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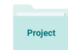

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Uncertainties in the temperature sensitivity of decomposition in tropical and subtropical ecosystems: Implications for models

Elisabeth A. Holland,[1] Jason C. Neff,[2] Alan R. Townsend,[3] and Becky McKeown[2]

Abstract. Tropical ecosystems play a central role in the global carbon cycle. Large changes in tropical temperature over geologic time and the significant responses of tropical ecosystems to shorter-term variations such as El Niño/La Niña argue for a robust understanding of the temperature sensitivity of tropical decomposition. To examine the responsiveness of heterotrophic respiration to temperature, we measured rates of heterotrophic respiration from a wide range of tropical soils in a series of laboratory incubations. Under conditions of optimal soil water and nonlimiting substrate availability, heterotrophic respiration rose exponentially with rising temperature. The mean Q_{10} measured across all temperature ranges in these short-term incubations was 2.37, but there was significant variation in Q_{10}*s* across sites. The source of this variation could not be explained by soil carbon or nitrogen content, soil texture, site climate, or lignin to nitrogen ratio. At the beginning of the incubation, heterotrophic respiration increased exponentially with temperature for all sites, despite the fact that the fluxes differed by an order of magnitude. When substrate availability became limiting later in the incubation, the temperature response changed, and heterotrophic response declined above 35°C. The documented changes in temperature sensitivity with substrate availability argue for using temperature relationships developed under optimal conditions of substrate availability for models which include temperature regulation of heterotrophic respiration. To evaluate the significance of this natural variation in temperature control over decomposition, we used the Century ecosystem model gridded for the areas between the tropics of Cancer and Capricorn. These simulations used the mean and upper and lower confidence limits of the normalized exponential temperature response of our experimental studies. We found that systems with the lowest temperature sensitivity accumulated a total of 70 Pg more carbon in soil organic carbon and respired 5.5 Pg yr^{-1} less carbon compared to the systems with the highest sensitivity.

1. Introduction

Net carbon dioxide uptake for an ecosystem is determined by small differences between photosynthesis and respiration temperature sensitivities [*Kirschbaum*, 2000; *Lloyd and Taylor*, 1994; *Townsend et al.*, 1992; *Woodwell and Houghton*, 1989]. As we scale to regional and global estimates of carbon flux, these small differences in photosynthesis and respiration determine whether an ecosystem or biome will be a net source or sink of CO_2 and are thus significant to the global carbon cycle [*Houghton et al.*, 1995; *Schimel et al.*, 1995; *Townsend et al.*, 1992]. While it is possible to use remote sensing techniques to constrain net primary production (cumulative net photosynthesis) over large regions and to examine the relationship to temperature [*Braswell et al.*, 1997], modeling is our only current means of extrapolating respiration fluxes over large areas. For this reason, it is important to develop a mechanistic and quantitative understanding of the factors that control decomposition, and the mathematical representation of this relationship is a central feature of virtually every ecosystem model.

Tropical and subtropical ecosystems process more carbon annually than any other region of the Earth [*Paul et al.*, 1989; *Raich and Potter*, 1995; *Schlesinger*, 1991; *Townsend et al.*, 1992] and are experiencing rapid changes in land cover and land use. Despite the importance of tropical and subtropical ecosystems to the global carbon cycle, our understanding of how these ecosystems function falls behind our understanding of temperate and high-latitude ecosystems. For example, a recent compilation of soil respiration studies included 106 temperate latitude studies, 39 high latitude studies, and 26 tropical and subtropical studies, a reflection of how few studies of tropical respiration have been done [*Raich and Schlesinger*, 1992]. There have been relatively few controlled laboratory studies of the factors which influence tropical decomposition rates. In field studies, temperature effects are complicated by numerous factors which act simultaneously to regulate respiration and by the unsolved problem of separating soil respiration from plant respiration processes. Recent reports of unexpectedly large and rapid changes in tropical land and sea temperatures over glacial-interglacial cycles [*Leyden*, 1995; *Stute*

[1]Max-Planck-Institut für Biogochemie, Jena, Germany, and National Center for Atmospheric Research, Boulder, Colorado.
[2]National Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado.
[3]Environmental, Population, and Organismic Biology, University of Colorado, Boulder, Colorado.

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et al., 1995; *Thompson et al.*, 1998] show that enhancing our understanding of the feedback between the climate and temperature regulation of tropical ecosystems is important for understanding current and geologic changes in atmospheric CO_2 concentrations [*Thompson et al.*, 1995].

There are two parallel and complimentary approaches to understanding large-scale carbon dioxide fluxes. Inverse analyses using the global CO_2 flask sampling network have provided us with insight into the relative strengths of sources and sinks in middle and high latitudes and offer an alternative to ecosystem modeling which cannot resolve many of the large scale features with confidence [*Ciais et al.*, 1995; *Rayner et al.*, 1996]. The inverse techniques currently have limited applicability in the tropics because of the limited number of flask sampling stations located at tropical latitudes [*Rayner et al.*, 1996; *Tans et al.*, 1990]. Furthermore, the complexity of atmospheric transport which is driven by strong vertical transport and convective storms in tropical regions [*Peixoto and Oort*, 1991], is poorly represented in transport models. For these reasons, ecosystem model-based analyses of this region are particularly important for furthering our understanding of how the tropics will interact with a changing environment and for diagnosing processes important at larger spatial scales.

The goals of our study were two: (1) We attempted to understand the variability of temperature regulation of heterotrophic respiration across the array of vegetation types, soils types, and land use found in the tropics. (2) We examined the implications of the resulting variability for ecosystem model-based estimates of decomposition and its feedbacks through nitrogen to net primary production and soil organic matter formation.

2. Materials and Methods

To achieve the stated goals, we first conducted a series of laboratory experiments to answer the following questions: How does temperature influence heterotrophic respiration across a broad range of tropical ecosystems? What is the shape of the response? Is the response consistent? How is the response influenced by substrate limitation? Can the variability in the temperature response among the sites be explained? We then incorporated the temperature responses and the estimated uncertainties from the laboratory experiments into the Century ecosystem model. The goal was to examine the implications of uncertainties in temperature regulation of decomposition for carbon and nitrogen fluxes from the tropics as a whole. The Century model was chosen because of its explicit representation of temperature regulation of decomposition, including the various and complicated feedbacks through substrate availability and the nitrogen cycle.

2.1 Laboratory Studies

Temperature regulation of heterotrophic respiration was assessed in soils from four general geographic locations; Brazil, Costa Rica, Hawai'i, and south Texas, and four soil types; Histosols, Inceptisols, Oxisols, and Mollisols, spanning a range of soil textures, organic matter content, and potentially, microbial community composition. There were 12 pasture or herbaceous sites, 3 woodland sites, 2 primary forest sites, and 1 secondary forest site represented in the soils sampled. Respiration rates were measured in the laboratory to determine "optimal" rates of respiration and to remove the influence of roots. Previous studies have shown that substrate carbon availability (and as a result length of the incubation) limits respiration and can complicate the interpretation of the respiration response to temperature [*Holland et al.*, 1995; *Townsend et al.*, 1997]. Field measurements of the relationship between respiration and temperature provide variable results, with Q_{10}s of 4 and 5 occasionally reported [*Raich and Schlesinger*, 1992]. However, respiration rates measured under optimal controlled conditions are more appropriate than field studies for the derivation of equations incorporated into models of microbial activity, heterotrophic respiration and terrestrial C exchanges for the following reasons: (1) Laboratory incubations are the only practical way of comparing responses across soils. (2) Field measurements of soil respiration include root respiration which likely responds differently to temperature than microbial respiration. (3) Using model equations based on lab incubations is the best approach to representing the direct effect of temperature on decomposition.

2.2. Site and Sampling Information

The sites were chosen to be broadly representative of tropical soils (Figure 1, Table 1). In all cases, soils were collected from sites with ongoing research on biogeochemical cycling [*Archer*, 1990; *Keller and Reiners*, 1994; *Hibbard*, 1995; *Hibbard et al.*, 2000; *Reiners et al.*, 1994; *Townsend et al.*, 1992; *Trumbore et al.*, 1995; *Vitousek and Sanford*, 1986]. Mean annual temperatures (MAT) for the sites ranged from 12.5 to 27°C, and mean annual rainfall ranged from 0.5 to 4 m. (Figure 1). We sampled the land use types and vegetation types available at each site including forests, savannas, and pastures.

