increase the rate of organic matter turnover. The work of Kemmitt et al. (2008) showed, however, that a very small microbial population can mineralize soil C at the same rate as a large one. The DOM comprises a heterogeneous mix of compounds (Marschner

and Kalbitz, 2003) with an overall negative charge (Curtin et al., 2011). As a charged (anionic) solute, DOM is subject to adsorption–desorption reactions with soil minerals (Moore et al., 1992). Thus, chemical factors must be important in controlling DOM release. Chemical perturbations that reduce the soil anion adsorption capacity can increase the DOM concentration. For example, raising the pH causes desorption of organic matter, which can stimulate mineralization (Curtin et al., 1998).

Several steps in the proposed mineralization model (Fig. 7) may be temperature sensitive. Raising the temperature may cause desorption of organic matter, thereby increasing the substrate supply. Information on the effects of temperature on DOM in the in situ soil solution is lacking because extracting solution from field-moist soils presents serious methodological difficulties (Adams, 1974); however, the concentration of organic matter in water extracts of soils has been shown to increase exponentially between 20 and 80°C (Chantigny et al., 2010). Less is known about the influence of temperature on water-extractable organic matter in the biologically important range (5–25°C), but our unpublished results indicate that it does increase across this range.

The uptake of DOM by the microbial biomass may also be temperature sensitive because temperature directly affects the activity of extracellular enzymes that catalyze the breakdown of large DOM molecules to bioavailable compounds (Miller and Dick, 1995; Skujins, 1976). In addition, mass transfer of DOM to the biomass is more rapid at higher temperatures because of the positive effect of temperature on solute diffusivity and the associated diffusion rate. As temperature increases, rapid uptake and utilization of DOM may promote further desorption of organic matter by maintaining a low concentration in solution and creating DOM concentration gradients. Collectively, these factors could increase the flux of DOM to microbial cells.

Temperature may influence the C utilization efficiency by the microbial biomass (i.e., the efficiency with which the C taken up is converted into microbial tissue). Temperature effects on C use efficiency are not well understood and soil C models often

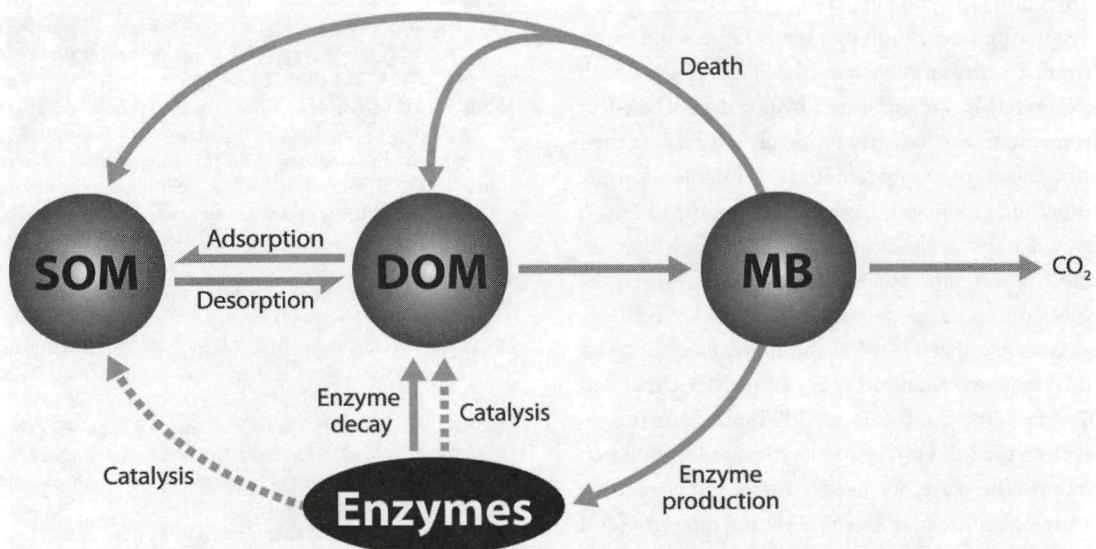


Fig. 7. Conceptual model of the C mineralization process: SOM is the solid-phase soil organic matter, DOM is dissolved organic matter, and MB is the microbial biomass.

