Predicting the temperature dependence of microbial respiration in soil: A continental-scale analysis

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[1] The production of CO_2 by soil microorganisms is an important component of the global carbon cycle, and its temperature sensitivity is poorly constrained in global models. To improve our understanding of the factors controlling the temperature dependence of soil microbial respiration, we analyzed the temperature sensitivity of labile soil organic carbon decomposition for 77 soils collected from a wide array of ecosystem types. Across all of the soils, the average Q_{10} value (the factor by which decomposition rates increase for a 10°C increase in temperature) was 3.0, but the range in Q_{10} values was substantial (2.2 to 4.6). A large percentage (45%) of the variation in Q_{10} values could be explained by the relative rate of microbial respiration per unit organic C, an analog for C quality. This result provides support for the "carbon quality-temperature" hypothesis that directly links the temperature dependence of microbial decomposition and the biochemical recalcitrance of soil organic carbon. A smaller percentage (17%) of the variability in Q_{10} values could be explained by the mean monthly temperature at the time of sampling, suggesting that microbial communities may adapt to the antecedent temperature regime. By showing that the Q_{10} of microbial respiration in soil is largely predictable under standardized incubation conditions, this work increases our understanding of the temperature sensitivity of labile soil organic carbon stores.

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1. Introduction

[2] Soil is the largest global pool of terrestrial C and the soil organic C pool (approximately 2400 Pg of C) is at least three times larger than the size of the atmospheric carbon pool [*Batjes*, 1996; *Jobbágy and Jackson*, 2000]. The conversion of soil organic C to CO_2 by microorganisms is an important component of the global carbon cycle. We know that the rate of microbial CO_2 production from soil strongly depends on soil temperature [*Kätterer et al.*, 1998; *Kirschbaum*, 1995; *Lloyd and Taylor*, 1994; *Waksman and Gerretsen*, 1931], however there is no consensus on the specific relationship. Because rates of soil microbial respiration are likely to be more sensitive to temperature than rates of net primary production [*Raich and Schlesinger*, 1992; *Schimel et al.*, 1994], the predicted increase in global temperatures could cause a net transfer of carbon from soils to the atmosphere. Without an improved, mechanistic perspective on the relationship between temperature and microbial respiration, we will not be able to accurately predict the impacts of climate change on global C dynamics [*Intergovernmental Panel on Climate Change*, 1996; *Kirschbaum*, 2000].

[3] The sensitivity of microbial respiration to temperature is commonly described by Q_{10}, the factor by which CO_2 production increases for a 10°C increase in temperature. While Q_{10} can be used to describe the temperature sensitivity of any chemical process, in this study Q_{10} refers specifically to the temperature sensitivity of microbial CO_2 production. The range of Q_{10} values reported for different soils and ecosystems (<2 to >6) is considerable [*Holland et al.*, 2000; *Kätterer et al.*, 1998; *Kirschbaum*, 1995]. Nonetheless, terrestrial carbon models such as Roth-C and CENTURY generally assume that the respiration-temperature relationship is constant, regardless of the characteristics of the ecosystem or soil in question [*Burke et al.*, 2003; *Melillo et al.*, 1995]. Since small differences in the assumed Q_{10} value can dramatically alter estimates of net soil carbon storage, our inability to accurately predict the temperature sensitivity of microbial respiration is a major source of uncertainty in terrestrial carbon models [*Holland et al.*, 2000; *Jones et al.*, 2003; *Lenton and Huntingford*, 2003].

[4] One reason for our poor understanding of the temperature dependency of soil CO_2 production is that few studies

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have quantitatively compared Q_{10} values across soil and ecosystem types or tried to evaluate the factors that control Q_{10}. Even the most comprehensive surveys [*Holland et al.*, 2000; *Howard and Howard*, 1993; *Ross and Cairns*, 1978] have directly measured Q_{10} values on fewer than 20 unique soil samples, and no specific mechanisms have been proposed to explain the variability in Q_{10} values. A meta-analysis of Q_{10} values from published studies is of limited utility because the variability in the methods of Q_{10} measurement makes it difficult to compare Q_{10} values across studies in a quantitative manner [*Burke et al.*, 2003; *Leifeld and Fuhrer*, 2005; *Reichstein et al.*, 2000]. For this study, we collected 77 distinct soils from across the United States and measured the short-term temperature sensitivity of microbial respiration of labile soil organic carbon pools under controlled laboratory conditions. We measured a suite of accompanying soil physical, chemical, and biological characteristics in order to examine relationships between these characteristics and the measured Q_{10} values.

[5] We hypothesize that the temperature sensitivity of microbial CO_2 production varies predictably across soil types. More specifically, we hypothesize that the Q_{10} measured at any given point in time will be inversely related to the quality of soil organic C being consumed by microorganisms. This "C quality-temperature" hypothesis, first proposed by *Bosatta and Ågren* [1999], is based on the fundamental chemical principle that the temperature sensitivity of a reaction is directly proportional to the net activation energy, as formulated in the Arrhenius equation [*Stryer*, 1995]. Since the enzymatic reactions required to metabolize simple organic C substrates are almost certain to have a lower net activation energy than the reactions required to metabolize structurally complex, low-quality, C substrates [*Ågren and Bosatta*, 2002; *Bosatta and Ågren*, 1999], we would expect an inverse relationship between soil organic C quality and the Q_{10} of microbial CO_2 production. *Fierer et al.* [2005] found strong support for this hypothesis in a study examining the temperature sensitivities of plant litter decomposition and the decomposition of individual C compounds. Other studies suggest that the "C quality-temperature" hypothesis may also apply to the decomposition of soil organic C pools [*Fierer et al.*, 2003a; *Knorr et al.*, 2005; *Leifeld and Fuhrer*, 2005; *Mikan et al.*, 2002]. To date, however, it is not clear that the "C quality-temperature" hypothesis can be used to predict the Q_{10} of microbial respiration across a wide range of ecosystems. If it can, we are likely to improve our ability to predict climate change impacts on soil C pools.