At all the sites, soils were sampled to 10 cm depth and refrigerated immediately after sampling. All the soil samples were shipped directly to the National Center for Atmospheric Research (NCAR) in Boulder, Colorado, in coolers packed with ice. Upon arrival, the soils were placed in a refrigerator at 4°C until the beginning of the incubations. The incubations for Brazil were started within 3 months after sample collection, while the Hawai'i, Costa Rica, and Texas incubations were started within 3 weeks of collection. Soils were sampled during the main growing season for the individual locations in 1993. The storage may have reduced substrate availability, and microbial death during storage and severing roots during sampling may have increased substrate availability. The sharp decrease in respiration in the incubations suggests a sharp decline in initial substrate availability (see section 4 for further discussion).

2.2.1. Brazil. We collected soils from the Fazenda Victoria site near Paragominas (2°59"S, 47°31"W) in the Para state of Brazil. Soils were sampled to 10 cm at two locations, a forest and a nearby pasture, for a total of 20 cores. The forests are characterized by deeply rooted tropical moist forests [*Nepstad et al.*, 1994] and are on highly weathered Kaolinitic Yellow Latosols (Haplustox in the U. S. Department of Agriculture (USDA) taxonomy). The pasture soils were from sites which were originally cleared in the late 1960s and are currently planted with *Panicum maximum* and *Brachiaria humidicola* (see *Trumbore et al.* [1995] for more details). Annual precipitation is 1.75 m and occurs mostly between November and June.

2.2.2. Costa Rica. We sampled soil from a total of nine sites: two forest sites; a primary and a secondary rainforest, and an age

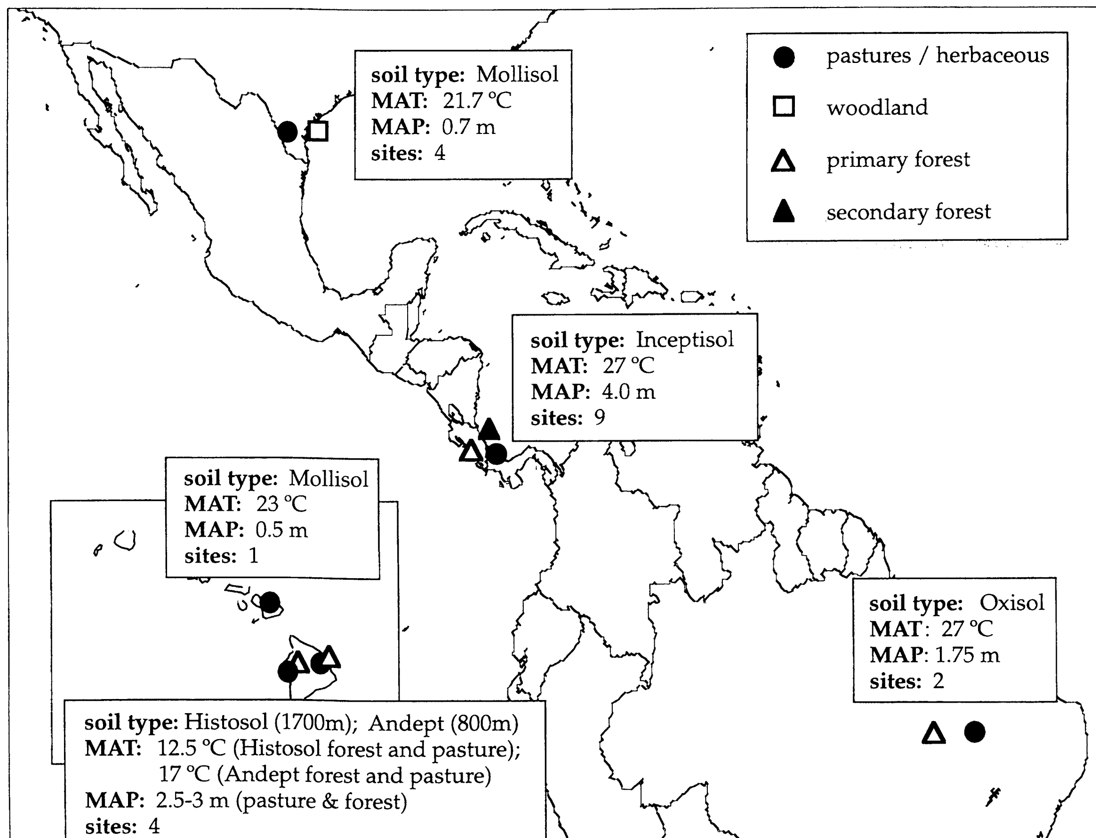


Figure 1. Map of the locations where soils were collected. In Hawai'i, we sampled two forests and two pastures located at 800 m and 1700 m on the island of Hawai'i and one degraded pasture on the island of Maui. In Texas, four different landscape types were sampled: herbaceous sites (H), groves (G), mottes (M), and woodlands (W). In Costa Rica, two forests in the La Selva Biological Station and seven nearby pastures were sampled. In Brazil, a single forest site and a single pasture site were sampled. MAP is mean annual precipitation, and MAT is mean annual temperature.

sequence of pastures ranging from a 2 year old pasture recently converted from tropical rainforest to a 25 year old pasture [*Keller and Reiners*, 1994; *Reiners et al.*, 1994; *Veldkamp and Keller,* 1997]. The pastures were 2, 3, 6, 10, 12, 18, and 25 years old for a total of seven pasture sites. The forest soils used in this study were collected from the La Selva Research Station in Sarapiqui Canton, Heredia Province, Costa Rica. Eight soils cores were taken at each location for a total of 72 cores. The site experiences mean annual rainfall of 3.96 m with a weak dry season, a MAT of 25.8°C and little seasonal variation in climate [*Sanford et al.*, 1994]. The secondary forest was logged between 1971 and 1981, and the pastures were established using slash and burn techniques.

2.2.3. Hawaii. We collected soils from two pastures and two forests on the slopes of Mauna Kea on the island of Hawai'i and from one pasture on the island of Maui [*Townsend and Vitousek,* 1995; *Vitousek et al.*, 1992, 1988]. Ten soil cores were sampled at each site for a total of 50 cores. We sampled from forests at 800 and 1700 m in the Laupahoehoe forest reserve and nearby pastures on Hawai'i. The forest sites are dominated by the widespread native *Metrosideros polymorpha* and *Acacia koa,* and the pastures are planted with *Pennisetum clandestinum*. Both pastures were converted from primary forest several decades ago. Soils at the high-elevation site are young organic Histosols developed on a ~5000 year old lava flow and experience a MAT of 12.5°C. At the lower site, soils are older allophanic Andepts developed from ash deposits that are ~20,000 years old with a MAT of 17°C. All four sites on Hawai'i receive 2.5-3 m rainfall annually with no significant dry season. The Maui pasture site was planted with *Cenchrus ciliaris* and was located on Mollisols at 300 m elevation with a MAT of 23°C. The Maui site receives only 0.5 m of rainfall annually and has a pronounced summer dry season.

2.2.4. Texas. The soils used in this experiment were collected at the La Copita Research area near Alice, Texas (27°40'N; 98°12'W). The semiarid subtropical climate of the region is characterized by hot summers and mild winters, with a mean annual temperature of 22.4°C and mean annual precipitation of 0.68 m. The length of the growing season varies between 260 and 300 days with an average of 289 days [*U. S. Department of Agriculture* (*USDA*), 1979]. The soils are fine, sandy loams, and the samples include both fine, loamy mixed hyperthermic Typic Argiustolls and fine, loamy mixed hyperthermic Pachic Argiustolls [*Scifres and Koerth,* 1987]. The vegetation is described as thorny brush/woodlands dominated by mesquite-colima/granjeño communities. Vegetation types in the area include savanna woodlands, in which woody plants develop in clusters beneath *Prosopis glandulosa* [*Archer*, 1989]. There is

