PERGAMON

Soil Biology & Biochemistry 33 (2001) 1103–1111

Soil Biology & Biochemistry

www.elsevier.com/locate/soilbio

Climatic influences on active fractions of soil organic matter

A.J. Franzluebbers[a,*], R.L. Haney[b], C.W. Honeycutt[c], M.A. Arshad[d], H.H. Schomberg[a], F.M. Hons[b]

[a]*US Department of Agriculture—Agricultural Research Service, J. Phil Campbell Sr. Natural Resource Conservation Center, 1420 Experiment Station Road, Watkinsville, GA 30677, USA*

[b]*Texas A&M University, Texas Agricultural Experiment Station, Department of Soil & Crop Sciences, College Station, TX 77843, USA*

[c]*US Department of Agriculture—Agricultural Research Service, New England Plant, Soil, and Water Laboratory, Orono, ME 04469, USA*

[d]*Agriculture and Agri-Food Canada, Northern Agriculture Research Centre, PO Box 29, Beaverlodge, Alberta, T0H 0C0, Canada*

Received 15 April 1999; received in revised form 5 November 1999; accepted 25 October 2000

Abstract

Biologically active fractions of soil organic matter are important in understanding decomposition potential of organic materials, nutrient cycling dynamics, and biophysical manipulation of soil structure. We evaluated the quantitative relationships among potential C and net N mineralization, soil microbial biomass C (SMBC), and soil organic C (SOC) under four contrasting climatic conditions. Mean SOC values were 28 ± 11 mg g^{-1} ($n = 24$) in a frigid–dry region (Alberta/British Columbia), 25 ± 5 mg g^{-1} ($n = 12$) in a frigid–wet region (Maine), 11 ± 4 mg g^{-1} ($n = 117$) in a thermic–dry region (Texas), and 12 ± 5 mg g^{-1} ($n = 131$) in a thermic–wet region (Georgia). Higher mean annual temperature resulted in consistently greater basal soil respiration (1.7 vs 0.8 mg CO_2–C g^{-1} SOC d^{-1} in the thermic compared with the frigid regions, $P < 0.001$), greater net N mineralization (2.8 vs 1.3 mg inorganic N g^{-1} SOC 24 d^{-1}, $P < 0.001$), and greater SMBC (53 vs 21 mg SMBC g^{-1} SOC, $P < 0.001$). Specific respiratory activity of SMBC was, however, consistently lower in the thermic than in the frigid regions (29 vs 34 mg CO_2–C g^{-1} SMBC d^{-1}, $P < 0.01$). Higher mean annual precipitation resulted in consistently lower basal soil respiration (1.1 vs 1.3 mg CO_2–C g^{-1} SOC d^{-1} in the wet compared with the dry regions, $P < 0.01$) and lower SMBC (31 vs 43 mg SMBC g^{-1} SOC, $P < 0.001$), but had inconsistent effects on net N mineralization that depended upon temperature regime. Specific respiratory activity of SMBC was consistently greater in the wet than the dry regions (≈ 33 vs 29 mg CO_2–C g^{-1} SMBC d^{-1}, $P < 0.01$). Although the thermic regions were not able to retain as high a level of SOC as the frigid regions, due likely to high annual decomposition rates, biologically active soil fractions were as high per mass of soil and even 2–3-times greater per unit of SOC in the thermic compared with the frigid regions. These results suggest that macroclimate has a large impact on the portion of soil organic matter that is potentially active, but a relatively small impact on the specific respiratory activity of SMBC. Published by Elsevier Science Ltd.

Keywords: Carbon mineralization; Climate; Nitrogen mineralization; Soil microbial activity; Soil microbial biomass; Soil organic carbon

1. Introduction

Macroclimatic influences on biologically active fractions of soil organic matter are not yet well understood. This limits cross-regional, environmental assessments (i.e. modeling approaches) of management systems that are based on the mechanisms of transformations and storage of organic matter. Reasons for this knowledge gap include: (i) complex interactive effects among precipitation, temperature, soil texture, and land use on active fractions; (ii) highly dependent relationship of active fractions on the level of soil organic C (SOC) within a region; and (iii) use of a wide array of methodologies to characterize active fractions that make comparisons across individual studies difficult.

Standing stock of SOC is generally greater in both colder and wetter climates compared with hotter and drier climates (Jenny, 1941; Jenkinson, 1988). Since soil microbial biomass C (SMBC) and mineralizable C are often highly related to the level of SOC (Woods and Schuman, 1986; Insam, 1990; Franzluebbers et al., 1994, 1996), separating these total and active fractions from that of climate can only be achieved with expression of active fractions per unit of SOC.

Insam et al. (1989) found that the ratio of SMBC-to-SOC tended to increase with higher mean annual temperature in an analysis of 12 frigid and mesic locations in North America with a precipitation-to-evaporation ratio of 0.49 ± 0.23.

* Corresponding author. Tel.: +1-706-769-5631; fax: +1-706-769-8962.
E-mail address: afranz@arches.uga.edu (A.J. Franzluebbers).

0038-0717/01/$ - see front matter Published by Elsevier Science Ltd.
PII: S0038-0717(01)00016-5

However, when nine predominantly thermic locations with a precipitation-to-evaporation ratio of 1.04 ± 0.28 were included in the analysis, the ratio of SMBC-to-SOC tended to decrease with higher temperature (Insam, 1990). It remains unclear whether mean annual temperature or mean annual precipitation has a more profound effect on soil microbial biomass and potential activity.

Although abundant information on biologically active soil fractions is available from various ecoregions in the world, synthesis of data is problematic. Protocols for measuring SMBC are numerous and results are not well correlated with each other across soil types and regions (Wardle and Parkinson, 1991; Martens, 1995). Different methods may measure a somewhat different fraction of microbial biomass (Wardle and Parkinson, 1991). Even when using the same method, estimates of SMBC can vary due to a wide range of efficiency factors (k_{EC} of 0.10–0.66) that would be necessary for different soils (Sparling and West, 1988; Martikainen and Palojärvi, 1990; Sparling et al., 1990; Wu et al., 1990). Variation in the ratio of SMBC-to-SOC due to macroclimatic influences may be of the same order of magnitude [25 ± 12 mg SMBC g^{-1} SOC (mean $\pm$ standard deviation among sites) (Insam et al., 1989; Insam, 1990)] as variation caused by methodology within studies [difference among methods was 13–54 mg g^{-1} in Horwath et al. (1996) and 2–22 mg g^{-1} in Beck et al. (1997)].