2. Methods

2.1. Soil Collection and Processing

[6] A total of 77 unique soils, representing a diverse array of soil and site characteristics, were collected from throughout the United States (Table 1). We restricted our sampling to soils that are unsaturated for most of the year. Soils were collected near the time of peak plant biomass at each site. The upper 5 cm of mineral soil was collected from 5–10 locations within each site and composited into a single bulk sample. All samples were shipped at field moisture content to the University of California, Santa Barbara, within a few days of collection. During shipping, soils were exposed to ambient temperatures. Immediately after arrival in the laboratory, soils were sieved to 4 mm, visible root fragments were removed, and soils were thoroughly homogenized.

[7] Prior to any analyses, all soils were adjusted to 35% of water-holding capacity, by drying at 20°C or wetting with deionized water, and equilibrated at 20°C for 10 days. Since the soils varied significantly in terms of their soil moisture contents at the time of collection, we adjusted the samples to a similar percentage of water holding capacity in order to accurately compare microbial processes across sites. Soils at the same percentage of water holding capacity should have similar soil water potentials [*Gulledge and Schimel*, 1998]. Gravimetric soil moisture contents were determined by drying soils at 120°C for 48 hours, with 100% of water holding capacity measured as the gravimetric water content of soil saturated and allowed to drain over 2 hours in a filter funnel.

2.2. Site Characterization

[8] Climate information for each site was estimated from historical average station data (1971–2000) provided by the National Oceanic and Atmospheric Administration, USA. Average annual soil moisture deficit (in mm H_2O) was estimated as the sum of the differences between mean monthly potential evapotranspiration (PET) and mean monthly precipitation. PET was estimated using Thornthwaite's method with a correction for latitude [*Thornthwaite*, 1948]. Ecosystem classification for each site follows *Bailey et al.* [1994].

2.3. Soil Analyses

[9] Total soil organic carbon and nitrogen contents were measured on a CE Elantech Model NC2100 elemental analyzer (ThermoQuest Italia, Milan, Italy) with combustion at 625°C and 900°C, respectively. Soil pH was measured after shaking a soil/water (1:1 w/v) suspension for 30 min. Particle size analyses were conducted at the Division of Agriculture and Natural Resources Analytical Laboratory, University of California Cooperative Extension (Davis, California) using a standard hydrometer method. Soil microbial biomass was estimated used the substrate induced respiration method described by *Fierer et al.* [2003b].

[10] Net N mineralization and microbial CO_2 production rates were measured on triplicate subsamples (4 g wet weight) over the course of a 50-day incubation at 20°C. After adjustment to 35% of water holding capacity and equilibration (see above), a series of 6–10 static incubations per sample were used to measure the average rate of soil CO_2 production for the 50-day incubation period, using the method described by *Fierer et al.* [2005]. Triplicate subsamples were harvested initially and at 50 days for the determination of K_2SO_4-extractable NH_4^+ and NO_3^-. Samples were extracted for 1 hour with 0.5 M K_2SO_4 and extract NH_4^+ and NO_3^- concentrations were measured on a Lachat autoanalyzer (Milwaukee, Wisconsin) using Lachat methods 31-107-06-5-A and 12-107-04-1-B, respectively. Net N mineralization was

Table 1. Site Information and Selected Characteristics of the Soils Used in This Study[a]