Table 1. Soil Characteristics of Sites Sampled

Site	Bulk Density, g cm^{-3}	%C	%N	C:N Ratio	Texture		
					%Sand	%Silt	%Clay
Brazil							
Pasture	1.20–1.22*	2.39(0.19)	0.23(0.02)	10.43	31,—	20(1)	49
Forest	0.96–1.02*	2.94(0.16)	0.28(0.01)	10.44	14.5(2.5)	18(1)	67.5
Costa Rica							
primary forest	0.62	5.27(0.66)	0.52(0.03)	10.11	34(10)	19.5(0.5)	46.5
secondary forest	0.64	3.25(0.56)	0.30(0.02)	10.75	28.5(2.5)	24.5(1.5)	47
2 year old pasture	0.78	4.15(0.88)	0.38(0.03)	10.79	21.5(0.5)	26.5(0.5)	52
3 year old pasture	0.83	4.23(0.72)	0.36(0.02)	11.89	31.5(0.5)	22.5(0.5)	46
6 year old pasture	0.82	4.62(1.31)	0.42(0.04)	11.05	24,—	24(2)	52
10 year old pasture	0.85	3.59(0.31)	0.33(0.01)	10.96	32(3)	25(1)	43
12 year old pasture	0.80	4.68(1.16)	0.38(0.02)	12.45	27,—	18.5(0.5)	54.5
18 year old pasture	0.98	3.27(0.47)	0.33(0.02)	9.99	31(1)	26(2.6)	43
25 year old pasture	0.80	4.65(0.61)	0.39(0.02)	11.84	23,—	20(2)	57
Hawaii							
800 m Forest	0.51	21.26(2.58)	1.13(0.16)	18.81			
800 m Pasture	0.59	18.07(0.74)	1.07(0.06)	16.89			
1700 m Forest	0.43	26.60(1.80)	1.95(0.11)	13.64			
1700 m Pasture	0.48	27.42(1.66)	1.95(0.10)	14.06			
Maui Pasture	0.85	2.50(0.28)	0.25(0.02)	10.00			
Texas							
Woodland	1.10†	2.34(0.46)	0.20(0.05)	11.54	60(2.9)	17(3)	23
Grove	1.14†	1.43(0.17)	0.12(0.01)	11.88	71(2)	15(2.5)	15
Motte	1.07†	2.18(0.23)	0.18(0.02)	12.18	70(1.7)	15(1)	15
Herbaceous	1.39†	0.84(0.05)	0.07(0.00)	12.88	70(0.8)	14(0.5)	16

Parenthese represent standard errors. Dash indicates only a single estimate which is an insufficient basis for calculation of a standard error

* From Trumbore *et al.* [1995].

† From Hibbard *et al.* [1995].

herbaceous vegetation located between shrub clumps, which is dominated by C4 grasses including *Paspalum setceum, Setaria geniculata, Bouteloua rigidseta,* and *Chloris cucullata*. We sampled soils from four distinct landscape types within the La Copita ecosystem: the herbaceous (H) areas between the shrub clumps, mottes (M), which were recently coalesced woody shrubs which still maintained relatively open canopy, groves (G), clumps of woody shrubs with a more closed canopy, and woodlands (W) which were continuous expanses of woody shrubs with a multitiered canopy, often located in seasonally inundated playas [*Hibbard*, 1995; *Hibbard et al.*, 2000]. Six soil cores were taken in each of the four vegetation classes.

2.3. Moisture Determinations

All soils were incubated at field capacity, the amount of water a soil will hold against gravity, to reduce the variability associated with soil moisture differences. To determine field capacity, we placed 40-50 grams of soil in a funnel that contained a coarse filter in the stem. We then added small amounts of water several times over 4-6 hours. Following the addition of water in excess of field capacity, we allowed the soils to drain overnight and determined gravemetric soil moisture the following day. We used 2-4 replicates for each site/land use/landscape class. Immediately prior to the incubations, sufficient water was added to bring the soils to field capacity (in all cases, field soil moisture was less than the soil moisture at field capacity).

2.4. CO_2 Sampling

Soils were preincubated overnight at the experimental temperature prior to the start of the 24-hour measurement period, in order to avoid transient effects in heterotrophic respiration associated with storage. Following the preincubation, we placed 10-15 grams of soil in plastic beakers in 1 L mason jars fitted with a Swagelok sampling port on the jar lid. Jar headspace samples were taken through this port and analyzed using a Shimadzu GC 8A gas chromatograph (oven temperature 70°C) equipped with a 3 m column packed with Haysep D (80/100 mesh) and a thermal conductivity detector manufactured by Carle Instruments. All the jars were well ventilated prior to the beginning of the incubation and ventilated again following the completion of each sampling. To test the linearity of CO_2 accumulation at the beginning of the incubation, we measured CO_2 concentrations at 1, 3, 5, and 24 hours. The rates of CO_2 accumulation were linear. For the first week of the incubations, CO_2 was accumulated for an hour, but the lower respiration rates later in the experiment required accumulation of CO_2 over 24 hours. Measurements were made following 3, 7, and 14 days of incubation for all of the sites. For soils from the Hawai'i, Brazil, and Texas sites, fluxes were measured for a maximum of 24 weeks following sampling to examine the decay in CO_2 flux with time. For the most part, our analysis focuses on fluxes measured on the first day following preincubation because substrate availability limited fluxes, particularly at the highest temperatures, after day 1. All fluxes were measured at the experimental temperature.

2.5. Additional Soil Characterizations

We determined total % carbon and % nitrogen for all the soil samples using a Carlo Erba CN analyzer (Carlo Erba Instruments, division of Fisons Instruments, Saddle Brook, New Jersey). Soil texture was determined by the Colorado Soil Testing Laboratory using the hygrometer technique [*Gee and Bauder*, 1986] .

Table 2a. The Parameters Which Best Describe the Exponential Relationship Between the Normalized Heterotrophic Respiration Flux and Temperature According to Equation (3) (Figure 2).

Site	k_1	k_2	r^2
Brazil			
forest	0.063	0.090	0.90
pasture	0.116	0.069	0.83
Costa Rica			
primary forest	0.931	0.031	0.79
secondary forest	0.354	0.043	0.65
2 year old pasture	0.563	0.046	0.69
3 year old pasture	0.311	0.059	0.78
6 year old pasture	0.417	0.059	0.83
10 year old pasture	0.333	0.055	0.88
12 year old pasture	0.385	0.058	0.95
18 year old pasture	0.318	0.055	0.84
25 year old pasture	0.559	0.049	0.93
Hawaii			
800 m pasture	1.578	0.064	0.95
1700 m pasture	7.702	0.041	0.93
800 m forest	3.774	0.039	0.83
1700 m forest	5.090	0.055	0.88
Maui pasture	2.589	0.037	0.90
Texas			
herbaceous	0.147	0.061	0.93
grove	0.393	0.048	0.90
motte	0.212	0.070	0.88
woodland	0.254	0.059	0.93

The fluxes were normalized to the flux at 45°C according to equation 2. The parameters were fit for the 20 individual sites sampled.

2.6. Calculations and Statistical Analyses

We took two different approaches to the comparison of the heterotrophic respiration (HR)/temperature relationship among the various sites. First, we calculated Q_{10} values as the ratio of the rate of heterotrophic respiration at two 10° temperature intervals according to the following equation [*van't Hoff*, 1898]:

$$Q_{10} = \frac{CO_2\text{flux} @ T_y}{CO_2\text{flux} @ T_{y-10}} \quad . \qquad (1)$$

Q_{10} values are commonly used and facilitate comparisons among sites and among temperature ranges. Second, we normalized the measured fluxes to the HR flux measured at 45°C according to the following equation:

$$\text{normalized flux} = \frac{CO_2\text{flux} @ T_y}{CO_2\text{flux} @ 45°C} \qquad (2)$$

where T is temperature. This approach facilitated the incorporation of the resulting equations into the terrestrial ecosystem model Century. We then fit the following two-parameter equation to the normalized heterotrophic respiration fluxes for each individual site and for all of the sites as a whole (Table 2a; Figure 2):

$$T_c = k_1 e^{k_2 T} \quad , \qquad (3)$$

where T_c is the temperature effect on decomposition and k_1 and k_2 are the exponential fit parameters. The parameter k_1 had the greatest influence on the y intercept, and k_2 influenced the slope of the relationship. The equation was fit using a nonlinear fitting routine including a number of analyses, which were done to ensure that the final estimated parameters were insensitive to the assigned starting values.

To examine the modeled sensitivity to the temperature parameterization, we calculated the ratio of the change in pools and fluxes to the change in k_2 the slope parameter in (3) (Table 2b):

$$\text{change in flux or pool} = \frac{\left| V_{\text{upper CI}} - V_{\text{lower CI}} \right|}{k_{2\,\text{upper CI}} - k_{2\,\text{lower CI}}} \qquad (4)$$

where V was the value of the Century simulation for the flux or the pool and k_2 was the slope parameter for (3).