Our objective was to assess the effects of gross climatic differences among four regions in North America on SMBC and mineralizable C and N. We collected soils from multiple sites, soil textural classes, management systems, and soil depths within a region to broaden our scope and help avoid these variables causing unintentional confounding effects. It is also difficult to obtain soils with the same textural class and management system in such diverse ecoregions. These conditions resulted in a wide range of SOC within a region so that active soil C and N fractions could be adequately regressed across a wide range in SOC.

2. Materials and methods

2.1. Soils and sites

Soils were collected from various depth increments down to 0.3 m from several long-term management sites in Alberta/British Columbia, Maine, Texas, and Georgia during April through June of 1992 to 1997 prior to planting of row crops or summer forage growth (October 1997 following crop growth in Maine) (Table 1). Management effects and further description of experimental setup can be found in Franzluebbers and Arshad (1996a,b, 1997) for samples collected in Alberta/British Columbia, in Haney (1997); Schomberg and Jones (1999) for samples collected in Texas, and in Lovell et al. (1997) and Franzluebbers et al. (1999c,d) for samples collected in Georgia. This paper is not concerned with management effects, but rather attempts to distinguish relationships among active soil C and N fractions due to climatic differences.

The four geographical regions we selected could be characterized relatively as frigid–dry [Alberta/British Columbia; 2°C mean annual temperature, 0.5 m mean annual precipitation (P), 0.9 mean annual precipitation/potential evapotranspiration (P/PET)], frigid–wet (Maine; 7°C, 1.1 m P, 1.9 P/PET), thermic–dry (Texas; weighted mean based on distribution of observations of 18°C, 0.6 m P, 0.6 P/PET), and thermic–wet (Georgia; 17°C, 1.3 m P, 1.4 P/PET).

2.2. Soil analyses

Potential C mineralization (CMIN) was determined from 15 to 120 g subsamples of soil under the following set of standard conditions. Soil was oven-dried (55°C, 48 h) and gently crushed to pass a 4.75-mm screen. Duplicate soil subsamples were moistened to 50% water-filled pore space following light tamping in a graduated jar and incubated at 25 ± 1°C in 1-l canning jars containing vials with 10 ml of 1.0 *M* NaOH to absorb CO_2 and water to maintain humidity. Alkali traps were replaced at 3 and 10 d and removed at 24 d. Carbon dioxide evolved was determined by titration of alkali with 1.0 *M* HCl (Anderson, 1982). Basal soil respiration (BSR) was calculated as the linear rate of CMIN during 3–24 d to avoid the majority of the flush of activity due to drying and rewetting. At 10 d, one of the subsamples was removed, fumigated with chloroform, and incubated separately for a further 10 d under the same conditions to determine the flush of CO_2–C representing SMBC using a k_C factor of 0.41 (Voroney and Paul, 1984). Determination of SMBC following rewetting of dried soil with 3–10 d of pre-incubation has been shown to yield, not only highly correlated, but also equivalent absolute estimates compared with those from field-moist soil (Franzluebbers et al., 1996; Franzluebbers, 1999b). Deviations from this standard protocol were using air-dried soil, sieving to pass a 5.6-mm screen, and adjusting water content to -10 to -30 kPa [equivalent to ~50% water-filled pore space (Franzluebbers, 1999a)] for soils in Alberta/British Columbia; sieving to pass a 6-mm screen, air-drying, and removing alkali traps at 3, 10, and 25 d for the Pullman CL soil in Texas; and oven-drying at 40°C, sieving to pass a 5-mm screen, adjusting water content to -10 to -30 kPa, and removing alkali traps at 1, 3, 7 (subsample fumigated), 17, and 24 d for the remaining soils in Texas. Results were not expected to be overly influenced by these minor variations in drying temperature (unpublished data, 1997), sieve size (Franzluebbers, 1999b), water adjustment (Franzluebbers, 1999a), and incubation period prior to fumigation (Franzluebbers et al., 1996).

Net N mineralization (NMIN) was determined from inorganic N (NO_3–N + NO_2–N + NH_4–N) concentration

Table 1
Soil and environmental characteristics of samples used to develop relationships among active soil C and N fractions (n = number of samples, T = mean annual temperature in °C, P = mean annual precipitation in mm, P/PET = precipitation/potential evapotranspiration in mm mm^{-1})