Soil Code	Location	Latitude, °N	Longitude, °W	Elevation, m	Dominant Plant Species	MAT, °C	MMT, °C	MAP, mm	% Organic C	Texture Class	pH	*B*	Q_{10}
BB1	Bear Brook, ME, USA	44.87	68.10	400	*Picea rubens*	6.1	18	1200	12.8	sandy loam	4.3	0.4	2.7
BB2	Bear Brook, ME, USA	44.87	68.10	400	*Fagus grandifolia, Acer rubrum, Acer saccharum, Betula alleghaniensis*	6.1	18	1200	5.2	sandy loam	4.6	0.4	2.8
BF1	Bousson Forest, PA USA	41.58	80.05	390	*Acer saccharum, Fagus grandifolia, Prunus serotina*	7.8	18	1000	6.4	loam	4.1	1.1	3.0
BF2	Bousson Forest, PA USA	41.58	80.05	390	*Acer saccharum, Fagus grandifolia, Prunus serotina*	7.8	18	1000	9.5	loam	3.6	0.6	3.5
BP1	Badlands National Park, SD	43.75	102.38	1000	*Agropyron smithii, Schizachyrium scoparium*	6.6	18	450	3.1	silt loam	7.5	3.0	2.8
BZ1	Bonanza Creek LTER, AK USA	64.80	148.25	300	*Picea glauca*	−2.9	11	260	3	silt loam	5.1	1.8	2.6
BZ2	Bonanza Creek LTER, AK USA	64.80	148.25	300	*Picea glauca*	−2.9	11	260	3	silt loam	5.2	2.8	2.6
BZ3	Bonanza Creek LTER, AK USA	64.80	148.25	300	*Picea glauca*	−2.9	11	260	3.7	silt loam	5.4	3.3	2.4
CA1	Cedar Mtn., AZ USA	36.05	111.77	2003	*Pinus edulis*	10.3	15	400	1.7	silt loam	7.3	2.7	2.6
CA2	Cedar Mtn., AZ USA	36.05	111.77	2003	*Juniperus monosperma*	10.3	15	400	2.2	silt loam	8.0	0.5	4.1
CC1	Cedar Creek LTER, MN USA	45.40	93.20	110	*Carex muhlenbergii, Andropogon gerardii, Poa pratensis,Schizachyrium scoparium*	5.8	18	720	1.9	sand	6.1	2.0	2.6
CF1	Catskills, NY USA	42.17	74.26	800	*Acer saccharum, Fagus grandifolia, Acer rubrum*	5.3	16	1300	2.6	loam	3.9	0.6	3.2
CF2	Catskills, NY USA	41.93	74.35	800	*Fagus grandifolia, Betula alleghaniensis, Acer saccharum*	5.3	16	1300	4.1	sandy loam	3.6	0.6	3.1
CF3	Catskills, NY USA	42.12	74.10	800	*Tsuga canadensis*	5.3	16	1300	4.3	silt loam	3.6	0.4	3.5
CL1	Calhoun Experimental Forest, SC USA	34.62	81.67	150	*Quercus* spp., *Carya* spp., *Acer rubrum*	15.9	22	1250	2.3	sandy loam	5.7	3.0	2.6
CL2	Calhoun Experimental Forest, SC USA	34.62	81.67	150	*Bromus* spp.	15.9	22	1250	2.3	sandy loam	5.6	1.9	3.0
CL3	Calhoun Experimental Forest, SC USA	34.62	81.67	150	*Pinus taeda*	15.9	22	1250	1.2	loamy sand	4.9	4.0	2.7
CL4	Calhoun Experimental Forest, SC USA	34.62	81.67	150	*Hordeum* sp.	15.9	22	1250	1.7	sandy loam	5.0	1.6	3.0
CM1	Clymer Meadow Preserve, TX USA	33.30	96.23	200	*Andropogon gerardii, Sorghastrum nutans, Schizachyrium scoparium*	18.5	25	850	3	silty clay	7.9	1.0	2.7
CO1	Fort Collins, CO USA	40.40	105.70	3800	*Geum rossii, Primula* spp., *Silene acaulis, Poa* spp.	−3.0	8	600	1.6	sand	6.1	5.5	2.6
CO2	Fort Collins, CO USA	40.58	105.33	2400	*Pinus contorta*	6.1	10	350	1.8	sandy loam	5.7	6.0	2.5
CO3	Shortgrass Steppe LTER, CO USA	40.80	104.83	1500	*Bouteloua gracilis, Buchloe dactyloides, Sphaeralcea coccinea*	9.3	14	322	0.8	sandy loam	6.0	4.0	3.0
CR1	Coffey Ranch, TX USA	33.93	97.23	250	*Schizachyrium scoparium, Andropogon gerardii, Panicum virgatum*	18.4	25	850	2.8	loam	8.0	0.6	4.1
DF1	Duke Forest, NC USA	35.97	79.08	163	*Pinus taeda, Liquidambar styraciflua, Liriodendron tulipifera, Cornus florida*	14.6	18	1100	2.8	sandy loam	5.4	5.5	2.4
DF2	Duke Forest, NC USA	35.97	79.08	163	*Liriodendron tulipifera, Liquidambar styraciflua, Carya* sp., *Ostrya virginiana*	14.6	18	1100	5.5	loam	6.8	4.2	2.7
DF3	Duke Forest, NC USA	35.97	79.08	150	*Quercus alba*	14.6	27	1100	1.7	loamy sand	5.1	2.1	2.7
GB1	Great Basin Experimental Range, UT USA	39.33	111.45	3750	*Poa* spp., *Achillea millefolium*	2.0	10	400	2.8	clay loam	6.8	1.5	2.9
GB2	Great Basin Experimental Range, UT USA	39.32	111.47	3290	*Populus tremuloides, Vicia americana, Bromus inermis understory*	2.0	13	400	6.9	loam	7.6	0.3	3.8
GB3	Great Basin Experimental Range, UT USA	39.32	111.48	3270	*Abies concolor, Picea engelmannii*	2.0	13	400	5.7	clay loam	7.2	0.6	3.0
GB4	Great Basin Experimental Range, UT USA	39.27	111.47	3735	*Penstemon rydbergii, Geranium richardsonii, Achillea millefolium*	2.0	10	400	3.6	clay loam	6.9	0.9	2.9
GB5	Great Basin Experimental Range, UT USA	39.35	111.58	2160	*Juniperus osteosperma, Artemisia tridentata, Bromus tectorum*	4.8	15	400	1.7	silt loam	8.2	1.9	3.2

Table 1. (continued)