assume a constant efficiency. For example, in the Century model, an efficiency of 55% is assumed (i.e., 45% of C taken up by the biomass is respired as CO<sub>2</sub>) (Parton et al., 1987). Incubation experiments by Steinweg et al. (2008) have shown that the utilization efficiency of added substrate (cellobiose) is greater at 15 than at 25°C, meaning that the soil biomass released more CO<sub>2</sub> per unit of assimilated C at the higher temperature. In our 85-d incubation, microbial biomass C decreased at higher temperatures (Table 7), even though the substrate supply is postulated to have increased with temperature. Reduced C use efficiency may have contributed to the decline in microbial C at higher temperatures, but a faster microbial death rate may be the dominant factor. The death rate of the microbial biomass is strongly temperature dependent (Joergensen et al., 1990). The latter researchers estimated that the turnover time of the microbial biomass at 15, 25, and 35°C was 139, 62, and 4 d, respectively.

A temperature response model for mineralization needs to include the living and nonliving organic matter because both can be sources of the CO<sub>2</sub>-C respired in response to temperature increases. The importance of the microbial biomass as a source of respired CO<sub>2</sub> may be particularly large at lower temperatures. The decline in MBC between 5 and 12°C represented an average of 40% of the C mineralization increase across that temperature interval. Between 18 and 25°C, the decline in MBC was equivalent to only 20% (on average) of the C mineralized across that temperature range. The high  $Q_{10}$  values reported in laboratory incubations at low temperature (Kirschbaum, 2006) may be partly due to the mineralization of microbial C. In time, the microbial biomass would presumably reach a stable level at each temperature. Thus, the microbial C source at higher temperature will be temporary, although the time required for the microbial biomass to reach a new equilibrium is open to question. While short-term laboratory incubations may provide an artificially high estimate of the temperature dependence of SOM mineralization, long incubation times are also undesirable because substrate depletion at higher temperatures can introduce a bias in the opposite direction (Kirschbaum, 2006).

In conclusion, the assumption of a temperature- and moisture-dependent first-order rate constant (the Stanford and Smith mineralization model) is not supported by our data. The effect of these environmental variables may be largely indirect via their influence on the substrate supply (amounts of soluble substrate reaching the microbial biomass). Based on the model in Fig. 7, we have suggested steps in the mineralization process that are likely to be sensitive to temperature and moisture; however, the model is largely conceptual and needs testing and validation. There is good evidence that DOM is the immediate substrate for the microbial biomass (Kemmitt et al., 2008; Marschner and Bredow, 2002; Marschner and Kalbitz, 2003) and that the release of DOM from the solid phase may be the rate-limiting step for mineralization. Therefore, we need a better understanding of the effect of temperature and moisture on the quantity (and composition) of DOM in the in situ soil solution, as well as on the physicochemical and biochemical controls on DOM release.

We have also shown that temperature has an effect on the size of the microbial biomass, with substantial reductions in microbial C between 5 and 25°C. This may significantly enhance the temperature response of C mineralization. This effect, which appears to have been overlooked in the debate over the temperature dependence of SOM mineralization (Agren and Wetterstedt, 2007; Davidson and Janssens, 2006; Kirschbaum, 2006), merits further investigation.

## ACKNOWLEDGMENTS

Funding for this work was provided by the Foundation for Research Science and Technology under Contract no. C02X0812. We thank Fran McCallum and Charles Wright for technical assistance, Glyn Francis for advice during the planning and initiation of the work, and Esther Meenken for assistance with data analysis.