Location	USDA soil classification	n	pH	T	P	P/PET	Land management and soil sampling depths (mm)
Dawson Creek, British Columbia (55°N, 120°W)	Donnelly silt loam (fine-loamy, mixed, frigid Typic Cryoboralf)	6	5.5	1	504	1.0	Barley (*Hordeum vulgare*) under conventional and no tillage (0–50, 50–125, 125–200)
Rolla, British Columbia (55°N, 120°W)	Donnelly sandy loam (coarse-loamy, mixed, frigid Typic Cryoboralf)	6	6.6	1	504	1.0	Wheat (*Triticum aestivum*), canola (*Brassica campestris*), barley rotation under conventional and no tillage (0–50, 50–125, 125–200)
Rycroft, Alberta (55°N, 118°W)	Falher clay (fine, montmorillonitic, frigid Typic Natriboralf)	6	5.7	2	449	0.9	Barley, wheat, pea (*Pisum sativum*) rotation under no and conventional tillage (0–50, 50–125, 125–200)
Beaverlodge, Alberta (55°N, 119°W)	Hythe clay loam (fine, montmorillonitic frigid Mollic Cryoboralf)	6	6.7	2	452	0.9	Barley, canola, pea rotation under conventional and no tillage (0–50, 50–125, 125–200)
Newport, Maine (45°N, 69°W)	Bangor silt loam (coarse-loamy, mixed, frigid Typic Haplorthod)	6	5.4	7	1070	1.9	Grass sod and potato (*Solanum tuberosum*) cropping (0–50, 50–100, 100–200)
Stillwater, Maine (45°N, 68°W)	Nicholville very fine sandy loam (coarse-silty, isotic, frigid Aquic Haplorthod) and Lamoine silt loam (fine, illitic, nonacid, frigid Aeric Epiaquept)	6	6.1	7	1070	1.9	Wheat, clover (*Trifolium pratense*), dry bean (*Phaseolus vulgaris*), maize (*Zea mays*) cropping (0–50, 50–100, 100–200)
Lubbock, Texas (33°N, 101°W)	Acuff loam (fine-loamy, mixed, thermic Aridic Paleustoll)	9	7.4	16	457	0.5	Sorghum (*Sorghum bicolor*) with 0–220 kg N ha^{-1} and 0–132 kg P ha^{-1} (0–100)
Amarillo, Texas (35°N, 101°W)	Pullman clay loam (fine, mixed, thermic Vertic Paleustoll)	56	6.0	17	425	0.5	Wheat, sorghum under conventional and no tillage with 0–55 kg N ha^{-1} (0–20, 20–40, 40–80, 0–100)
Stephenville, Texas (32°N, 98°W)	Windthorst fine sandy loam (fine, mixed, thermic Udic Paleustalf)	20	6.5	18	750	0.8	Bermudagrass (*Cynodon dactylon*) hay receiving 0–450 kg N ha^{-1} dairy manure (0–100)
College Station, Texas (30°N, 96°W)	Weswood silty clay loam (fine, mixed, thermic Fluventic Ustochrept)	18	8.2	20	978	0.9	Sorghum, wheat, soybean (*Glycine max*) under conventional and no tillage (0–100)
Overton, Texas (32°N, 94°W)	Bowie fine sandy loam (fine-loamy, siliceous, thermic Plinthic Paleudult)	8	5.9	20	1050	1.0	Bermudagrass hay receiving 0–450 kg N ha^{-1} as poultry manure (0–100)
Corpus Christi, Texas (27°N, 97°W)	Victoria clay (fine, montmorillonitic, hyperthermic Udic Pellustert)	6	8.0	22	765	0.6	Sorghum, maize under conventional and reduced tillage with 0–60 kg N ha^{-1} (0–100)
Farmington, Georgia (33°N, 83°W)	Appling, Cecil, Grover, Louisa, Madison, Pacolet, and Wedowee loamy sand, sandy loam, loam, sandy clay loam (clayey, kaolinitic, thermic Typic Kanhapludults)	54	6.0	17	1250	1.4	Bermudagrass pasture receiving N via inorganic, clover (*Trifolium incarnatum*), poultry litter sources under low and high cattle grazing pressures (0–20, 20–40, 40–60)
Watkinsville, Georgia (34°N, 83°W)	Cecil sandy loam (clayey, kaolinitic, thermic Typic Kanhapludult)	77	6.0	17	1250	1.4	Cotton (*Gossypium hirsutum*), rye (*Secale cereale*) under no tillage with various frequencies and intensities of tillage; tall fescue (*Festuca arundinacea*) with and without endophyte (*Neotyphodium coenophialum*) (0–25, 25–75, 75–150, 150–300)

Table 2
Association of active soil C and N fractions with soil organic C (SOC) as influenced by climatic region ($n = 284$) ($CMIN_{0-3\ d}$ is the flush of CO_2–C evolved following rewetting of dried soil during 3 d of incubation (mg kg^{-1} soil), $CMIN_{0-24\ d}$ is cumulative carbon mineralization during 24 d of incubation (mg kg^{-1} soil), BSR is basal soil respiration (mg kg^{-1} soil d^{-1}), SMBC is soil microbial biomass carbon (mg kg^{-1} soil), $NMIN_{0-24\ d}$ is net nitrogen mineralization during 24 d of incubation (mg kg^{-1} soil), and SOC is soil organic carbon (g kg^{-1} soil). $*P \leq 0.1$, $**P \leq 0.01$, and $***P \leq 0.001$)

Source of variation	$CMIN_{0-3\ d}$	$CMIN_{0-24\ d}$	BSR	SMBC	$NMIN_{0-24\ d}$
Variability explained (%)					
SOC alone	26.4***	35.2***	34.7***	31.3***	15.3***
Thermic (Texas + Georgia) vs frigid (Alberta + Maine)	13.7***	21.2***	22.0***	35.9***	24.1***
Wet (Maine + Georgia) vs dry (Alberta + Texas)	9.4***	0.0	1.1**	8.5***	3.5***
Alberta + Georgia vs Maine + Texas	0.8*	0.3	0.1	0.0	4.5***
Regression coefficients (microbial biomass or activity = $\beta_0 + \beta_1$ SOC)					
β_0	− 12.6	− 116.3	− 4.9	111.5	− 1.3
β_1 [Alberta/British Columbia (AB), frigid–dry]	5.1	23.9	0.89	26.9	0.75
β_1 [Maine (ME), frigid–wet]	7.7	22.3	0.69	15.4	1.74
β_1 [Texas (TX), thermic–dry]	9.7	45.6	1.71	59.4	2.83
β_1 [Georgia (GA), thermic–wet]	14.5	48.2	1.61	46.6	2.76

at 0 and 24 d of incubation using Cd reduction and salicylate–nitroprusside autoanalyzer techniques from 2 *M* KCl extracts (Bundy and Meisinger, 1994). At 0 and 24 d, soil was oven-dried (55°C, 48 h), sieved to pass a 2-mm screen, and a 10-g subsample shaken with 20 ml of 2 *M* KCl for 30 min. Soils from Texas were dried at 60°C and a 7-g subsample shaken with 28 ml of 2 *M* KCl. Soils from Alberta/British Columbia were analyzed for NH_4–N using a citrate buffer autoanalyzer technique.

Soil organic C and N were determined either by dry combustion for soils in Maine and Georgia ($pH < 7$) or dichromate oxidation with heating to 150°C for 1 h and Kjeldahl digestion for soils in Alberta/British Columbia and Texas (Bremner and Mulvaney, 1982; Nelson and Sommers, 1982). The presence of carbonates in soils from Alberta/British Columbia and Texas led us to choose wet oxidation procedures for analysis in those regions.