Analysis of variance (ANOVA) tests [*Statview*, 1999] were used to examine differences in heterotrophic respiration rates and Q_{10} values among temperatures and among the sites sampled. For both the ANOVA tests applied to both the fluxes and Q_{10}s, we tested for differences among sites, temperature of incubation, and site by temperature interactions. In addition, for each site, we tested for the differences among or between the land uses (Brazil), time since forest to pasture conversion (Costa Rica), and landscape type (Texas). The Hawai'i site was excluded from the ANOVA analyses because statistical analysis of the fluxes, Q_{10}s and the sensitivity of heterotrophic respiration to temperature have been presented elsewhere [*Holland et al.*, 1995; *Townsend et al.*, 1997].

3. Model Analyses

We used the Century terrestrial ecosystem model [*Parton et al.*, 1987, 1994] to examine the impact of variable temperature regulation of decomposition and heterotrophic respiration on tropical carbon and nitrogen pools and fluxes. The analysis was done using the global version of Century developed by B. Mckeown, D. S. Ojima, W. J. Parton, W. Pulliam, and D. S. Schimel [*Schimel et al.*, 1996, 1997]. The model was run exclusively for the tropics extending from the tropic of Capricorn to the tropic of Cancer (23°S to 23°N). The model initialization was done by running the model for 2000 years for each grid cell using the best fit parameters which best described the aggregate data (equation (3), Table 2b). Grid cell size was 0.5° by 0.5°. The model run was then extended for 200 years using each of the three different parameter sets to describe the temperature equations: the best fit, the lower 95% confidence interval, and the upper 95%

Table 2b. Same as Table 2a Except That the Exponential Equation (3) was Fit to the Data for All of the Sites Combined

	Lower 95% C. I.	Best Fit	Upper 95% C. I.
k_1	0.066	0.092	0.117
k_2	0.049	0.054	0.060

These parameters were used for the Century model runs. C. I., confidence interval.

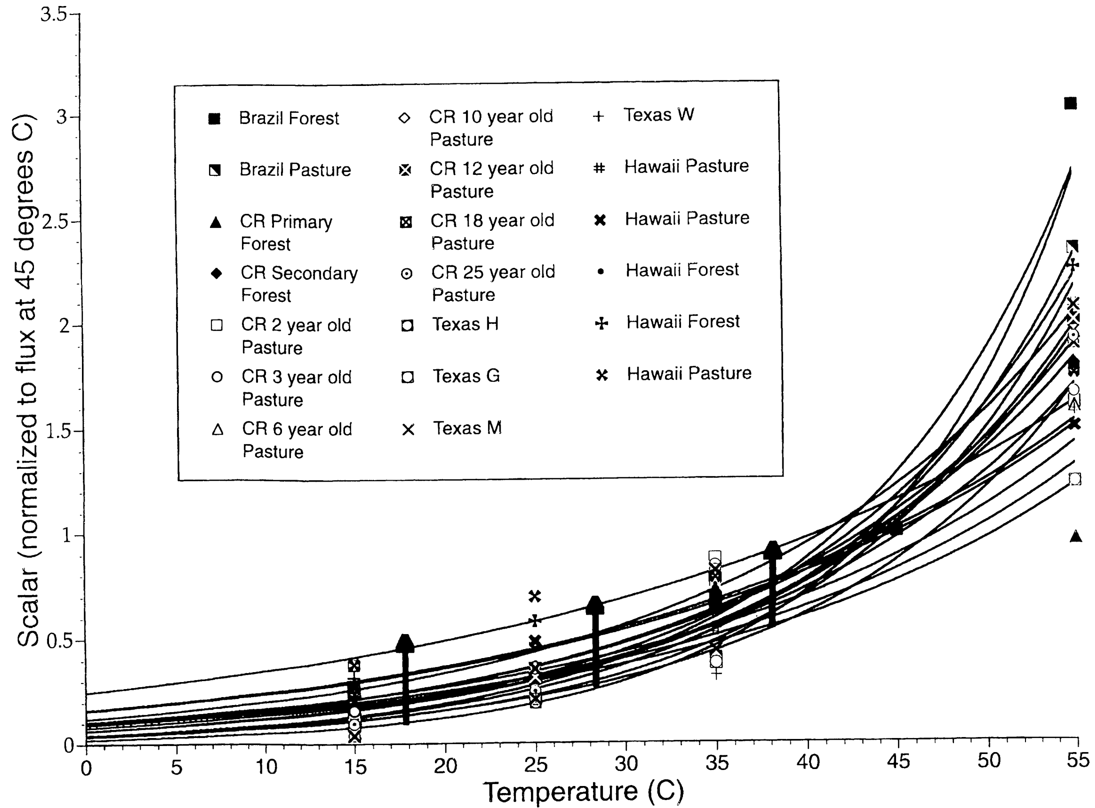


Figure 2. The variation in the CO_2 flux normalized to the flux at 45°C with temperature. The parameters which describe both the exponential rise in normalized CO_2 flux and the calculated Q_{10} for the individual sites are provided in Tables 2a and 2b and Figures 6 and 7. The parameters describing the exponential increase and their standard deviations calculated for all of the sites lumped together were used for the Century simulations and are provided in Table 2a.

confidence interval (Table 2b). The results shown are the average of the last 5 years of the 200 year runs.

Temperature and moisture regulation of microbial processes within Century act through a single decomposition factor which is calculated as the cross product of the effect of temperature and moisture [*Parton et al.*, 1987, 1994]. The original temperature function in Century was a generalized Poisson density function [*Parton and Innis,* 1972]:

$$\text{Effect of temperature} = \left(\frac{t\max - t}{t\max - topt}\right)^{tshr} e^{\left(\frac{tshr}{tshl}\right)\left(1-\left(\frac{t\max - t}{t\max - topt}\right)^{tshl}\right)} \quad (5)$$

where *t*opt is the temperature where $f(x)$ = 1, or the optimum temperature, *t*opt=35°C; *t*max is the temperature where $f(x)$ declines to 0.0, *t*max = 45°C; *t*shr is the shape parameter for the part of the curve to the right of *t*opt, *t*shr = 0.2; *t*shl is the shape parameter for the part of the curve to the left of *t*opt, *t*shl = 2.63. The effect of temperature is a 0-1 scalar between temperatures of 0 and 35°C. In the Century runs described in section 4.2, we replaced the generalized Poisson density function with the exponential function described in Table 2b and (3).

The regulation of microbial activity by moisture is a modified logistic function [*Parton and Innis,* 1972]:

$$\text{Effect of moisture} = \frac{a}{1 + be^{-cx}}, \quad (6)$$

where x is the ratio of precipitation plus stored water to potential evapotranspiration [*Parton et al.*, 1987], a is 1, the maximum values of $f(x)$, a scalar, b = 30 is the control parameter for the value of $f(x)$ when x = 0.0, and c = -8.5 is the control parameter for the values of "x" at the inflection point of the curve.

In Century, defac is calculated first and then multiplied by the maximum decay rate for an individual pool. Thus it influences the decay rate of both the carbon and nitrogen pools throughout the model.

