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Climate dependence of heterotrophic soil respiration from a soil-translocation experiment along a 3000 m tropical forest altitudinal gradient

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Summary

Tropical ecosystems play a key role in the global carbon cycle, but their response to global warming is not well understood. Altitudinal gradients offer the unique possibility of undertaking *in situ* experimental studies of the influence of alterations in climate on the carbon (C) cycle. In a soil-translocation experiment we took replicate soil cores at 3030 m, 1500 m, 1000 m and 200 m above sea level along an altitudinal gradient in tropical forest in Peru, and exchanged (i.e. translocated) them among these sites to observe the influence of altered climatic conditions on the decomposition of soil organic matter under natural field conditions. Soil respiration rates of the translocated soil cores and adjacent undisturbed soils were measured twice a month from April 2007 to October 2007. The temperature sensitivity of heterotrophic respiration in each core was examined using a Lloyd & Taylor function and a simple modified third-order polynomial fit. Calculated Q_{10} values decreased with decreasing altitude using both mathematical functions (2.53–1.24 according to the Lloyd & Taylor function, and 2.56–0.63 using the polynomial fit). Soil organic C-stocks increased markedly and linearly with altitude, but surprisingly the average total soil respiration rate did not vary significantly with altitude along the transect (3.98–4.31 μmol CO_2 m^{-2} s^{-1}). This implies an increase with elevation of absolute C allocation to below-ground allocation.

Introduction

Tropical forests play a major role in the global carbon (C) cycle. Approximately 46% of the world's living biomass and 11% of the soil C stocks are stored within these ecosystems (Brown & Lugo, 1982; Lewis, 2006). Furthermore, C return-rates from soils to the atmosphere are generally at a maximum in tropical moist forests where temperature and moisture are often not limiting (Luo & Zhou, 2006). Changes in environmental conditions will affect the C cycle of these ecosystems not only directly, but also through possible feedback effects (Davidson & Janssens, 2006).

The amount of C sequestered in ecosystems equates to the balance of C inputs and losses over time, and is related to both biotic (e.g. substrate quality) and abiotic (e.g. temperature) conditions (Garten & Hanson, 2006). Elevation gradients traverse large differences in temperature and moisture under otherwise similar environmental conditions (e.g. lithology, seasonality), providing a useful natural framework for examining controls on the terrestrial C cycle. For example, Leuschner *et al.* (2007) studied the C allocation of leaves and roots along an altitudinal gradient in tropical montane forest in Ecuador, finding a clear shift towards below-ground allocation in the root-to-shoot ratio with increasing altitude. Graefe *et al.* (2008) observed increasing root longevity with increasing elevation in the same forest. However, it is not just C allocation processes that alter with altitude, soil processes influencing decomposition rates also vary strongly with climatic conditions at different elevations (Schawe *et al.*, 2007).

In general, an increase in the stock of soil organic matter (SOM) with elevation has been widely reported (Townsend *et al.*, 1995; Garten *et al.*, 1999; Trumbore *et al.*, 1999). However, the influence of changed climatic conditions on the soil respiration rate (R_s) remains a matter of debate, especially when considered in forest ecosystems at different altitudes. The dependence of R_s on temperature can be described with various functions, as reviewed by Fang & Moncrieff (2001). Depending on the function applied, calculated temperature sensitivities and the consequent predicted soil CO_2 effluxes under warming can vary considerably. Kätterer *et al.* (1998) reviewed several incubation studies and concluded that temperature sensitivities might vary over different ranges of

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temperature, with, in general, predictions of greater temperature sensitivities at lower temperatures.

In the present paper, we examine the influence of warming on heterotrophic R_s by reporting on the translocation of cores along an altitudinal gradient of almost 3000 m in a tropical forest in the Peruvian Andes. We measured the CO_2 effluxes twice each month during the dry season of 2007. A Lloyd & Taylor (1994) function in combination with a quadratic soil moisture function was then fitted to the data to examine the influences of differences in temperature and soil provenance on the calculated temperature sensitivity in R_s.

Materials and methods

Site description

The soil translocation experiment was performed along an altitudinal tropical forest transect down the east flank of the Peruvian Andes, a region with continuous forest cover ranging from high-elevation cloud-forest through to lowland Amazon rainforest. The experiment was established as part of an interdisciplinary study by the Andes Biodiversity and Ecosystem Research Group (ABERG). Soil monoliths (cores) were translocated among the following sites: Wayqecha (site A, upper-montane cloud-forest, 3030 m above sea level (asl)), San Pedro (site B, lower-montane cloud-forest 1500 m asl), Tono (site C, sub-montane rainforest 1000 m asl) and Tambopata (site D, lowland rainforest 200 m asl) (Table 1). Mean annual air temperature increases steadily from site A to site D, whilst annual rainfall reaches a maximum at 1000 m asl at site C. Approximately 25% of total rainfall occurs during the dry season from April to October. There are large shifts in taxonomic composition along the gradient: the dominant tree families are *Clusiaceae* and *Cunoniceae at* site A, *Clethraceae* at site B, *Elaeocarpaceae* and *Fabaceae* at site C and *Moraceae* and *Fabaceae* at site D.