2.3. Statistical analyses

Data in the analyses represent means from 3 to 13 replications, which were independent samples taken from the field, per treatment—depth combination. Regression analyses were performed using the general linear model procedure of SAS (SAS Institute Inc., 1990) to obtain four slope estimates (i.e. one for each region) with a common intercept. Regression with a common intercept for all regions allowed us to analyze slopes only, which simplified the interpretation of statistical parameters by not allowing slope and intercept estimates to covary. Multiple-parameter regressions often lead to strong correlations among parameters, which are difficult to interpret separately (Kätterer et al., 1998). Significant differences among slopes were tested with orthogonal contrasts to distinguish effects of (i) temperature class [thermic (Texas, Georgia) vs frigid (Alberta/British Columbia, Maine)], (ii) precipitation class [wet (Maine, Georgia) vs dry (Alberta/British Columbia, Texas)], and (iii) the interaction between temperature and precipitation classes.

3. Results and discussion

3.1. Temperature effect on biologically active fractions relative to soil organic C (SOC)

Mean SOC values were 28 ± 11 mg g^{-1} ($n = 24$) in Alberta/British Columbia, 25 ± 5 mg g^{-1} ($n = 12$) in Maine, 11 ± 4 mg g^{-1} ($n = 117$) in Texas, and 12 ± 5 mg g^{-1} ($n = 131$) in Georgia. It has been previously found that soils from colder regions contain more SOC than soils from hotter regions (Jenny, 1941; Jenkinson, 1988). Lower temperature, especially in winter when it falls below a threshold for activity, limits decomposition of organic matter resulting in accumulation with time. It should also be noted that total C input via plant production is also likely lower throughout the year in a frigid region, suggesting that actual turnover of organic matter input would be much slower than in a thermic region.

Ratios of $CMIN_{0-3\ d}$-to-SOC, $CMIN_{0-24\ d}$-to-SOC, BSR-to-SOC, SMBC-to-SOC, and $NMIN_{0-24\ d}$-to-SOC were all consistently greater in the thermic (Texas and Georgia) than in the frigid (Alberta/British Columbia and Maine) regions (Figs. 1–3) (Table 2). Greater active fractions relative to SOC in the thermic than in the frigid regions may have been a consequence of longer time for plant production and subsequent development of biologically active soil fractions from these substrates. Suitable environmental conditions for plant and soil biological activity in the frigid regions occur primarily during the short summer with suboptimal temperatures limiting activity for a large portion of the year. In the long-term, decomposition of organic inputs to soil may be halted prematurely in frigid regions, such that partially decomposed organic C accumulates. These partially decomposed substrates may then undergo further

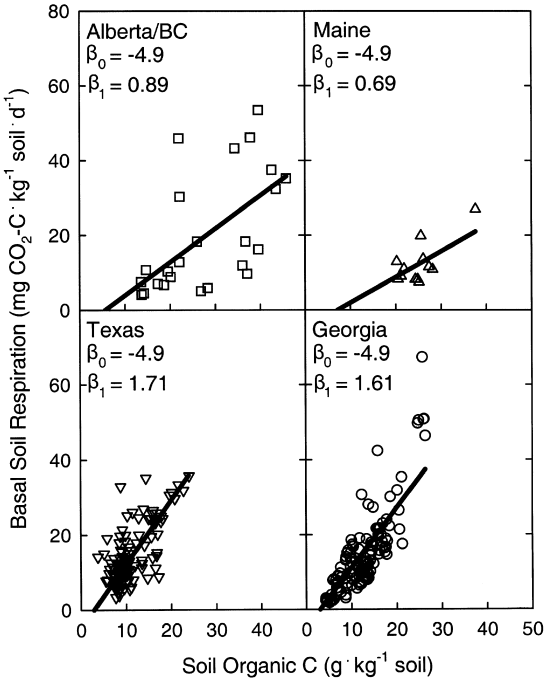

Fig. 1. Relationship of basal soil respiration with soil organic C (BSR-to-SOC) in surface soils from frigid–dry (Alberta/British Columbia), frigid–wet (Maine), thermic–dry (Texas), and thermic–wet (Georgia) climates. Significance of difference in slope among climatic regions is noted in column 4 of Table 2.

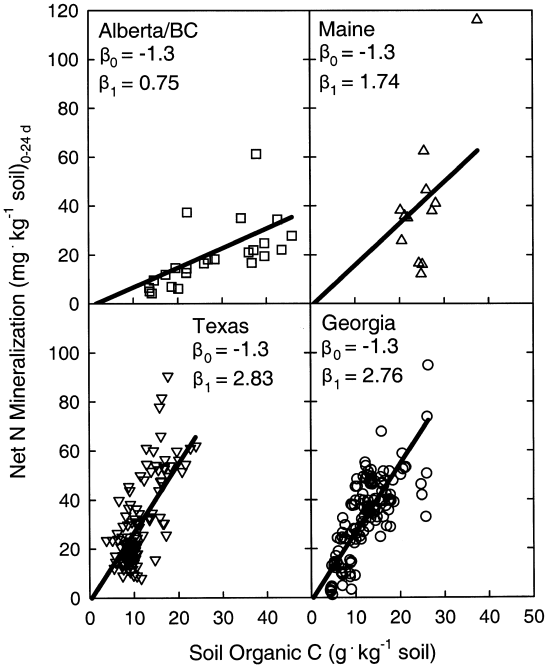

Fig. 3. Relationship of net N mineralization during 24 d with soil organic C ($NMIN_{0-24\ d}$-to-SOC) in surface soils from frigid–dry (Alberta/British Columbia), frigid–wet (Maine), thermic–dry (Texas), and thermic–wet (Georgia) climates. Significance of difference in slope among climatic regions is noted in column 6 of Table 2.