4. Results and Discussion

4.1. Incubation Results: Heterotrophic respiration.

The short-term CO_2 fluxes from all incubated tropical soils rose exponentially with temperature, up to 55°C, a relatively high temperature (Figure 3, measured on day 1). The range of

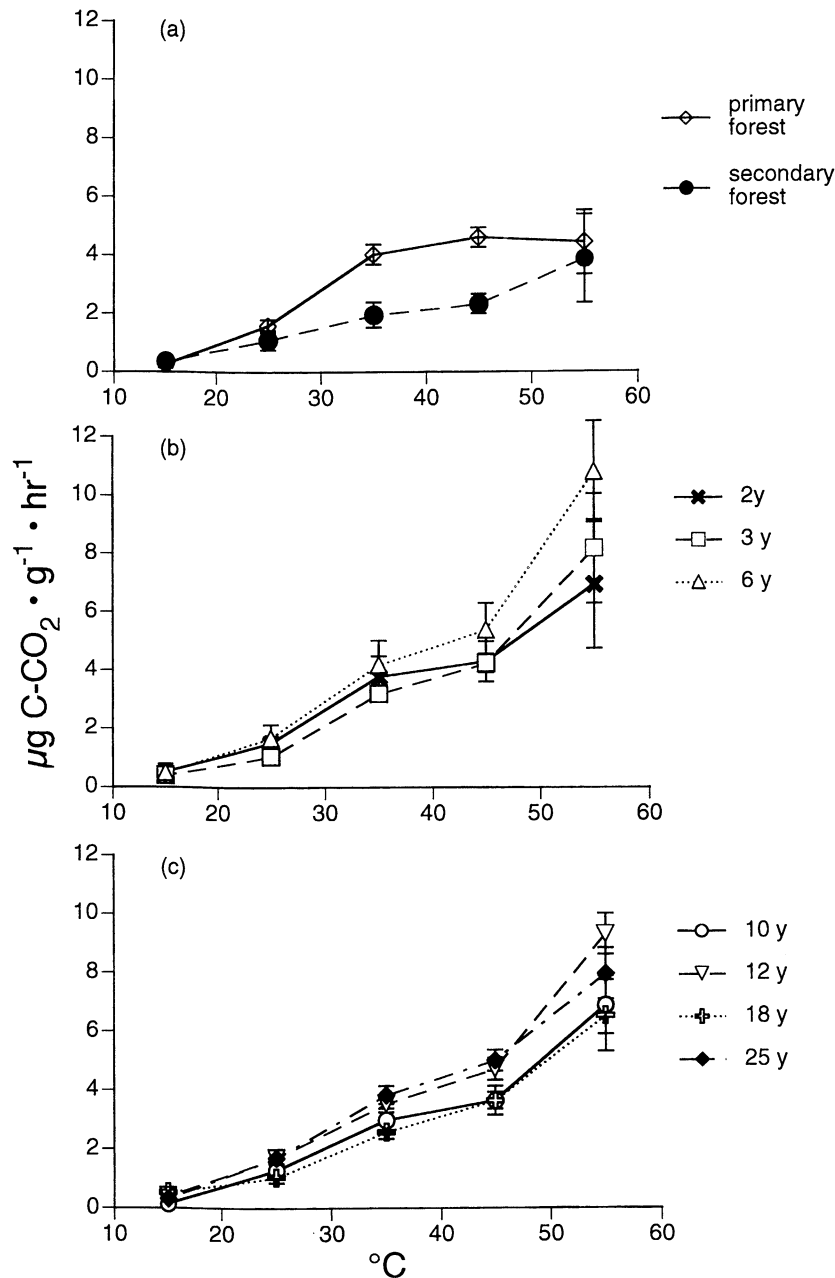


Figure 3. The variation in heterotrophic respiration flux with temperature for the (a-c) Costa Rican, (d) Texas, and (e) Brazilian sites. CO_2 fluxes for the Hawai'i sites are provided by Holland *et al.* [1995].

temperatures used in these incubations spanned the range of surface soil temperatures experienced at tropical latitudes. It is not unusual for surface soil temperatures to exceed 45°-50°C, while the soil below remains cooler because litter, soil, and soil water buffer the deeper soils from the dramatic changes experienced at the surface [*Geiger*, 1965]. The persistent rise in heterotrophic respiration with high temperatures is consistent with even the earliest studies of soil respiration [*Lundegårdh*, 1921], where he stated that "the CO_2 percentage rises rapidly with temperature up to ~60°C and this is no doubt largely due to the fact that the CO_2 production is a biological process, induced by bacteria and fungi." Many field and laboratory studies have demonstrated a similar exponential rise in soil respiration with temperature [*Peterjohn et al.*, 1994; *Townsend et al.* 1997; *Kätterer et al.*, 1998].

Heterotrophic respiration (HR) fluxes spanned orders of magnitude from 0.2 to 120 μg CO_2 -C g^{-1} h^{-1} including the Hawai'i data not shown here [*Holland et al.*, 1995] (Figure 3). Using the bulk densities from Table 1 and the depth of sampling (10 cm), the measured rates can be converted to mg CO_2-C m^{-2} h^{-1} and compared to field measurements of soil respiration. The range of laboratory heterotrophic respiration rates was 12.6-1349 mg CO_2-C m^{-2} h^{-1} with the greatest fluxes from the Hawai'i Histosols. The highest measured values were greater than the highest field measurements of soil respiration reported in the review by *Singh*

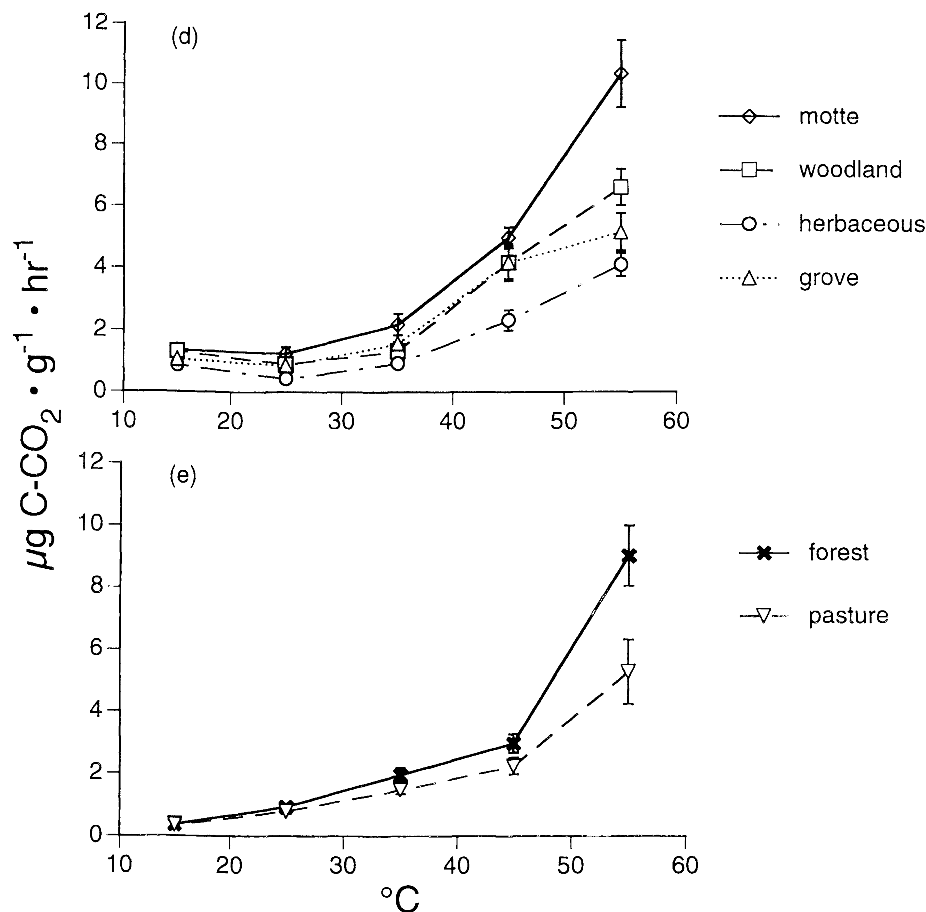


Figure 3. (continued)

and Gupta [1977] (697 mg CO_2-C g^{-1} h^{-1} for a second growth Costa Rican rainforest) and were also greater than the limited number of annual average soil respiration rates compiled by *Raich and Schlesinger* [1992]. Our measurements considered only heterotrophic respiration and did not include the substantial root respiration flux (20-70%) included in field measurements of soil respiration [*Paul and Clark*, 1996; *Raich and Schlesinger*, 1992]. The highest incubation temperatures were greater than the annual average temperatures experienced in the field.

Heterotrophic respiration rates were strongly correlated with the wide range of soil organic carbon (SOC) and soil organic nitrogen (SON) contents of the soils sampled (Table 1; Figure 4). In the development of these relationships, we used the fluxes measured at 25°C, the temperature which most closely corresponded to the mean annual temperature of the various sites (Figure 1). The consistency of the relationship over the various sites argues that the correlation between heterotrophic respiration and soil organic carbon and nitrogen would be strong no matter the temperature, but the coefficients of the regression equation may vary. The Hawai'i sites were excluded because they have very high organic matter contents, which led to a spurious coefficient of determination (Table 1). However, the strength of the correlation reflects both the recent inputs of actively cycling carbon, which dominate heterotrophic respiration, and the soil carbon pools, which, because of the longer turnover time, dominate soil organic carbon content.