## REFERENCES

- Adams, F. 1974. Soil solution. In: E.W. Carson, editor, *The plant root and its environment*. Univ. of Virginia Press, Charlottesville. p. 441–481.
- Agren, G.I., and J.A.M. Wetterstedt. 2007. What determines the temperature response of soil organic matter decomposition? *Soil Biol. Biochem.* 39:1794–1798. doi:10.1016/j.soilbio.2007.02.007
- Allison, S.D., M.D. Wallenstein, and M.A. Bradford. 2010. Soil-carbon response to warming dependent on microbial physiology. *Nat. Geosci.* 3:336–340. doi:10.1038/ngeo484
- Alvarez, R., O.J. Santanatoglia, and R. Garcia. 1995. Effect of temperature on soil microbial biomass and its metabolic quotient in situ under different tillage systems. *Biol. Fertil. Soils* 19:227–239. doi:10.1007/BF00336164
- Benedetti, A., and G. Sebastiani. 1996. Determination of potentially mineralizable nitrogen in agricultural soil. *Biol. Fertil. Soils* 21:114–120. doi:10.1007/BF00336002
- Cabrera, M.L. 1993. Modeling the flush of nitrogen mineralization caused by drying and rewetting soils. *Soil Sci. Soc. Am. J.* 57:63–66. doi:10.2136/sssaj1993.03615995005700010012x
- Campbell, C.A., B.H. Ellert, and Y.W. Jame. 1993. Nitrogen mineralization potential in soils. In: M.R. Carter, editor, *Soil sampling and methods of analysis*. Lewis Publ., Boca Raton, FL. p. 341–349.
- Campbell, C.A., Y.W. Jame, and G.E. Winkleman. 1984. Mineralization rate constants and their use for estimating nitrogen mineralization in some Canadian prairie soils. *Can. J. Soil Sci.* 64:333–343. doi:10.4141/cjss84-035
- Chantigny, M.H., D. Curtin, and M.H. Beare. 2010. Influence of temperature on water-extractable organic matter and ammonium production in mineral soils. *Soil Sci. Soc. Am. J.* 74:517–524. doi:10.2136/sssaj2008.0347
- Condron, L.M., S. Sinaj, R.W. McDowell, J. Dudler-Guela, J.T. Scott, and A.K. Methere. 2006. Influence of long-term irrigation on the distribution and availability of soil phosphorus under permanent pasture. *Aust. J. Soil Res.* 44:127–133. doi:10.1071/SR05065
- Curtin, D., M.H. Beare, M.H. Chantigny, and L. Greenfield. 2011. Controls on the extractability of soil organic matter in water over the 20 to 80°C temperature range. *Soil Sci. Soc. Am. J.* 75:1423–1430. doi:10.2136/sssaj2010.0401
- Curtin, D., C.A. Campbell, and A. Jalil. 1998. Effects of acidity on mineralization: pH-dependence of organic matter mineralization in weakly acidic soils. *Soil Biol. Biochem.* 30:57–64. doi:10.1016/S0038-0717(97)00094-1
- Davidson, E.A., and I.A. Janssens. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440:165–173. doi:10.1038/nature04514
- Deans, J.R., A.E. Molina, and C.E. Clapp. 1986. Models for predicting potentially mineralizable nitrogen and decomposition rate constants. *Soil Sci. Soc. Am. J.* 50:323–326. doi:10.2136/sssaj1986.03615995005000020014x
- GenStat Committee. 2005. The guide to GenStat 8. Parts 1–3. VSN Int., Oxford, UK.
- Gregorich, E.G., M.H. Beare, U. Stoklas, and P. St. Georges. 2003. Bioavailability of soluble organic matter in maize cropped soils. *Geoderma* 113:237–252. doi:10.1016/S0016-7061(02)00363-4
- Griffin, D.M. 1981. Water and microbial stress. *Adv. Microb. Ecol.* 5:91–136.