Soil Code	Location	Latitude, °N	Longitude, °W	Elevation, m	Dominant Plant Species	MAT, °C	MMT, °C	MAP, mm	% Organic C	Texture Class	pH	*B*	Q_{10}
GB6	Great Basin Experimental Range, UT USA	39.33	111.45	3750	*Lupinus perennis, Bromus inermis, Achillea millifolium, Taraxicum officinales*	2.0	10	400	2.2	clay	7.2	1.6	2.5
HF1	Harvard Forest, MA USA	42.50	72.17	300	*Quercus rubra, Acer rubrum, Quercus velutina*	7.0	15	1100	12.7	sandy loam	4.3	1.4	2.8
HF2	Harvard Forest, MA USA	42.50	72.17	300	*Pinus resinosa*	7.0	15	1100	9.6	sandy loam	4.0	1.0	3.4
HI1	Kohala Peninsula, HI USA	20.08	155.70	200	*Pennisetum clandestinum*	22.8	25	250	1.1	loam	6.5	0.4	4.0
HI2	Kohala Peninsula, HI USA	20.08	155.70	700	*Pennisetum clandestinum*	22.0	25	750	15.8	sandy loam	6.3	0.5	3.1
HI3	Kohala Peninsula, HI USA	20.08	155.70	1000	*Pennisetum clandestinum*	22.0	25	1000	18.2	loamy sand	6.5	0.3	3.6
HI4	Kohala Peninsula, HI USA	20.1	155.70	1500	*Pennisetum clandestinum*	21.2	25	1500	10.8	loam	4.9	1.1	2.9
HJ1	H.J. Andrews Experimental Forest, OR USA	44.22	122.15	700	*Pseudotsuga menziesii, Tsuga heterophylla, Thuja plicata*	9.4	17	2000	6.9	sandy loam	5.4	0.5	3.1
HJ2	H.J. Andrews Experimental Forest, OR USA	44.22	122.15	700	*Alnus rubra, Rhododendron macrophyllum*	9.4	17	2000	7.6	sandy loam	5.4	0.4	3.2
IE1	Institute for Ecosystem Studies, NY USA	41.80	73.75	75	*Poa pratensis, Galium aparine, Solidago* sp.	8.6	21	1200	2.7	sandy loam	5.3	2.9	3.0
IE2	Institute for Ecosystem Studies, NY USA	41.80	73.75	75	*Anthoxanthum odoratum, Coronilla varia, Galium aparine, Schizachyrium scoparium*	8.6	21	1200	4.1	sandy loam	5.5	3.0	2.6
IE3	Institute for Ecosystem Studies, NY USA	41.80	73.75	75	*Galium aparine, Solidago* sp., *Phleum pratensis, Poa pratensis*	8.6	21	1200	6.4	sandy loam	5.7	2.1	2.8
IE4	Institute for Ecosystem Studies, NY USA	41.80	73.75	75	*Dactylis glomerata, Phleum pratensis, Poa pratensis, Anthoxanthum odoratum, Galium aparine*	8.6	21	1200	3.3	sandy loam	6.3	3.0	2.9
IE5	Institute for Ecosystem Studies, NY USA	41.80	73.75	75	*Anthoxanthum odoratum, Datcylis glomerata, Galium aparine, Solidago* sp.	8.6	21	1200	5.3	sandy loam	5.6	3.8	2.9
IT1	Itasca Lake State Park, MN USA	47.17	95.17	550	*Acer saccharum, Corylus cornuta, Populus tremuloides*	3.0	18	750	6.3	sandy loam	5.8	2.0	2.5
IT2	Itasca Lake State Park, MN USA	47.18	95.17	550	*Pinus resinosa*	3.0	18	750	3.9	loamy sand	5.4	2.2	2.8
KP1	Konza Prairie LTER, KS USA	39.10	96.60	100	*Andropogon gerardii, Sorghastrum nutans, Poa pratensis*	12.5	20	835	6.1	silt loam	6.4	1.0	2.7
KP2	Konza Prairie LTER, KS USA	39.10	96.60	100	*Andropogon gerardii, Sorghastrum nutans, Schizachyrium scoparium*	12.5	20	835	4.6	silt loam	6.5	1.0	2.9
KP3	Konza Prairie LTER, KS USA	39.10	96.60	100	*Juniperus virginiana*	12.5	20	835	6.9	silt loam	7.9	0.2	3.9
LQ1	Luquillo LTER, Puerto Rico	18.30	65.83	1000	*Tabebuia rigida*	19.3	25	5000	13.9	silt loam	4.9	0.4	3.5
LQ2	Luquillo LTER, Puerto Rico	18.30	65.83	400	*Dacryodes excelsa*	21.5	28	3500	4.1	silty clay loam	5.0	1.8	3.0
LQ3	Luquillo LTER, Puerto Rico	18.30	65.83	700	*Cyrilla racemiflora*	20.5	27	4500	6.4	sandy loam	4.7	1.7	3.0
MD1	Mojave Desert, CA USA	34.90	115.60	1171	*Larrea tridentata, Ambrosia dumosa, Yucca schidigera*	21.0	16	150	0.4	sandy loam	7.7	10.2	2.4
MD2	Mojave Desert, CA USA	34.90	115.65	967	*Larrea tridentata, Ambrosia dumosa, Yucca shidigera*	21.0	16	150	0.1	loamy sand	7.9	16.3	2.3
MD3	Mojave Desert, CA USA	35.2	115.87	776	*Larrea tridentata, Ambrosia dumosa*	21.0	16	150	0.6	loamy sand	8.1	11.9	2.9
MP1	Mary's Peak, OR USA	49.47	123.53	1300	*Poa* spp., *Bromus* spp.	8.8	17	2200	10.7	sandy loam	4.6	0.4	3.1
MP2	Mary's Peak, OR USA	49.47	123.53	1300	*Abies procera*	8.8	17	2200	9.9	sandy loam	4.4	0.6	3.0
RT1	USDA Grassland Research Center, Riesel, TX USA	31.47	96.87	50	*Prosopis glandulosa, Gleditsia triacanthos, Ulmus crassifolia*	18.1	27	840	3.9	silty clay loam	7.9	0.3	3.9
RT2	USDA Grassland Research Center, Riesel, TX USA	31.47	96.87	50	*Andropogon gerardii, Schizachyrium scoparium*	18.1	27	840	3.8	silty clay loam	8.1	0.2	4.6
SA1	Sunset Crater, AZ USA	35.37	111.55	1905	*Pinus edulis*	10.3	15	400	2.3	sand	6.9	3.0	2.2
SA2	Sunset Crater, AZ USA	35.37	111.55	1905	*Juniperus monosperma*	10.3	15	400	2.5	sand	8.1	1.4	3.1
SB1	Santa Barbara, CA USA	34.47	119.80	500	*Ceanothus megacarpus, Adenostoma fasciculatum*	15.0	15	550	2.7	loam	7.9	2.6	3.0
SN1	Sierra Nevada Mts., CA USA	36.45	118.17	3000	*Pinus jeffreyi, Abies concolor*	3.6	8	600	4.3	loamy sand	5.0	2.8	2.5
SN2	Sierra Nevada Mts., CA USA	36.45	118.17	3000	*Artemisia tridentata, Ceanothus prostratus*	3.6	8	600	1.7	loamy sand	5.7	4.9	2.6
SP1	Sequoia National Park, CA USA	36.62	118.63	3215	*Calamagrostis breweri, Carex* spp., *Salix arctica, Vaccinium caespitosum*	3.6	9	750	8.1	loamy sand	5.1	0.8	2.6
SR1	Sedgwick Reserve, CA USA	34.70	120.05	300	*Quercus douglasii, Bromus* spp.	17.2	15	500	4.6	loam	6.8	1.4	2.8

Table 1. (continued)