Substrate availability is a key determinant of the temperature response of heterotrophic respiration [*Anderson and Domsch*, 1986; *Pohhacker and Zeh*, 1995; *Winkler et al.*, 1996]. Using the long-term incubation of the Brazilian soils as an example, heterotrophic respiration rose exponentially with temperature only during the first few days of incubation (Figure 5). Subsequently, the maximum flux dropped to lower and lower temperatures. After one week of incubation, the flux peaked at 45°C and between 10 and 24 weeks of incubation, the average flux peaked at 35°C. The greater demands for substrate and higher turnover rates at higher temperatures quickly depleted the easily metabolized substrate. More available carbon results in greater heterotrophic respiration [*Anderson and Domsch*, 1986; *Holland et al.*, 1995; *Townsend et al.*, 1997]. At higher temperatures, the rate of decomposition required to sustain higher respiration rates depleted the available substrate. The temperature response must be considered in light of substrate availability. The calculation of temperature response when substrate is abundant, as was done here, is considerably different than if the temperature response had been calculated after 1or 2 weeks of incubation as has been commonly done.

The $Q_{10}s$ for all of these tropical sites and across the temperature ranges between 15° and 55°C show a distribution with occasional high values observed in a long tail above the mean (Figure 6). The Q_{10} occurrences in our data peak between 1 and 1.25 with most values falling between 1 and 2. The mean Q_{10}

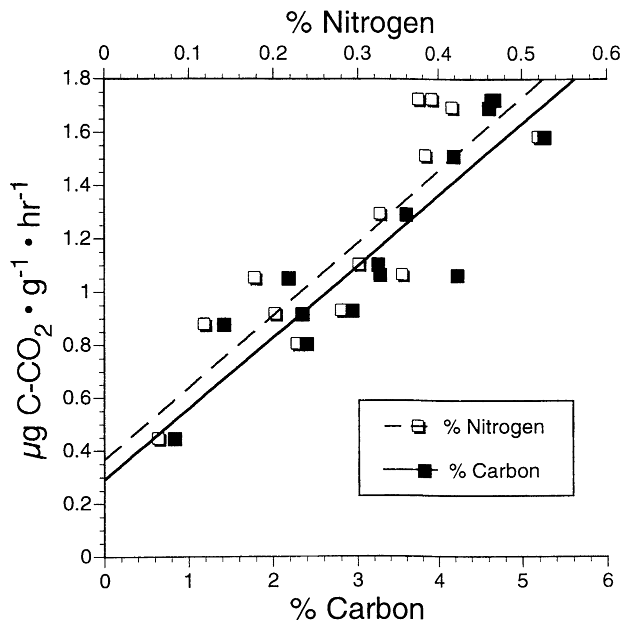


Figure 4. The linear correlation between the heterotrophic respiration (HR) flux and % C and % N in the soil organic matter. The Hawai'i sites were excluded from the graph. HR = 0.27 (SOC) -0.29, r^2 = 0.82 and HR= 2.73 (SON) - 0.37, r^2 = 0.73. The relationship was developed using the HR fluxes measured at 25°C, the incubation temperature which most closely corresponded to the mean annual temperature of the sites (Figure 1).

estimated for heterotrophic respiration in this study of tropical soils was 2.37, compared to the Q_{10} of 2.4 estimated by *Raich and Schlesinger* [1992] in their global compilation of Q_{10} values for field soil respiration measurements. By contrast, *Fung et al.* [1987] reported lower Q_{10} values of 1.4-1.6 for tropical and subtropical woody vegetation in their compilation of soil CO_2 fluxes and its temperature dependence.

Overall, the mean and range of our laboratory-based estimates of Q_{10} values for heterotrophic respiration declined slightly with increasing incubation temperature (Table 3; P = 0.059). The decline in Q_{10} with rising temperature was greatest below 45°C. These results are consistent with studies of temperate soil respiration by *Schleser* [1982] and *Kirschbaum* [1995]. In a field study, *Boone et al.* [1998] describe a decline in Q_{10} with decreasing carbon inputs. *Townsend et al.* [1997] reported a slight but statistically insignificant decline in Q_{10} in their laboratory examination of the temperature dependence of the slow and active soil organic matter pools. This array of field and laboratory studies argues for an interaction between substrate availability and calculated Q_{10}. Substrate limitation is a key determinant of the apparent strength of the respiration response to temperature, and if this is not controlled, interpretation of fluxes in terms of microbial metabolism can be inconsistent or misleading [*Anderson and Domsch*, 1986; *Holland et al.*, 1995; *Townsend et al.*, 1997; *Giardina and Ryan*, 2000; *Valentini et al.*, 2000; *Grace and Rayment*, 2000]. Q_{10} calculations are derived from the theoretical basis for calculation of activation energies based on the change of the rate of biochemical reactions with temperature (the Arrhenius equation). A fundamental requirement of the Arrhenius calculation is that the reaction not be substrate limited. This requirement is often neglected in the calculation of Q_{10}s. Recent global calculations underscore the importance of accurate understanding and representation of the interaction between substrate availability and the temperature response of respiration [*Grace and Rayment,* 2000].

Normalized fluxes more consistently rose with temperature than the raw HR fluxes themselves (Figures 2 and 5; Table 2a). For the individual sites, the slope parameter, k_2, varied between 0.031 (Costa Rican primary forest site) and 0.090 (Brazilian forest site). The y intercept parameter, k_1, varied over a much wider range from 0.063 (Brazilian forest site) to 7.702 (1700 m pasture on the Island of Hawai'i). When all of the sites were combined together, the slope parameter, k_2, was 0.054, and the y intercept parameter, k_1, was 0.092. Both values fell near the middle of the range of parameters determined for the individual sites, and the confidence intervals reflect the variability in the parameters determined for the individual sites.

We learned a number of key points from these laboratory investigations. First, although modeling analyses frequently use a single Q_{10} value (typically 2), we found considerable variability in the Q_{10}s both between sites and across temperatures (Table 3). Second, there was a consistent exponential increase in heterotrophic respiration with rising temperature when substrate was abundant, but the response changed as substrate availability declined (Figure 5). The strength of the exponential response of decomposition to temperature varied with geographic location, but within a single location, only the Costa Rican chronosequence showed a temperature sensitivity that differed significantly (P = 0.001). For all the sites combined, the variability was not correlated with any of the following: mean annual temperature of the site, soil organic carbon (%), soil organic nitrogen (%), soil texture, lignin content, lignin:N ratio, or C:N ratio (Tables 1 and 3). Thus, as in our previous studies, the regression analyses do not explain the uncertainty in the temperature sensitivity of heterotrophic respiration but argue that the variability may be driven by microbial community dynamics interacting with substrate availability [*Schimel and Gulledge*, 1998; *Holland et al.*, 1995; this study].

4.2. Model Analysis

Within Century, temperature regulation of many of the microbiological processes; decomposition, heterotrophic respiration, and nitrogen mineralization, act through a single decomposition factor "defac," which incorporates the influence of both temperature and moisture (Plate 1). Defac is the cross product of the temperature equation and the moisture equation [*Parton et al.*, 1987]. The temperature portion of the defac formulation exerts much greater control over defac than does the moisture portion because it has a much greater dynamic range. We performed three simulations using in turn the best fit and the upper and lower confidence intervals of the temperature parameters. Defac differed by more than two-fold when the temperature equation was changed from the lower to the upper bound of the 95% confidence interval for k_1 and k_2. There was a change in magnitude of defac among the three simulations, but the spatial pattern of the three simulations were quite similar.