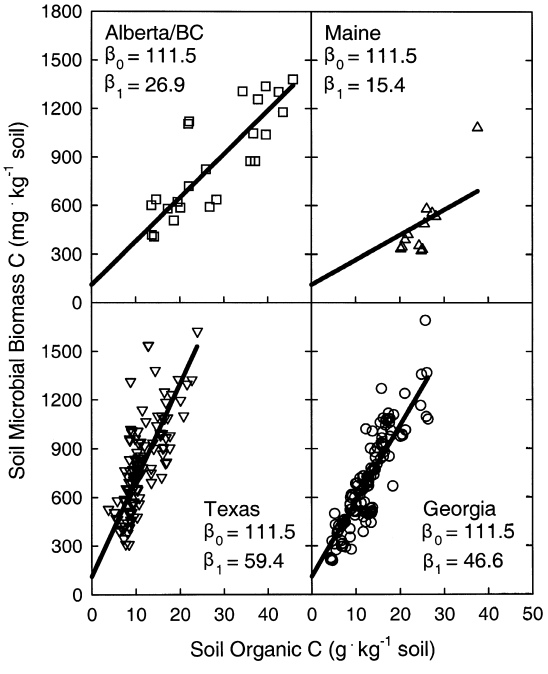

Fig. 2. Relationship of soil microbial biomass C with soil organic C (SMBC-to-SOC) in surface soils from frigid–dry (Alberta/British Columbia), frigid–wet (Maine), thermic–dry (Texas), and thermic–wet (Georgia) climates. Significance of difference in slope among climatic regions is noted in column 5 of Table 2.

chemical transformations under sub-optimal conditions of decomposition leading to long-lasting sequestration of this organic matter. Accumulation of resistant SOC in frigid regions may be the reason that active soil C and N fractions became a smaller fraction of total C compared with thermic regions. It is also possible that the species and functional composition of the microbial biomass between frigid and thermic regions is significantly different because of major differences in climate controls and resource availability.

The consistent temperature effect on the ratio of SMBC-to-SOC corroborates an observation by Franzluebbers and Arshad (1996a) that soils from Alberta/British Columbia (0.9 P/PET) contained a lower ratio of SMBC-to-SOC ($CHCl_3$ fumigation–incubation) than a Fluventic Ustochrept in Texas (20°C, 1.0 m P, 0.9 P/PET) (an independent data set not used in this study). Powlson and Jenkinson (1976) also reported a somewhat lower ratio of SMBC-to-SOC ($CHCl_3$ fumigation–incubation) in arable soils from England compared with Nigeria. In an analysis of soils from 21 locations in North America, Insam et al. (1989) found no significant effect of temperature on the ratio of SMBC-to-SOC (substrate-induced respiration). In contrast, Grisi et al. (1998) reported that three temperate British soils tended to have a higher ratio of SMBC-to-SOC ($CHCl_3$ fumigation–extraction) (23 ± 10 mg SMBC g^{-1} SOC) than three tropical Brazilian soils (17 ± 4 mg SMBC g^{-1} SOC). Differences in method of determination of SMBC may be one explanation for inconsistent temperature effects

among studies, since correlations among SMBC methods are not always strong (Wardle and Ghani, 1995; Franzluebbers et al., 1999a,b). Also, major differences in soil mineralogical, chemical, and physical properties among these locations, as well as differences in land use history, could have altered soil biological responses differently than the pattern we observed.

Insam (1990) reported that BSR was negatively correlated with mean annual temperature, primarily because SOC decreased with increasing temperature. However, when we calculated BSR per unit of SOC found in the Insam (1990) study, no effect of mean annual temperature on BSR-to-SOC was observed. Mean annual temperature and precipitation were correlated ($r = 0.79$, $n = 21$) in the studies of Insam et al. (1989); Insam (1990). Although we did not evaluate as many locations as Insam et al. (1989), locations in our study were factorially separated to distinguish between gross temperature and precipitation effects. Our findings of greater BSR-to-SOC in the thermic compared with the frigid regions also seem to be in contrast to the results of (i) Powlson and Jenkinson (1976), where the ratio of CMIN-to-SOC was not different between soils from Nigeria and England and (ii) Grisi et al. (1998), where soils from Brazil had less than half the ratio of CMIN-to-SOC compared with soils from England. Tropical soils, such as those in Nigeria and Brazil, may have unique biogeochemical characteristics that are different from the soils and climatic controls in our study. Our data encompass the frigid and thermic regions only, but not the hyperthermic region of the tropics. Further work is needed to test the consistency of relationships within and outside of the climatic boundaries we studied.

3.2. Precipitation effect on biologically active fractions relative to soil organic C

Precipitation had no significant effect on SOC when data were averaged across soils, management systems, and sampling depths. Others have reported general increases in SOC with increasing precipitation (Jenny, 1941; Sparling, 1992), which would potentially lead to higher plant production and organic C input, but also greater decomposition.

Mean annual precipitation affected biologically active soil fractions relative to SOC (Table 2), but effects were generally much smaller (0–10% of variation explained) than those due to temperature (14–36% of variation explained). Ratios of BSR-to-SOC and SMBC-to-SOC were $23 \pm 15\%$ lower in the wet than the dry regions (Figs. 1 and 2) (Table 2). However, ratio of $CMIN_{0-24\ d}$-to-SOC was unaffected by precipitation regime partly because a portion of this estimate (i.e. $CMIN_{0-3\ d}$) increased with increasing precipitation. The flush of CO_2 evolved during 3 d may have been greater in soils of the wet than the dry regions, partly because soils in Maine and Georgia (i.e. wet region) were dried at 55°C prior to incubation, while soils in Alberta/British Columbia and Texas (i.e. dry region) were dried at either 22 or 40°C. Higher drying temperature causes an increase in initial C mineralization (i.e. 0–3-d flush), but does not affect steady-state C mineralization (unpublished data, 1998). Lower ratios of BSR-to-SOC and SMBC-to-SOC in wet than in dry regions were also observed for other soils in North America (Insam, 1990) and in New Zealand (Sparling, 1992).

The effect of precipitation on the ratio of $NMIN_{0-24\ d}$-to-SOC was dependent upon temperature regime (Table 2). Ratio of $NMIN_{0-24\ d}$-to-SOC was greater in the wet (Maine) than the dry (Alberta/British Columbia) part of the frigid region, but was unaffected by precipitation in the thermic region. It is unclear why the soils from Alberta/British Columbia had a lower ratio of $NMIN_{0-24\ d}$-to-SOC than soils from Maine. The ratio of $CMIN_{0-24\ d}$-to-$NMIN_{0-24\ d}$ was significantly affected by region, averaging 23 in Alberta/British Columbia, eight in Maine, 10 in Texas, and 11 in Georgia. Net N mineralization from soils in Alberta/British Columbia was clearly lower (Fig. 3) than from all other regions and the reason for this difference is unclear. It may be that more resistant organic matter in frigid, dry regions leads to greater immobilization of N, more so than in other regions.