Soil Code	Location	Latitude, °N	Longitude, °W	Elevation, m	Dominant Plant Species	MAT, °C	MMT, °C	MAP, mm	% Organic C	Texture Class	pH	*B*	Q_{10}
SR2	Sedgwick Reserve, CA USA	34.68	120.05	300	*Bromus* spp., *Hordeum murinum*	17.2	15	500	3.3	loam	7.0	3.3	2.8
SV1	Sevilleta LTER, NM USA	34.33	106.73	1480	*Larrea tridentata*	13.5	20	210	0.3	sandy loam	8.3	7.2	3.2
SV2	Sevilleta LTER, NM USA	34.33	106.73	1480	*Bouteloua eriopoda, Bouteloua gracilis*	13.5	20	210	0.2	loamy sand	8.4	9.2	2.9
SV3	Sevilleta LTER, NM USA	34.33	106.73	1480	*Larrea tridentata, Bouteloua eriopoda*	13.5	20	210	0.3	loamy sand	8.3	8.3	3.0
SV4	Sevilleta LTER, NM USA	34.33	106.73	1480	*Larrea tridentata, Bouteloua eriopoda*	13.5	20	210	0.3	loamy sand	8.3	9.3	3.1
TL1	Toolik Lake LTER, AK USA	68.63	149.58	894	*Eriophorum vaginatum*	–9.3	6	400	7.0	loam	4.6	1.2	2.7
TL2	Toolik Lake LTER, AK USA	68.63	149.58	894	*Salix* spp., *Betula nana*	–9.3	6	400	15.8	silt loam	6.5	0.5	3.2
TL3	Toolik Lake LTER, AK USA	68.63	149.58	894	*Vaccinium* spp.	–9.3	6	400	5.4	loam	4.2	3.1	2.4
VC1	Valles Caldera, NM USA	35.90	106.55	2746	*Picea engelmannii, Populus tremuloides*	2.5	7	500	5.7	sandy loam	5.6	3.0	2.8
VC2	Valles Caldera, NM USA	35.90	106.55	2733	*Blepharoneuron tricholepis, Potentilla fruticosa, Poa pratensis, Achillea millefolium*	2.5	7	500	3.4	loam	6.0	2.0	2.9

[a]MAT, mean annual temperature; MMT, mean monthly temperature for the month when samples were collected; MAP, mean annual precipitation; *B*, relative carbon availability (see equation (1) in section 2). The dominant plant species at each site were determined in a qualitative manner at the time of sample collection.

calculated as the change in total extractable nitrogen over the course of the 50-day incubation.

2.4. Q_{10} Determination

[11] We estimated Q_{10} values from incubations of short duration in order to characterize the temperature sensitivity of the more labile SOM fractions. With longer incubations, organic C pools become depleted over time, altering the apparent Q_{10} [*Burke et al.*, 2003; *Mikan et al.*, 2002; *Reichstein et al.*, 2000]. After the 10-day equilibration period (see above), soil samples (4 g wet weight) were weighed into individual 50-mL plastic tubes sealed with gas-tight lids fitted with rubber septa. Rates of microbial CO_2 production were simultaneously measured at five temperatures (10°–30°C, 5°C increments) with duplicate samples per temperature. Samples were placed in five separate controlled temperature incubators and soil temperatures were measured using Type K thermocouples and a Campbell CR10x (Logan, Utah) data logger to measure the actual soil temperatures during the assay. After a 1-hour equilibration at the target temperature, headspace CO_2 concentrations were measured with an infrared gas analyzer (Licor Model LI-6252). CO_2 concentrations were measured again after 6–24 hours and microbial respiration rates were calculated as the net rate of CO_2 accumulation in the headspace. Headspace CO_2 concentrations were kept below 0.5% in all cases. A similar method of measuring Q_{10} values was previously utilized by *Fierer et al.* [2005]. The dependence of microbial respiration on temperature was described by the equation

$$y_T = Be^{kT}, \tag{1}$$

where y_T is the respiration rate at any given temperature (in μg C-CO_2 g soil organic C^{-1} h^{-1}), T is temperature in °C, and B and k are the exponential fit parameters describing the y intercept and slope, respectively, of the line describing the temperature-respiration relationship. This exponential equation accurately described the data obtained for each sample ($r^2 > 0.95$ in all cases). We used Q_{10} instead of k to describe the temperature sensitivity of decomposition because Q_{10} values are more straightforward to interpret. Q_{10} is calculated from equation (2),

$$Q_{10} = e^{10k}. \tag{2}$$

[12] We used the parameter B as an index of relative organic C quality, the fraction of the total soil organic C pool that can be mineralized over a given period of time [see *Fierer et al.*, 2005]. The parameter B provides a robust estimate of soil organic C bioavailability from soils incubated under controlled conditions. While conventional indices based on elemental ratios or C fractions, such as lignin:N or C:N ratios, are often used to estimate carbon quality in long-term litter decomposition studies [*Hobbie*, 1996], these indices are not useful estimators of organic C quality in mineral soils and they are not good predictors of organic C availability at specific points in time [*Fierer et al.*, 2005]. The measurement of the specific rate of microbial respiration, as done here, is a type of "biological" fraction-

Table 2. Q_{10} and B Values for the Soils Included in This Study With the Soils Grouped Into General Ecosystem Categories[a]

Ecosystem Type	Number of Soils	Range of B Values	Average B	Range of Q_{10} Values	Average Q_{10}
Boreal Forest/Tundra	7	0.5–5.5	2.6 (0.6)	2.4–3.2	2.7 (0.1)
Humid Temperate Forest	20	0.4–5.5	1.6 (0.4)	2.4–3.5	2.9 (0.1)
Humid Temperate Grassland	18	0.2–3.8	1.6 (0.3)	2.6–4.6	3.1 (0.1)
Dry Forest	7	0.3–6.0	2.5 (0.6)	2.2–3.8	2.8 (0.2)
Dry Grassland/Shrubland	18	0.5–16.3	5.0 (1.0)	2.3–4.1	2.9 (0.1)
Tropical Forest/Grassland	7	0.3–1.8	0.9 (0.2)	2.9–4.0	3.3 (0.2)
All Soils	77	0.2–16.3	2.6 (0.3)	2.2–4.6	3.0 (0.1)

[a]Standard errors of the mean Q_{10} and B values are indicated in parentheses.

ation of soil organic carbon pools and remains the most accurate method for estimating substrate availability to soil microorganisms at any given point in time [*Robertson and Paul*, 2000].

[13] *Reichstein et al.* [2005] have illustrated that, for an individual set of data points, the error terms for B and Q_{10} will be negatively correlated due to inherent statistical model properties [see also *Draper and Smith*, 1981]. If we had estimated B and Q_{10} separately using replicate samples, this autocorrelation would be removed. However, we do not expect the existence of this autocorrelation to affect the results reported here since B and Q_{10} are estimated from 77 independent data sets (one data set for each of the soil samples included in this study). There is no a priori expectation that Q_{10} and B should be correlated across the range of soils tested.