The uncertainty associated with the temperature sensitivity of decomposition resulted in substantial differences in modeled carbon and nitrogen fluxes and pools. The simulations using the lowest temperature sensitivity accumulated the most soil organic carbon and nitrogen because lower above-ground and

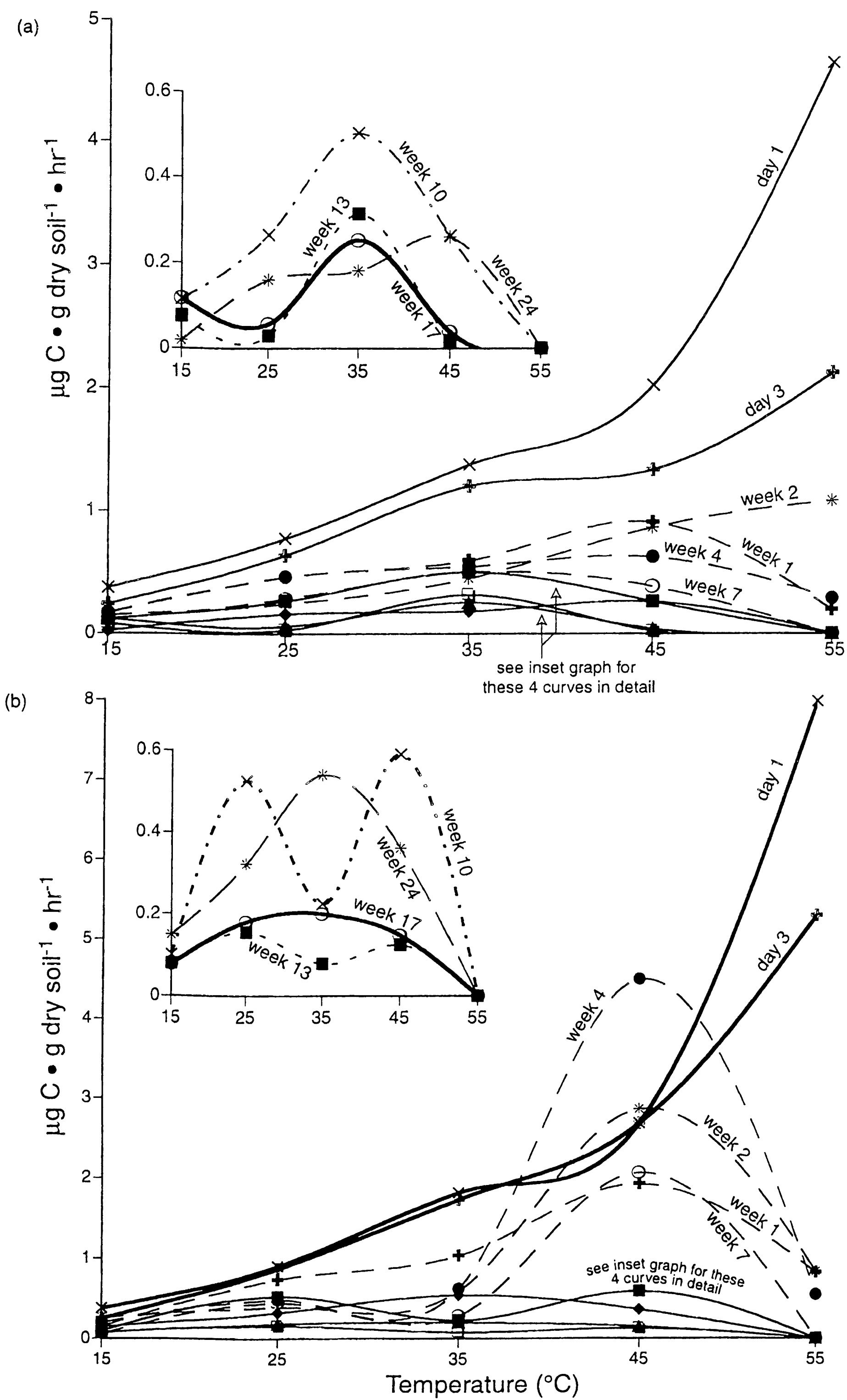


Figure 5. Time series of heterotrophic respiration for long term incubation of the (a) Brazilian forest and (b) pasture.

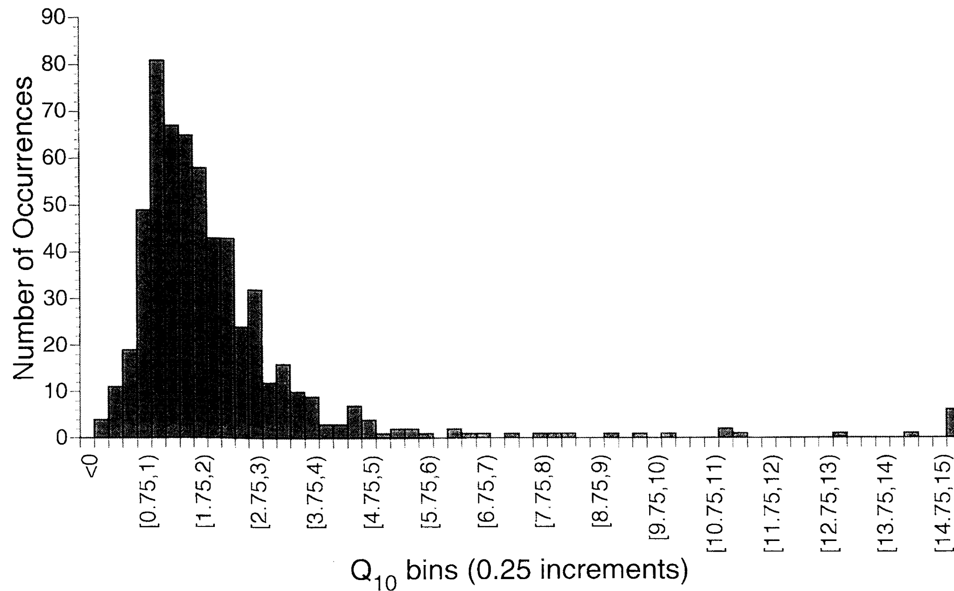


Figure 6. The distribution of the Q_{10} values binned in 0.25 unit increments across all sites and all temperature ranges. The mean Q_{10} value is 2.37, the median is 1.74, and the standard deviation is 3.16.

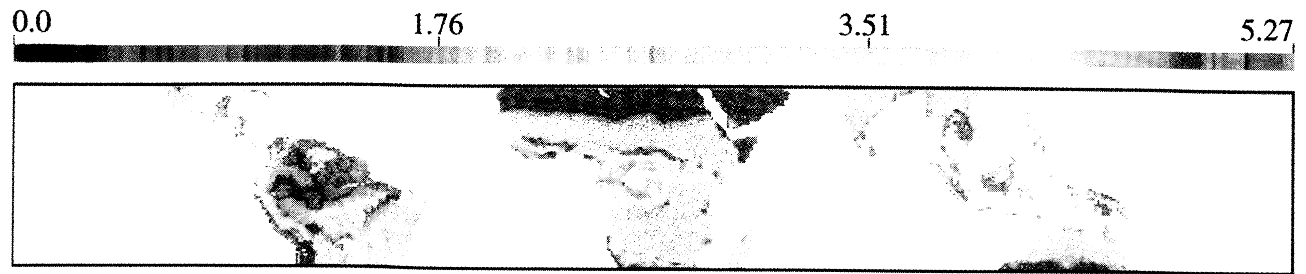
belowground net primary production was accompanied by less decomposition (Table 5). The simulation with the greatest temperature sensitivity had the greatest NPP because of a more active nutrient cycle, but the greater NPP was counteracted by greater rates of decomposition resulting in the smallest soil organic matter stocks. In all cases, tropical forests and savannas dominated the fluxes and the pools followed in order by grasslands, deserts, and wetlands (Plate 1; Tables 4 and 5). Simulations using the laboratory based estimate of temperature sensitivity resulted in a 47 Pg C change in soil carbon storage (to