- Hassink, J. 1994. Effect of soil texture on the size of the microbial biomass and on the amount of C and N mineralized per unit of microbial biomass in Dutch grassland soils. *Soil Biol. Biochem.* 26:1573–1581. doi:10.1016/0038-0717(94)90100-7
- Haynes, R.J., and R. Tregurtha. 1999. Effects of increasing periods under intensive arable and vegetable production on biological, chemical and physical indices of soil quality. *Biol. Fertil. Soils* 28:259–266. doi:10.1007/s003740050491
- Horwarth, W.R., and E.A. Paul. 1994. Microbial biomass. In: R.W. Weaver, editor, *Methods of soil analysis. Part 2. Microbiological and biochemical properties*. SSSA Book Ser. 5. SSSA, Madison, WI. p. 753–773.
- Joergensen, R.G., P.C. Brookes, and D.S. Jenkinson. 1990. Survival of soil microbial biomass at elevated temperatures. *Soil Biol. Biochem.* 22:1129–1136. doi:10.1016/0038-0717(90)90039-3
- Kalbitz, K., J. Schmerwitz, D. Schwesig, and E. Matzner. 2003. Biodegradation of soil-derived dissolved organic matter as related to its properties. *Geoderma* 113:273–291. doi:10.1016/S0016-7061(02)00365-8
- Keeney, D.R., and J.M. Bremner. 1966. Comparison and evaluation of laboratory methods of obtaining an index of soil nitrogen availability. *Agron. J.* 58:498–503. doi:10.2134/agronj1966.00021962005800050013x
- Keeney, D.R., and D.W. Nelson. 1982. Nitrogen—Inorganic forms. In: A.L. Page et al., editors, *Methods of soil analysis. Part 2. Microbiological and biochemical properties*. Agron. Monogr. 9. ASA and SSSA, Madison, WI. p. 643–698.
- Kemmitt, S.J., C.V. Lanyon, I.S. Waite, Q. Wen, T.M. Addiscott, N.R.A. Bird, et al. 2008. Mineralization of native soil organic matter is not regulated by the activity or composition of the soil microbial biomass. *Soil Biol. Biochem.* 40:61–73. doi:10.1016/j.soilbio.2007.06.021
- Kirschbaum, M.U.F. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biol. Biochem.* 27:753–760. doi:10.1016/0038-0717(94)00242-S
- Kirschbaum, M.U.F. 2006. The temperature dependence of organic matter decomposition: Still a topic of debate. *Soil Biol. Biochem.* 38:2510–2518. doi:10.1016/j.soilbio.2006.01.030
- Linn, M.D., and J.W. Doran. 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and nontilled soils. *Soil Sci. Soc. Am. J.* 48:1267–1272. doi:10.2136/sssaj1984.03615995004800060013x
- MacDonald, N.W., D.R. Zak, and K.S. Pregitzer. 1995. Temperature effects on the kinetics of microbial respiration and net mineralization of N and S. *Soil Sci. Soc. Am. J.* 59:233–240.
- Marschner, B., and A. Bredow. 2002. Temperature effects on release and ecologically relevant properties of dissolved organic matter in sterilised and biologically active samples. *Soil Biol. Biochem.* 34:459–466. doi:10.1016/S0038-0717(01)00203-6
- Marschner, B., and K. Kalbitz. 2003. Controls of bioavailability and biodegradability of dissolved organic matter in soils. *Geoderma* 113:211–235. doi:10.1016/S0016-7061(02)00362-2
- Miller, M., and R.P. Dick. 1995. Thermal stability and activities of soil enzymes as influenced by crop rotations. *Soil Biol. Biochem.* 27:1161–1166. doi:10.1016/0038-0717(95)00045-G
- Moore, T.R., W. Desouza, and J.F. Koprivnjak. 1992. Control on the sorption of dissolved organic carbon by soils. *Soil Sci.* 154:120–129. doi:10.1097/00010694-199208000-00005
- Motavalli, P.P., C.A. Palm, W.J. Parton, E.T. Elliott, and S.D. Frey. 1994. Comparison of laboratory and modeling simulation methods for estimating soil carbon pools in tropical forest soils. *Soil Biol. Biochem.* 26:935–944. doi:10.1016/0038-0717(94)90106-6