2.5. Statistical Analyses

[14] Soil and site variables with non-normal data distribution were log-transformed prior to performing analyses. Normality pretransformation and posttransformation was checked with quantile plots. All statistical analyses were conducted using Systat [*Systat*, 2000]. Correlations between measured soil variables and Q_{10} values were examined using linear regression analyses. Correlations and the corresponding residuals were checked graphically to screen for possible nonlinear correlations. Multivariate models were compared using the Akaike information criteria [*Burnham and Anderson*, 2002], a model selection technique balancing model fit and parsimony.

3. Results

[15] Across all soils, the average measured Q_{10} value was 3.0 (median = 2.9), but the range in Q_{10} values (2.2–4.6) was considerable (Table 2). In general, soils collected near one another had similar Q_{10} values (Table 1), though this was not always the case (e.g., the soils from Toolik Lake, Alaska). We grouped the soils into general vegetation categories (grassland, coniferous forest, deciduous forest, and shrubland) and found no significant differences in the average Q_{10}s across these broadly defined vegetation categories (P = 0.20). There were differences in measured Q_{10} values across ecosystem types (Table 2) but these differences were not significant (P = 0.08). While the sample sizes were relatively small (N = 7 in both cases), soils from tropical ecosystems had the highest average Q_{10} (3.3) with soils from polar and tundra ecosystems having the lowest average Q_{10} (2.7) of the six ecosystem categories.

[16] Of all the soil and site variables measured, only two variables were significantly correlated with Q_{10} (Table 2): relative substrate quality (B from equation (1)) and the mean monthly temperature for the sampling month (MMT). Individually, relative substrate quality and MMT explained 44% and 17%, respectively, of the variability in Q_{10} values across all soils (Figure 1 and Table 3). Relative substrate quality was negatively correlated with Q_{10}; decomposition in soils with organic C pools of lower lability was more temperature sensitive than decomposition in soils with abundant mineralizable organic C (Figure 1a). MMT was

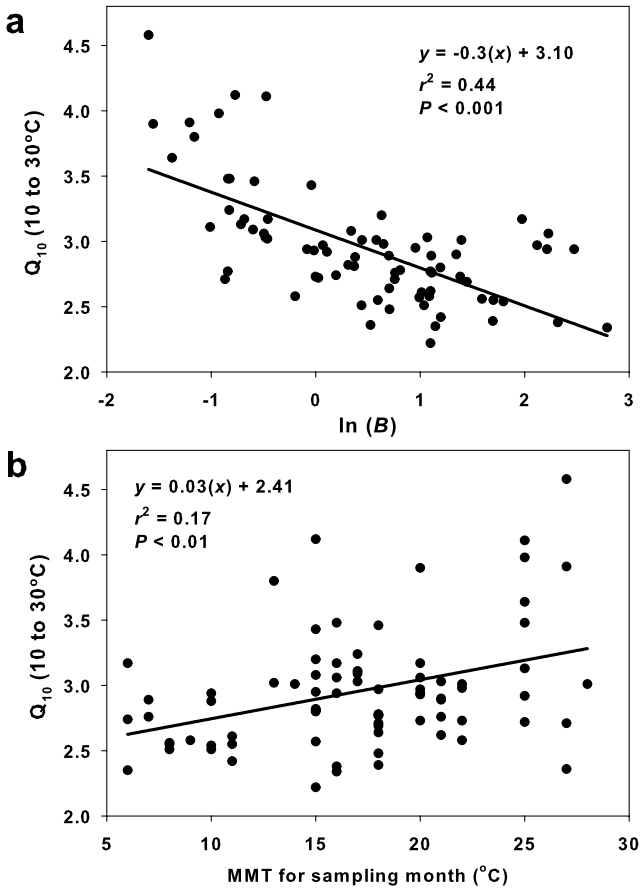

Figure 1. The relationship between measured Q_{10} values and (a) the ln of parameter B and (b) the mean monthly temperature for the month the samples were collected. B is an index of relative substrate quality and is obtained from equation (1) (see section 2).

Table 3. Linear Correlations Between Soil and Site Variables and Measured Q_{10} Values[a]

Soil/Site Variable	Range of Values	Correlation with Q_{10} r
Relative substrate quality (B in equation (1))[b]	0.2–16.3	−0.67[c]
MMT for sampling month, °C	6–28	0.41[d]
% silt + clay	8–84	0.34
CO_2 production rate,[b] μg C-CO_2 g soil^{-1} d^{-1}	0.5–23.1	−0.34
Minimum MMT, °C	−23–22	0.30
MAT, °C	−9–23	0.30
Annual range in MMT, °C	2–31	−0.25
C:N ratio	4.6–37.7	−0.23
pH	3.6–8.4	0.22
Maximum MMT, °C	7–32	0.21
% organic C	0.1–18.2	0.21
Soil moisture deficit,[b] cm H_2O yr^{-1}	−411–108	−0.08
Microbial biomass,[b] μg C-CO_2 g soil^{-1} d^{-1}	0.7–18.4	−0.07
Net N mineralization, μg N g soil^{-1} d^{-1}	−0.8–1.7	−0.02

[a]MAT, mean annual temperature; MMT, mean monthly temperature (historical averages); SMD, average annual soil moisture deficit. Variables are listed in order of the strength of their correlation; except for the first two cases, no correlations were significant at the $P = 0.10$ level.
[b]Values log-transformed in order to normalize data before performing correlation analyses.
[c]Correlation with Bonferroni-corrected significance at $P < 0.001$ level.
[d]Correlation with Bonferroni-corrected significance at $P < 0.01$ level.

positively correlated with Q_{10}, as soils that experienced higher average temperatures during the sampling month tended to have higher Q_{10} values (Figure 1b). None of the other climatic characteristics examined were significant predictors of Q_{10} (Table 3). Together, MMT and relative substrate quality (B) could explain 53% of the variability in Q_{10} values ($Q_{10} = -0.26*\ln B + 0.02*\text{MMT} + 2.7$, $r = 0.73$, $P < 0.001$). The addition of other variables to the model did not significantly improve model fit.