3.3. Temperature and precipitation effects on specific activities of microbial biomass

Specific activities of SMBC (i.e. $CMIN_{0-3\ d}$-to-SMBC, $CMIN_{0-24\ d}$-to-SMBC, BSR-to-SMBC, and $NMIN_{0-24\ d}$-to-SMBC) were significantly affected by climate, but generally less affected by temperature (1–3% of variability explained) than by precipitation (1–15% of variability explained) regime (Table 3) (Fig. 4). Ratios of $CMIN_{0-3\ d}$-to-SMBC, $CMIN_{0-24\ d}$-to-SMBC, and BSR-to-SMBC in the thermic regions were consistently lower ($20 \pm 5\%$) than those in the frigid regions. Ratio of $NMIN_{0-24\ d}$-to-SMBC was also lower in the wet-thermic region (Georgia) than in the wet-frigid region (Maine), but greater in the dry-thermic region (Texas) than in the dry-frigid region (Alberta/British Columbia). The reason for this interaction is unclear. Lower specific activities of SMBC in the thermic than in the frigid regions suggest either (i) less readily mineralizable C and N are available for maintenance of microbial biomass in thermic regions or (ii) mineralization of C and N from the greater pool of intermediately-available organic matter in the frigid regions contributes little to microbial biomass. Further work is needed to verify these hypotheses. If we consider the ratio of BSR-to-SMBC as potential turnover of SMBC, then our results would be consistent with observations made by Wardle (1998), where the turnover rate of SMBC was greater with increasing latitude (i.e. lower mean annual temperature).

Ratios of $CMIN_{0-3\ d}$-to-SMBC, $CMIN_{0-24\ d}$-to-SMBC, BSR-to-SMBC, and $NMIN_{0-24\ d}$-to-SMBC were all consistently lower in the dry than in the wet regions (Table 3). The dry regions had specific activity ratios $66 \pm 22\%$ of those in the wet regions. Soils in the wet regions may have had more

Table 3
Association of mineralizable C and N with soil microbial biomass C (SMBC) as influenced by climatic region ($n = 284$) ($CMIN_{0-3\ d}$ is the flush of CO_2–C evolved following rewetting of dried soil during 3 d of incubation (mg kg^{-1} soil), $CMIN_{0-24\ d}$ is cumulative carbon mineralization during 24 d of incubation (mg kg^{-1} soil), BSR is basal soil respiration (mg kg^{-1} soil d^{-1}), $NMIN_{0-24\ d}$ is net nitrogen mineralization during 24 d of incubation (mg kg^{-1} soil), and SMBC is soil microbial biomass carbon (mg kg^{-1} soil). $*P \le 0.1$, $**P \le 0.01$, $***P \le 0.001$)

Source of variation	$CMIN_{0-3\ d}$	$CMIN_{0-24\ d}$	BSR	$NMIN_{0-24\ d}$
Variability explained (%)				
SMBC alone	38.1***	61.5***	64.5***	30.0***
Thermic (Texas + Georgia) vs frigid (Alberta + Maine)	3.2***	1.7***	1.1**	2.1***
Wet (Maine + Georgia) vs dry (Alberta + Texas)	14.5***	3.1***	0.7**	15.3***
Alberta + Georgia vs Maine + Texas	1.1***	0.1	0.0	9.0***
Regression coefficients (mineralizable C or N = $\beta_0 + \beta_1$ SMBC)				
β_0	− 21.2	− 148.1	− 6.0	2.6
β_1 [Alberta/British Columbia (AB), frigid–dry]	0.18	0.85	0.032	0.021
β_1 [Maine (ME), frigid–wet]	0.40	1.16	0.036	0.086
β_1 [Texas (TX), thermic–dry]	0.15	0.69	0.026	0.035
β_1 [Georgia (GA), thermic–wet]	0.28	0.92	0.031	0.044

readily mineralizable C and N available for maintenance of microbial biomass because of more continuous input of plant-derived organic inputs than soils in the dry regions. However, the possibility of greater availability of substrates did not contribute to parallel increases in SMBC. Insam (1990) reported a weak positive, but insignificant effect of precipitation on the ratio of BSR-to-SMBC. We were able to document statistically significant changes in biologically active soil fractions due to macroclimatic influences, perhaps because we utilized a regression approach with numerous observations along a gradient in soil organic matter within a region. This allowed more power to test the difference in slopes of active fractions among regions. For example, our approach of regressing SMBC on SOC resulted in F-values for temperature, precipitation, and temperature × precipitation contrasts of 327, 77, and 0, respectively. In comparison, F-values using absolute ratios of SMBC-to-SOC in our study [the approach employed by Insam (1990)] were only 185, 30, and 0, respectively.

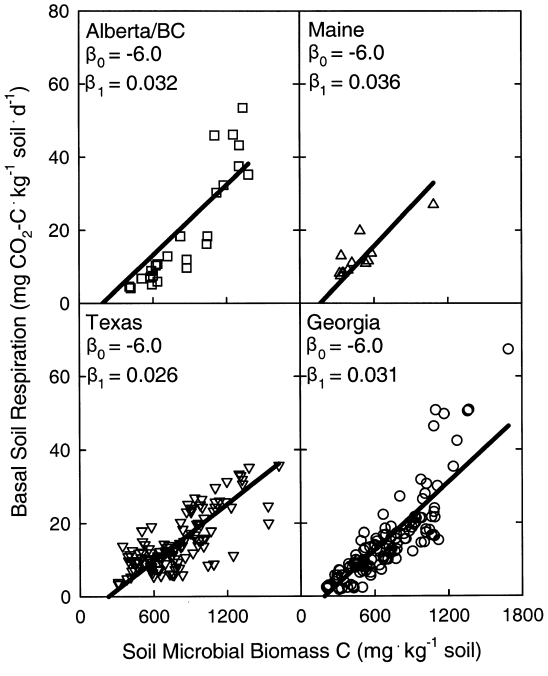

Fig. 4. Relationship of basal soil respiration with soil microbial biomass C (BSR-to-SMBC) in surface soils from frigid–dry (Alberta/British Columbia), frigid–wet (Maine), thermic–dry (Texas), and thermic–wet (Georgia) climates. Significance of difference in slope among climatic regions is noted in column 4 of Table 3.