- Orchard, V.A., and F.J. Cook. 1983. Relationship between soil respiration and soil moisture. *Soil Biol. Biochem.* 15:447–453. doi:10.1016/0038-0717(83)90010-X
- Parton, W.J., D.S. Schimel, C.V. Cole, and D.S. Ojima. 1987. Analysis of factors controlling organic matter levels in Great Plains grasslands. *Soil Sci. Soc. Am. J.* 51:1173–1179. doi:10.2136/sssaj1987.03615995005100050015x
- Paul, E.A., and F.E. Clark. 1996. *Soil microbiology and biochemistry*. 2nd ed. Academic Press, San Diego.
- Paul, K.I., P.J. Polglase, A.M. O'Connell, J.C. Carlyle, P.J. Smethurst, and P.K. Khanna. 2003. Defining the relation between soil water content and net nitrogen mineralization. *Aust. J. Soil Res.* 54:39–47.
- Rinnan, R., A. Michelsen, E. Baath, and S. Jonasson. 2007. Fifteen years of climate change manipulations alter soil microbial communities in a subarctic heath ecosystem. *Global Change Biol.* 13:28–39. doi:10.1111/j.1365-2486.2006.01263.x
- Schimel, J.P., and J. Bennett. 2004. Nitrogen mineralization: Challenges of a changing paradigm. *Ecology* 85:591–602. doi:10.1890/03-8002
- Schjønning, P., I.K. Thomsen, P. Moldrup, and B.T. Christensen. 2003. Linking soil microbial activity to water- and air-phase contents and diffusivities. *Soil Sci. Soc. Am. J.* 67:156–165. doi:10.2136/sssaj2003.0156
- Schlesinger, W.H. 1997. *Biogeochemistry: An analysis of global change*. 2nd ed. Academic Press, San Diego.
- Schwalm, C.R., C.A. Williams, K. Schaefer, A. Arneth, D. Bonal, N. Buchmann, et al. 2010. Assimilation exceeds respiration sensitivity to drought: A FLUXNET synthesis. *Global Change Biol.* 16:657–670. doi:10.1111/j.1365-2486.2009.01991.x
- Skopp, J., M.D. Jawson, and J.W. Doran. 1990. Steady-state aerobic microbial activity as a function of soil water content. *Soil Sci. Soc. Am. J.* 54:1619–1625. doi:10.2136/sssaj1990.03615995005400060018x
- Skujins, J. 1976. Extracellular enzymes in soil. *CRC Crit. Rev. Microbiol.* 4:383–421. doi:10.3109/10408417609102304
- Stanford, G., and E. Epstein. 1974. Nitrogen mineralization–water relations in soils. *Soil Sci. Soc. Am. Proc.* 38:103–107. doi:10.2136/sssaj1974.03615995003800010032x
- Stanford, G., M.H. Frere, and D.H. Schwaninger. 1973. Temperature coefficient of soil nitrogen mineralization. *Soil Sci.* 115:321–323. doi:10.1097/00010694-19730400-00009
- Stanford, G., and S.J. Smith. 1972. Nitrogen mineralization potentials of soils. *Soil Sci. Soc. Am. Proc.* 36:465–472. doi:10.2136/sssaj1972.03615995003600030029x
- Stark, J.M., and M.K. Firestone. 1995. Mechanisms for soil moisture effects on activity of nitrifying bacteria. *Appl. Environ. Microbiol.* 61:218–221.
- Steinweg, J.M., A.F. Plante, R.T. Conant, E.A. Paul, and D.L. Tanaka. 2008. Patterns of substrate utilization during long-term incubations at different temperatures. *Soil Biol. Biochem.* 40:2722–2728. doi:10.1016/j.soilbio.2008.07.002
- Vance, E.D., P.C. Brookes, and D.S. Jenkinson. 1987. An extraction method for measuring microbial biomass C. *Soil Biol. Biochem.* 19:703–707. doi:10.1016/0038-0717(87)90052-6
- Zak, D.R., W.E. Holmes, N.W. MacDonald, and K.S. Pregitzer. 1999. Soil temperature, matric potential, and the kinetics of microbial respiration and nitrogen mineralization. *Soil Sci. Soc. Am. J.* 63:575–584. doi:10.2136/sssaj1999.03615995006300030021x

Copyright of Soil Science Society of America Journal is the property of American Society of Agronomy and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.