[17] Although the parameter B (from equation (1)) was estimated from relatively short-term incubations (<24 hours, see section 2), we observed a strong correlation ($r = 0.98$, $P < 0.001$) between B values (log-transformed) and the average rates of CO_2 production, (in μg C-CO_2 g soil organic C^{-1} h^{-1}, also log-transformed) measured over the course of the 50-day microbial respiration assays. No other soil or site characteristics measured here were significantly correlated with B ($P > 0.40$ in all cases, data not shown).

4. Discussion

4.1. Variability in Q_{10}

[18] Across all soils the average Q_{10} value was 3.0. However, the range in measured Q_{10} values was reasonably large (Table 1) and the assumption of a single "average" Q_{10} value is unrealistic. The large range in measured Q_{10} values is particularly striking considering that Q_{10} values were measured for an identical period of time and all of the soils were adjusted to the same percentage of water holding capacity. Other studies measuring microbial decomposition under controlled conditions have also reported a high degree of variability in measured Q_{10} values between different types of soil and litter [*Fierer et al.*, 2005; *Holland et al.*, 2000; *Kätterer et al.*, 1998; *Kirschbaum*, 1995; *Ross and Cairns*, 1978].

[19] The extreme sensitivity of biome-level soil C models to changes in Q_{10} has been highlighted by *Townsend et al.* [1992] and *Lenton and Huntingford* [2003]. Our large range in measured Q_{10} values suggests that the use of a single Q_{10} in soil carbon models could lead to significant errors in estimating the sensitivity of SOM pools to climate change. If the average Q_{10} is estimated correctly, variability in Q_{10} values at small spatial scales would have only a minimal affect on the accuracy of models examining SOM dynamics over large areas, where many ecosystem/soil types are integrated into a single model. However, models examining SOM dynamics at higher spatial resolutions (local or regional scales) may be significantly improved by explicitly considering the variability in Q_{10} values and applying soil-specific Q_{10} values [*Canadell et al.*, 2000; *Burke et al.*, 2003]. Of course, since Q_{10} is most strongly correlated with relative organic carbon quality (the parameter B), a parameter that is most easily measured in the laboratory, the determination of soil-specific Q_{10} values is no easy task. If methods can be developed to more rapidly estimate B values across a range of soil types, our ability to parameterize soil-specific Q_{10} values will be dramatically improved.

4.2. Q_{10} and Organic Carbon Quality

[20] There was a strong negative relationship between the relative quality of soil organic carbon and Q_{10} values across the wide range of soils examined. SOM quality alone (the parameter B) explained 44% of the variability in Q_{10} values (Table 3). This finding supports the carbon quality-temperature hypothesis which predicts that the mineralization of low-quality substrates will have a higher Q_{10} than the mineralization of more labile substrates. The inverse relationship between Q_{10} and substrate quality (which we define as microbial CO_2 production per unit organic C) appears to be a general pattern, having been observed in both experimental studies (Table 4) and modeling studies [*Hyvönen et al.*, 2005; *Knorr et al.*, 2005].

[21] Here we used potential microbial CO_2 production as a bio-assay to index C quality (B). The *Bosatta and Ågren* [1999] "carbon quality-temperature" hypothesis defines C quality biochemically, as the number of enzymatic steps

Table 4. Other Published Experimental Studies in Which an Inverse Relationship Between Measured Q_{10} Values and Substrate Quality Has Been Observed[a]

Reference	Study Characteristics	Temperature Range of Q_{10} Measurements	Range in Measured Q_{10} Values	Description of Results
		Time Course Studies		
Fierer et al. [2005]	53-day incubation of 24 litter samples	10°–30°C	2.1–3.4	significant relationships between Q_{10} and B with incubation time
Fang et al. [2005]	100-day incubation of 4 soils	4°–44°C	2.0–2.6	over the course of the incubation, respiration rates decreased by ≈60% and Q_{10}s increased by ≈10%
		Variable Substrate Studies		
Leifeld and Fuhrer [2005]	4 fractionated soils	5°–25°C	3–15	across the different soil fractions, Q_{10}s were inversely related to CO_2 production rate
Fierer et al. [2005]	24 grass litters	10°–30°C	2.1–3.4	generally strong relationship between B and Q_{10} across a range of litter types
Mikan et al. [2002]	5 arctic tundra soils	0.5°–14°C	4.6–9.4	strong relationship between B and Q_{10} ($r^2 = 0.94$)
Fierer et al. [2003a]	6 soils from depth profile	10°–35°C	2.8–4.1	large decrease in B with soil depth corresponded to significant increase in Q_{10}
this study	77 soils	10°–30°C	2.2–4.6	significant inverse relationship between Q_{10} and B

[a]Substrate quality is defined as microbial CO_2 production per unit total organic C. "Time course studies" are those studies in which an individual soil or litter type was incubated over time and Q_{10} was measured at specific intervals during the incubation as substrate quality declined with time. "Variable substrate studies" refers to those studies where Q_{10} were values were determined simultaneously on >3 distinct litter or soil types. Because of methodological differences between studies, we have not attempted to compare these studies in a quantitative manner.

required to mineralize the organic C to CO_2. However, some of the organic C pools in mineral soils are likely to be protected from microorganisms ("stabilized") by physico-chemical mechanisms, such as adsorption to mineral surfaces or inclusion inside aggregates. The means by which soil organic C is protected from microbial mineralization is likely to have a large effect on both B and Q_{10} of the particular organic C pool being mineralized [*Thornley and Cannell*, 2001]. By defining C quality as the rate of microbial CO_2 production per unit organic C, we are effectively combining biochemically and physico-chemically protected C pools in our estimation of B. If all of the organic C was biochemically protected, we would expect the Q_{10} and C quality relationship to be stronger. Indeed, this may explain why the correlations between C quality and Q_{10} appear to be particularly robust in studies examining plant litters [*Fierer et al.*, 2005] and organic soils [*Mikan et al.*, 2002], where physico-chemical protection of organic C is limited. A more detailed accounting of the C protection mechanisms in each soil may improve our ability to predict the biochemical lability of soil organic C pools and, consequently, the temperature sensitivity of microbial CO_2 production in soil.