Biologically active soil C and N fractions as a function of SOC were not related to P/PET (data not shown). Insam (1990) reported that P/PET was a major determinant of variability in SMBC-to-SOC among 12 sites in North America. Our data suggest that effects of temperature and precipitation on biologically active soil C and N fractions as a portion of SOC are, for the most part, independent. We did, however, observe that specific activities of SMBC were positively related to P/PET. For example, ratio of $CMIN_{0-24\ d}$-to-SMBC increased 334 mg g^{-1} 24 d^{-1} for every 1 m m^{-1} of P/PET ($r^2 = 0.95$, $n = 4$), ratio of BSR-to-SMBC increased 6 mg $^{-1}$ d^{-1} ($r^2 = 0.77$), and ratio of $NMIN_{0-24\ d}$-to-SMBC increased 43 mg g^{-1} 24 d^{-1} ($r^2 = 0.76$). In comparisons of ecosystems, higher BSR-to-SMBC has been suggested as an indication of disturbance or stress (Odum, 1985) and of soil maturity or rehabilitation (Insam and Haselwandter, 1989). However in our study, less stress (i.e. increasing P/PET) led to increasing specific activities of SMBC. We believe that differences in specific activities along this climatic gradient reflect differences in substrate availability, substrate quality, and microbial utilization, rather than ecosystem stress or development. The positive relationship between specific activities and P/PET that we report contradicts that reported by Insam (1990), where the ratio of BSR-to-SMBC decreased significantly ($r^2 = 0.45$) with an increase in P/PET. Differences in methodology for determining SMBC may have contributed to these contradictory findings and/or the strong correlation between temperature and precipitation may have confounded the results of Insam (1990). We did not evaluate

as many sites as Insam (1990), but our results were consistent whether specific activity was calculated with C or N mineralization. Further work is needed to clarify this discrepancy among studies. We suggest that further work be conducted on more soils in different ecoregions to validate the initial relationships developed.

4. Conclusions

Mean annual temperature had a greater influence on biological properties expressed per unit of SOC than did mean annual precipitation. Although thermic regions are not able to retain as large a portion of organic inputs as SOC compared with frigid regions due to high annual decomposition rates, biologically active components of soil organic matter in thermic regions were as high per mass of soil and 2.3 ± 0.7-times greater per unit of SOC than in frigid regions. Ratios of BSR-to-SOC and SMBC-to-SOC in the wet regions were 23 ± 15% lower than in the dry regions. Macroclimate influenced specific activities of SMBC less (13 ± 12% of variation) than active fractions of SOC (29 ± 10% of variation). This implies that, on an absolute basis, microbial activity and biomass are much more intimately linked across major differences in climate than microbial biomass/activity and total organic C. Differences in climate, therefore, alter the quantity of various fractions of organic matter that are less utilized by microorganisms. The frigid and wet regions had a greater pool of biologically unavailable organic matter than the thermic and dry regions. We did not distinguish whether this biologically unavailable fraction was composed more of intermediately available or resistant fractions.

Acknowledgements

We appreciate the work of Mr A. David Lovell, Mr Steven W. Knapp, and Ms Georgette Trusty in the field and laboratory.

References

Anderson, J.P.E., 1982. Soil respiration. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.). Methods of Soil Analysis, Part 2: Chemical and Microbiological Properties. 2nd ed. American Society of Agronomy and Soil Science Society of America, Madison, WI, pp. 837–871.

Beck, T., Joergensen, R.G., Kandeler, E., Makeschin, F., Nuss, E., Oberholzer, H.R., Scheu, S., 1997. An inter-laboratory comparison of ten different ways of measuring soil microbial biomass C. Soil Biology & Biochemistry 29, 1023–1032.

Bremner, J.M., Mulvaney, C.S., 1982. Nitrogen-total. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.). Methods of Soil Analysis, Part 2: Chemical and Microbiological Properties. American Society of Agronomy and Soil Science Society of America, Madison, WI, pp. 595–624.

Bundy, L.G., Meisinger, J.J., 1994. Nitrogen availability indices. In: Weaver, R.W., Angle, J.S., Bottomley, P.S. (Eds.). Methods of Soil Analysis, Part 2: Microbiological and Biochemical Properties. Soil Science Society of America, Madison, WI, pp. 951–984.

Franzluebbers, A.J., 1999a. Microbial activity in response to water-filled pore space of variably eroded southern Piedmont soils. Applied Soil Ecology 11, 91–101.

Franzluebbers, A.J., 1999b. Potential C and N mineralization and microbial biomass from intact and increasingly disturbed soils of varying texture. Soil Biology & Biochemistry 31, 1083–1090.

Franzluebbers, A.J., Arshad, M.A., 1996a. Soil organic matter pools during early adoption of conservation tillage in northwestern Canada. Soil Science Society of America Journal 60, 1422–1427.

Franzluebbers, A.J., Arshad, M.A., 1996b. Soil organic matter pools with conventional and zero tillage in a cold, semiarid climate. Soil and Tillage Research 39, 1–11.

Franzluebbers, A.J., Arshad, M.A., 1997. Soil microbial biomass and mineralizable carbon of water-stable aggregates. Soil Science Society of America Journal 61, 1090–1097.

Franzluebbers, A.J., Hons, F.M., Zuberer, D.A., 1994. Long-term changes in soil carbon and nitrogen pools in wheat management systems. Soil Science Society of America Journal 58, 1639–1645.

Franzluebbers, A.J., Haney, R.L., Hons, F.M., Zuberer, D.A., 1996. Determination of microbial biomass and nitrogen mineralization following rewetting of dried soil. Soil Science Society of America Journal 60, 1133–1139.