Table 3. Q_{10} Values for Each Temperature Range Measured

Q_{10}	25°, 15°C	35°, 25°C	45°, 35°C	55°, 45°C
Brazil				
forest	3.1 (0.4)	2.2 (0.3)	1.7 (0.2)	3.4 (0.4)
pasture	3.1 (1.2)	2.0 (0.2)	1.5 (0.1)	2.3 (0.2)
Costa Rica				
forest	15.6 (8.3)	2.7 (0.2)	1.2 (0.1)	1.0 (0.2)
secondary forest	4.1 (1.6)	6.4 (3.4)	2.2 (1.0)	1.4 (0.4)
2 year old pasture	2.6 (0.5)	2.6 (0.2)	1.1 (0.1)	1.5 (0.4)
3 year old pasture	6.6 (4.8)	3.4 (0.5)	1.4 (0.1)	1.9 (0.3)
6 year old pasture	8.5 (7.3)	3.5 (0.9)	1.4 (0.2)	2.1 (0.2)
10 year old pasture	4.8 (0.2)	3.4 (1.0)	1.4 (0.3)	1.9 (0.3)
12 year old pasture	5.5 (1.7)	2.1 (0.1)	1.4 (0.1)	2.1 (0.2)
18 year old pasture	1.2 (0.2)	3.1 (0.8)	1.5 (0.2)	2.0 (0.5)
25 year old pasture	3.1 (0.6)	2.4 (0.2)	1.3 (0.1)	1.6 (0.2)
Hawaii				
800 m pasture	1.8 (0.4)	1.6 (0.3)	1.8 (2.0)	2.2 (0.3)
1700 m pasture	2.0 (0.3)	1.5 (0.2)	1.6 (0.2)	1.7 (0.3)
800 m forest	1.6 (0.3)	1.6 (0.3)	1.6 (0.3)	1.5 (0.2)
1700 m forest	2.8 (0.4)	1.2 (0.1)	1.7 (0.1)	1.9 (0.4)
Maui pasture	1.9 (0.3)	1.3 (0.2)	1.3 (0.2)	1.9 (0.3)
Texas				
herbaceous	0.5 (0.1)	2.2 (0.2)	2.7 (0.4)	2.0 (0.4)
grove	1.3 (0.4)	1.7 (0.1)	2.7 (0.4)	1.3 (0.2)
motte	1.1 (0.1)	2.1 (0.2)	3.1 (1.1)	1.9 (0.4)
woodland	0.8 (0.2)	1.5 (0.2)	3.2 (0.2)	1.7 (0.2)
All sites combined				
mean	2.3 (0.1)	2.2 (0.1)	1.8 (0.1)	1.9 (0.1)
median	1.9	2.0	1.5	1.8
range	0.3-7.8	0.4-9.6	0.4-9.1	0-5.8

Values in parentheses are standard errors. Q_{10} values greater than ten were excluded from the analysis.

a) decomposition factor (defac), best fit — data maximum 7.03



b) soil organic carbon (somtc), best fit — data range 0.0 - 29075.

c) heterotrophic respiration, best fit — data maximum 1273.

Plate 1. (a) The decomposition factor (defac), best fit. (b) Soil organic carbon (somtc), best fit. (c) Heterotrophic respiration, best fit (Table 2b).

Table 4. The Ratio of the Change in Pools and Fluxes to the Change in the Parameter k_2, the Slope Parameter Which Had the Most Influence on the Results

	Forests	Savannas	Grasslands	Deserts	Wetlands	Total
		Standing pools				
ΔSOC (Pg C)/ Δk_2	4273	1582	90	293	62	6364
ΔSON (Pg N)/ Δk_2	86	77	4.8	13	2.5	244
		Fluxes				
ΔHR (Pg C)/ Δk_2	432	4.2	5.1	4.1	5.3	487
Δnet N mineralized (Pg N)/ Δk_2	11.3	0.083	0.0089	0.146	0.128	12.6

See text for more information.
SOC, soil organic carbon.
SON, soil organic nitrogen.
HR, heterotrophic respiration.

20 cm depth) and a 4.8 Pg C yr^{-1} change in heterotrophic respiration fluxes for tropical forests alone. Carbon fluxes changed by 53% across the range of temperature sensitivities (the lowest value was used as the reference point for the percent change calculation). Simulations of tropical forests were substantially more sensitive to the change in temperature parameterization than any of the other biomes considered, suggesting that water limitation of decomposition played a larger role in savannas, grasslands, deserts, and wetlands. The changes in carbon and nitrogen fluxes were significantly less than changes in carbon and nitrogen storage.

Simulated soil organic nitrogen pool and net nitrogen mineralization values were much less sensitive to the change in temperature parameterization than their carbon counterparts (Tables 4 and 5). Total soil organic nitrogen content differed by 5% difference across the range of temperature sensitivities, and the spatial median net nitrogen mineralization increased by two-fold across the range of temperature sensitivities. In tropical forests, the simulated regional average C:N ratio of soil organic matter ranged from 13.8 to 16.18 between the upper and lower temperature sensitivity simulations. The narrowing of C:N ratios of soil organic matter with higher temperature sensitivities reduces immobilization and fuels net N mineralization. The rise in net N mineralization, which is nitrogen available for plant uptake, also allows a drop in the C:N ratio of the vegetation inputs to decomposition, providing another source of decreased immobilization demand for N. Thus, in addition to the direct effect of the temperature function on net N mineralization, comparable in size to the direct effect on heterotrophic respiration (~20%), there was the strong indirect effect operating through the C:N ratio of the metabolic, microbial, and slow soil organic matter pools.

Unlike much of the rest of the terrestrial biosphere, plant growth in undisturbed moist tropical forests frequently is additionally limited by some combination of "rock-derived" elements, including phosphorus (P) and calcium (Ca) which have inorganic sources and are strongly biologically recycled [*Cuevas and Medina*, 1988; *Vitousek and Sanford*, 1986]. *McKane et al.* [1995] argue that nutrient availability will constrain increases in tropical C storage to a maximum of 63 Mg of carbon for predicted future climates. However, the nature and strength of such nutrient limitation across variations in climate and soil types within the tropics is variable and uncertain [*Matson et al.*, 1999; *McKane et al.*, 1995], making it difficult to project how temperature-driven

Table 5. Summary of the Impact of the Variability of Temperature Regulation on Tropical Carbon and Nitrogen Pools and Fluxes

	Forests	Savannas	Grasslands	Deserts	Wetlands	Total
Area x 10^6 km^2	22	21	0.82	5.3	1.5	50
		Standing pools				
Soil organic carbon, Pg† C*						
upper 95% CI†	152	34.9	3.07	8.48	1.84	200
best fit	175	42.7	3.53	9.99	2.16	233
lower 95% CI	199	52.3	4.06	11.7	2.52	270
Soil organic, nitrogen, Tg N‡						
upper 95% CI	11,348	2,894	296	718	145	15,401
best fit	12,190	3,297	323	790	159	16,760
lower 95% CI	12,296	3,740	349	864	172	18,090
		Fluxes				
Heterotrophic respiration, Pg yr^{-1}						
upper 95% CI	13.67	2.53	0.182	0.167	0.184	16.73
best fit	11.5	2.35	0.156	0.147	0.157	14.26
lower 95% CI	8.92	2.07	0.126	0.122	0.126	11.37
Net N mineralization, Tg N yr^{-1}						
upper 95% CI	281	60.1	3.27	4.99	3.57	354
best fit	219	56.6	2.75	4.25	2.88	286
lower 95% CI	157	50.1	2.19	3.38	2.16	215

*Petagrams, 10^{15} g.
†CI, confidence interval.
‡Teragrams, 10^{12} g.

changes in heterotrophic respiration might interact with nutrient cycling. The complexity of tropical nutrient cycling is an important limitation of ecosystem models which do not represent the element cycles of phosphorus, calcium or other base cations which are likely to play important roles in tropical biogeochemistry. The analysis presented here illustrates how temperature interacts with N availability to influence tropical carbon exchange. The multiple interactions of temperature and the cycling of other elements should be the subject of additional experimental and modeling-based analyses.

5. Conclusions

Overall, the results of this study underscore the sensitivity of tropical carbon and nitrogen cycling to the temperature-decomposition relationship despite relatively constant diurnal and seasonal temperatures for tropical ecosystems. The laboratory results point out a number of key lessons for extrapolating information on heterotrophic respiration to model relationships. When substrate is abundant, the overall temperature response is exponential but variable. The variability is not accounted for by differences in easily measured quantities like soil texture, soil organic matter content, lignin:N, C:N, or mean annual precipitation or temperature, suggesting that the variability is driven by other factors. We demonstrated the interaction with substrate availability, but it is likely that microbial community dynamics are an important factor. Short- and long-term incubations provide very different results regarding the temperature sensitivity of decomposition because of the strong substrate limitation which occurs in long-term incubations. The model results underscore the need to explicitly consider the uncertainty associated with key relationships, such as temperature regulation of decomposition in regional and global simulations, and the need to pay close attention to issues of substrate availability when examining decomposition/temperature relationships. Temperature responses of ecosystem components, including decomposition, rank among the best described aspects of ecosystem dynamics, but our understanding is far from complete, and we need critical evaluation of ecosystem response to global change scenarios to understand the strengths and weakness of commonly used models [*VEMAP Members*, 1995].

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E. A. Holland, Max-Planck-Institut für Biogochemie. Postfach 10 01 64. 07701 Jena. Germany. (eholland@bgc-jena.mpg.de)

B. McKeown and J.C. Neff, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523.

A. R. Townsend, Environmental, Population, and Organismic Biology, N122 Ramaley, Campus Box 34, University of Colorado, Boulder, CO 80303.

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