Soil core translocation design

Soil cores were translocated in plastic tubes with an internal diameter of 10 cm in April 2007. At all four forest sites, the litter and upper soil layers were removed and plastic sampling tubes inserted vertically into the soil to excavate 50 cm of intact mineral soil. The upper soil layer differed among sites: a classic organic layer (Oh) was found at sites A and B, but at sites C and D the Oh layer was missing, and instead was replaced by a thin layer comprising a mixture of mineral soil and partly decomposed organic matter, which, following Scheffer & Schachtschabel (2002), we term the Aa layer. As both Oh and Aa layers were much richer in organic matter than the underlying mineral soils, we use a collective term 'organic topsoils' to refer to both. Soil compaction as a result of coring was minimal ($< 4\%$) because of the moist soil conditions during the sampling period. The organic topsoils were sieved using a 1-cm mesh to remove all coarse roots, the fresh weight per m^3 quantified, and the corresponding amount of organic material per tube area temporarily stored in re-sealable plastic bags for transport. The lengths of the plastic tubes were cut to contain 50 cm of intact soil core and the refilled organic topsoil with 5 cm of free space left in the top of the tube. Each core was equipped with a 10-cm long soil moisture probe (Echo EC-10, Decagon, Pullman, WA, USA) mounted within the mineral soil layer; the sensor cables were trained out of the cores trough a small borehole in the side wall, which was subsequently sealed with silicon rubber. The bottom of each tube was covered with a 63-µm nylon mesh to prevent roots growing into the tube and to stabilize the soils within the tubes, while still allowing moisture drainage. Twelve soil cores were extracted at each site; three of these were re-installed at the same sites as controls, and three were translocated to each of the other three sites. To insert the cores at the new sites, holes were drilled with a hand auger of 12-cm diameter and the cores inserted carefully into the bore holes. The gaps around the tubes were filled with soil, and the organic topsoils from their original sites replaced on the mineral soil surface inside the tubes. To maintain moisture at contents similar to those experienced at the sites of origin of each soil, cores were capped with suitably sized removable funnels/collars to increase/reduce the total rainfall incident on each of the soil monoliths to amounts similar to that which would have been experienced by the monolith at its original location. Three additional cores were taken at site A and installed at 2350 m above sea level to partially fill the altitude gap between sites A and B.

At each of the four sites, a soil moisture probe was installed at 5-cm depth in the native soil and connected to a data logger (Echo EM-50, Decagon). Water content (WC) in these undisturbed sites was recorded every 30 minutes.

Soil analysis

At each site, initial soil samples for chemical and physical analysis were taken using thin-walled metal tubes of 35 mm diameter. The samples were stratified according to the different soil horizons into

Table 1 Site description of the transect (3000 m altitudinal transect in tropical forest) with mean annual air temperature (MAT) and mean annual precipitation (MAP) (C.A.J. Girardin, unpublished data)

	Site	Altitude	Coordinates	MAT / °C	MAP / mm
A	Wayqecha	3030	13°11′29”S/71°35′24”W	12.5	1700
B	San Pedro	1500	13°02′52”S/71°32′34”W	18.3	2600
C	Tono	1000	12°53′25”S/71°33′17”W	21.3	3100
D	Tambopata	200	12°49′50”S/69°16′11”W	26.4	2700

organic topsoils (as removed before the core sampling), humic layers and mineral layers. Mineral layers were subdivided into B_1 and B_2 layers to obtain analytical results for the translocated soil-core depths. All soil samples were immediately air-dried in Peru and later oven-dried to constant mass at 40°C in the UK and then crushed and sieved to 2 mm. Stones and roots were removed and the fine earth density calculated. Total C and nitrogen (N) concentrations and the $\delta^{13}C$ values of milled subsamples were quantified with a Finnigan Delta Plus-XL mass spectrometer; $\delta^{13}C$ results are reported as per mil (‰) deviations from the V-PDB standard for carbon (Bird *et al*., 2007). pH was measured with an electrode in a mixture of dry soil and 0.01 M $CaCl_2$ at a ratio of 1:10 after shaking the mixture for 17 hours (Thunjai *et al*., 2001). Particle size analyses for all mineral layers were determined by laser diffraction (Beckmann Coulter LS230, Krefeld, Germany).