Franzluebbers, A.J., Haney, R.L., Hons, F.M., 1999a. Relationships of chloroform fumigation-incubation to soil organic matter pools. Soil Biology & Biochemistry 31, 395–405.

Franzluebbers, A.J., Haney, R.L., Hons, F.M., Zuberer, D.A., 1999b. Assessing biological soil quality with chloroform fumigation–incubation: why subtract a control?. Canadian Journal of Soil Science 79, 521–528.

Franzluebbers, A.J., Langdale, G.W., Schomberg, H.H., 1999c. Soil carbon, nitrogen, and aggregation in response to type and frequency of tillage. Soil Science Society of America Journal 63, 349–355.

Franzluebbers, A.J., Nazih, N., Stuedemann, J.A., Fuhrmann, J.J., Schomberg, H.H., Hartel, P.G., 1999d. Soil carbon and nitrogen pools under low- and high-endophyte-infected tall fescue. Soil Science Society of America Journal 63, 1687–1694.

Grisi, B., Grace, C., Brookes, P.C., Benedetti, A., Dell'Abate, M.T., 1998. Temperature effects on organic matter and microbial biomass dynamics in temperate and tropical soils. Soil Biology & Biochemistry 30, 1309–1315.

Haney, R.L., 1997. Soil carbon and nitrogen dynamics as affected by inputs of dairy manure and poultry litter. M.S. Thesis, August 1997, Texas A&M University.

Horwath, W.R., Paul, E.A., Harris, D., Norton, J., Jagger, L., Horton, K.A., 1996. Defining a realistic control for the chloroform fumigation–incubation method using microscopic counting and ^{14}C-substrates. Canadian Journal of Soil Science 76, 459–467.

Insam, H., 1990. Are the soil microbial biomass and basal respiration governed by the climatic regime? Soil Biology & Biochemistry 22, 525–532.

Insam, H., Haselwandter, K., 1989. Metabolic quotient of the soil microflora in relation to plant succession. Oecologia 79, 174–178.

Insam, H., Parkinson, D., Domsch, K.H., 1989. Influence of macroclimate on soil microbial biomass. Soil Biology & Biochemistry 21, 211–221.

Jenkinson, D.S., 1988. Soil organic matter and its dynamics. In: Wild, A. (Ed.). Russell's Soil Conditions and Plant Growth. 11th ed.. Longman, London, pp. 564–607.

Jenny, H., 1941. Factors of Soil Formation. McGraw-Hill, New York.

Kätterer, T., Reichstein, M., Andrén, O., Lomander, A., 1998. Temperature dependence of organic matter decomposition: a critical review using literature data analyzed with different models. Biology and Fertility of Soils 27, 258–262.

Lovell, A.D., Wilkinson, S.R., Stuedemann, J.A., Seman, D.H., Franzluebbers, A.J., 1997. Broiler litter and grazing pressure impacts on soil organic C and N pools. In: Agronomy Abstracts. American Society of Agronomy, Madison, WI, p. 217.

Martens, R., 1995. Current methods for measuring microbial biomass C in soil: potentials and limitations. Biology and Fertility of Soils 19, 87–99.

Martikainen, P.J., Palojärvi, A., 1990. Evaluation of the fumigation–extraction method for the determination of microbial C and N in a range of forest soils. Soil Biology & Biochemistry 22, 792–802.

Nelson, D.W., Sommers, L.E., 1982. Total carbon, organic carbon, and organic matter. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.). Methods of Soil Analysis, Part 2: Chemical and Microbiological Properties. American Society of Agronomy and Soil Science Society of America, Madison, WI, pp. 539–579.

Odum, E.P., 1985. Trends expected in stressed ecosystems. Bioscience 35, 419–422.

Powlson, D.S., Jenkinson, D.S., 1976. The effects of biocidal treatments on metabolism in soil. II. Gamma irradiation, autoclaving, air-drying and fumigation. Soil Biology & Biochemistry 8, 179–188.

SAS Institute Inc., 1990. SAS User's Guide: Statistics, Version 6 Ed. SAS Institute, Cary, NC.

Schomberg, H.H., Jones, O.R., 1999. Carbon and nitrogen conservation in dryland tillage and cropping systems. Soil Science Society of America Journal 63, 1359–1366.

Sparling, G.P., 1992. Ratio of microbial biomass carbon to soil organic carbon as a sensitive indicator of changes in soil organic matter. Australian Journal of Soil Research 30, 195–207.

Sparling, G.P., West, A.W., 1988. A direct extraction method to estimate soil microbial C: calibration in situ using microbial respiration and ^{14}C labelled cells. Soil Biology & Biochemistry 20, 337–343.

Sparling, G.P., Feltham, C.W., Reynolds, J., West, A.W., Singleton, P., 1990. Estimation of soil microbial C by a fumigation–extraction method: use on soils of high organic matter content, and a reassessment of the k_{EC}-factor. Soil Biology & Biochemistry 22, 301–307.

Voroney, R.P., Paul, E.A., 1984. Determination of k_C and k_N in situ for calibration of the chloroform fumigation–incubation method. Soil Biology & Biochemistry 16, 9–14.

Wardle, D.A., 1998. Controls of temporal variability of the soil microbial biomass: a global-scale synthesis. Soil Biology & Biochemistry 13, 1627–1637.

Wardle, D.A., Ghani, A., 1995. Why is the strength of relationships between pairs of methods for estimating soil microbial biomass often so variable?. Soil Biology & Biochemistry 27, 821–828.

Wardle, D.A., Parkinson, D., 1991. A statistical evaluation of equations for predicting total microbial biomass carbon using physiological and biochemical methods. Agriculture, Ecosystems and Environment 34, 75–86.

Woods, L.E., Schuman, G.E., 1986. Influence of soil organic matter concentrations on carbon and nitrogen activity. Soil Science Society of America Journal 50, 1241–1245.

Wu, J., Joergensen, R.G., Pommerening, B., Chaussod, R., Brookes, P.C., 1990. Measurement of soil microbial biomass C by fumigation–extraction—an automated procedure. Soil Biology & Biochemistry 22, 1167–1169.