4.3. Q_{10} and the Ambient Temperature Regime

[22] A modest though statistically significant portion (17%, Table 3) of the variation in Q_{10} values can be solely explained by site climate characteristics, specifically the MMT at the site for the month of sample collection, despite the fact that all soils were exposed to ambient temperatures during shipping and soils were equilibrated at 20°C for 10 days prior to the Q_{10} measurements. Since there is no significant correlation between MMT and B ($P > 0.5$), the apparent influence of MMT on Q_{10} is independent of the B/Q_{10} relationship. One possible explanation for this result is that the microbial communities in each soil have adapted to their antecedent temperature regime, the mean seasonal temperature. We know that the temperature optima of microorganisms can vary widely [*Madigan et al.*, 1997] and that microorganisms are able to adapt to the temperature regime of a particular environment [*Cooper et al.*, 2001; *Hahn and Pockl*, 2005]. Therefore we might expect that communities that are adapted to warm temperatures would maximize their activities at higher mean temperatures than those communities adapted to cooler temperatures. Likewise, communities adapted to high temperatures should have lower activities (relatively) when exposed to low temperatures than those communities adapted to cooler temperature regimes. As a consequence of any thermoadaptation, we would expect communities adapted to higher antecedent temperatures to exhibit higher Q_{10}s across the range of temperatures tested (10°–30°C), than those communities adapted to cooler temperatures, yielding the observed relationship between MMT and Q_{10}. At this point, this mechanism is merely hypothetical and further research is necessary to determine the prevalence of thermoadaptation by microbial communities and its role in determining the temperature dependency of SOM decomposition.

4.4. Assay Methods and the Estimation of Q_{10}

[23] For this study we estimated Q_{10} by incubating replicate soil samples for less than 24 hours at five different temperatures. The specific characteristics of the chosen Q_{10} assay method (incubation time, the range of temperatures, parallel versus sequential incubations) can strongly influence estimates of Q_{10} [*Burke et al.*, 2003; *Leifeld and Fuhrer*, 2005; *Mikan et al.*, 2002; *Reichstein et al.*, 2000]. For this reason, we have not attempted to quantitatively compare the Q_{10} values reported here with the Q_{10} values reported in other laboratory-based studies. However, it is

important to mention some of the specific advantages and limitations of the Q_{10} assay used here.

[24] The short-duration incubation approach we used was chosen to minimize changes in the sizes of organic C pools over the course of Q_{10} assays. Longer incubations can underestimate Q_{10} because C pools are depleted over time [*Mikan et al.*, 2002]. Likewise, by simultaneously incubating separate replicate soil samples at each temperature, we minimize changes in soil C pools that can occur when individual soil samples are sequentially incubated at a range of temperatures. In this study, temperature-induced shifts in the sizes of soil C pools should have a minimal effect on Q_{10} estimations. Even at the highest assay temperature (30°C) the amount of soil organic C mineralized during the incubation was relatively small (30 to 320 μg C-CO_2 g soil organic C^{-1}).

[25] With our methodology, Q_{10} was measured at a single point in time after soils were equilibrated for a 10-day period so the reported Q_{10} values will only reflect the temperature sensitivity of the more labile soil organic carbon pools. If the soils were equilibrated for a longer period of time before measuring Q_{10}, we would expect the estimated Q_{10} values to be higher owing to an overall decrease in C quality as the more labile C pools are depleted over time. Only with incubations of longer duration can we begin to understand the temperature sensitivities of more recalcitrant soil organic C pools. Despite the limitations of our ''snapshot'' method for measuring Q_{10}, the method provides a controlled and replicable method of comparing Q_{10}s across a wide variety of soil types.

[26] It is also important to recognize that the apparent temperature dependency of microbial decomposition may not be equivalent in field and laboratory conditions. In the field, factors such as soil moisture, nutrient availability, root respiration, and C availability are likely to interact with temperature [*Gulledge and Schimel*, 2000; *Rustad et al.*, 2000], potentially obscuring any relationship between C quality and the Q_{10} of microbial respiration. This may partly explain the discrepancy between the median Q_{10} of 2.9 reported here and the median Q_{10} of 2.4 for total soil CO_2 efflux, as reported from a comprehensive survey of field-based studies [*Raich and Schlesinger*, 1992]. Likewise, in projecting these results to changes in temperature over longer periods of time (years to decades), other factors that may have an important influence on the temperature sensitivity of decomposition, including shifts in C pools, shifts in microbial community composition, and physico-chemical stabilization reactions, will also need to be considered. This work provides an approach for considering how the immediate temperature sensitivity of microbial respiration in soil changes as all those other factors shift over time.

4.5. Absolute Versus Relative Responses to Temperature

[27] Here we show an inverse relationship between C quality and Q_{10}. However, total C emissions from a soil are a function of basal respiration, temperature sensitivity, and total C stocks. Thus absolute changes in overall C respired will be a function of all three of these variables. Here we show that the relative (not the absolute) response of CO_2 production to temperature is greater for soils with low C quality. However, because those soils with low C qualities are likely to have lower basal rates of microbial CO_2 production, a relatively large increase on a small basal level (for a low-quality soil) may be a smaller absolute amount of C respired than a smaller increase over a larger basal value (for a high-quality soil). Additionally, absolute responses should be driven by total C supply and soils vary enormously in the sizes of their total C stocks. This distinction between absolute and relative responses may explain why soil warming experiments [*Luo et al.*, 2001; *Oechel et al.*, 2000] have observed a decrease in the apparent temperature sensitivity of respiration as labile C pools are depleted by warming, lowering the absolute response of CO_2 production to temperature [*Knorr et al.*, 2005].

5. Summary

[28] To our knowledge, this study is the first to compare the temperature dependence of microbial decomposition across a wide range of soil types. Our goal was not to identify a single, average Q_{10} value that best describes the temperature sensitivity of soil microbial respiration across a range of ecosystems. Rather, we focused on the variability in Q_{10} values and the identification of those biotic and abiotic factors that influence the temperature sensitivity of soil microbial respiration. We found that by considering only two variables, MMT and carbon quality (B), we could predict more than 50% of the variability in Q_{10} values. The predictive power of this model is impressive considering that the soils included in this survey represent a broad range of soil and site characteristics. This work represents an important first step toward understanding the fundamental mechanisms governing the temperature dependence of SOM decomposition.

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