Soil respiration measurements

R_s was measured using a Li-Cor 8100 (Li-Cor, Nebraska, USA) portable infrared gas analyser equipped with a proprietary 10-cm survey chamber. For the first 2 months after translocation, effluxes from all cores were measured each week, and thereafter twice each month until the end of the dry season in mid-October. The increase in CO_2 concentration within the closed chamber was measured for 150 s, and the flux rates calculated based on an exponential best fit equation (Healy *et al*., 1996; Kutzbach *et al*., 2007). Every tube was measured twice on each occasion, and the R_s rates averaged before any further calculation. The soil water content within the tubes, the air temperature in the chamber and the soil temperature at 10-cm depth (outside the tubes) were also recorded at the same time. Before the measurements were taken, the funnels or collars were detached and any new leaf litter removed from the tubes. In addition to the measurement of heterotrophic R_s from the soil cores in the tubes, the 'native' R_s, including litter and root respiration, was measured on three permanently installed soil collars at each site. These plastic collars had been pushed gently 3 cm into the ground, taking care not to cut any roots, but enabling all sources of soil CO_2 efflux from the soil to be captured.

Calculation of climate sensitivity

To express the climate dependence of R_s, various equations have been considered, as reviewed by Fang & Moncrieff (2001). Here, we used a Lloyd & Taylor (1994) function to calculate the temperature sensitivity and combined it with a simple quadratic function for the relation between water content (WC) and R_s (Martin & Bolstad, 2005):

$$R_s = (a \times e^{-E_0/(T_S - T_0)}) \times (b \times WC + c \times WC^2), \qquad (1)$$

where a, E_0, T_0, b and c are fitted parameters. This temperature function was proposed to give a better and unbiased relationship between R_s and soil temperatures than the original Arrhenius function (Fang & Moncrieff, 2001). This function is not valid for temperatures near to 0°C because of the singularity of the equation at that temperature (Tuomi *et al*., 2008), but as the study sites are in the tropics, this should not be of any concern. The function was fitted to the measured values of R_s by means of minimizing the least square regressions through the Levenberg-Marquardt algorithm, using the software package STATISTICA 6.0.

Results

Soil properties

Descriptions of the physical and chemical soil properties for all sites are given in Table 2. All organic topsoils (Oh and Aa) were characterized by a large porosity and root density, and acid pH values, between 2.4 and 3.4. The pH values were less acidic in the deeper soil horizons for all four altitudes, ranging from 3.8 to 4.4. At the rainforest sites C and D, the thin Aa layer directly overlaid very weathered mineral B layers. The mineral B layers at site C were very silty, with a large fraction (54%) of fine-silt particles in the size range 2–20 µm, whereas the B layers at site D had large sand contents (44–49%). These large sand contents were caused by the geomorphology of site D, as it was situated on an ancient terrace of the Tambopata River. At the highest elevation site, the sampled soil depth of 67 cm corresponded well with the total soil depth, whereas total soil depth increased considerably at lower altitudes. The amount of soil organic carbon (SOC) within the organic topsoil plus the top 50 cm of mineral soil (±1 STD) decreased linearly with altitude from 25.7 (±3.3) kg C m^{-2} at site A to 13.3 (±1.2) kg C m^{-2} at site B, 9.0 (±0.5) kg C m^{-2} at site C and 4.1 (±0.9) kg C m^{-2} at site D (correlation coefficient $R^2 = 0.99$). However, the translocated soil cores do not represent the total soil C-stocks, especially at the lower elevations where soils can be several metres deep. $\delta^{13}C$ values increased at all sites with increasing depth, although this change in $\delta^{13}C$ with soil depth tended to decline with altitude ($R^2 = 0.74$, $P = 0.14$). In general, differences in $\delta^{13}C$ between the organic topsoils and the mineral layers were larger than the differences observed between equivalent samples from along the transect.

Total R_s along the altitudinal transect

R_s values for undisturbed 'native' soil along the transect during the dry season of 2007 are shown in Figure 1. The repeated R_s measurements of each of the three soil collars at each site were averaged for every measurement day and are given together with the standard deviations. For site D, measurements could only be taken during three field periods in May, June and October 2007, as site access was difficult. Soil temperatures at 10-cm depth varied from 9.4 to 24.4°C along the transect, but despite having the lowest mean temperature, the effluxes measured at site A included both the smallest (3.18 µmol m^{-2} s^{-1}) and largest (5.11 µmol m^{-2} s^{-1}) values recorded throughout the study. The average native CO_2 efflux (±1 STD) at site A was 4.18 (±0.19) µmol m^{-2} s^{-1} with a mean soil temperature (range) at 10 cm depth of

Table 2 Soil properties along a 3000 m altitudinal transect in tropical forest. Values for texture represent proportions (%) of sand/silt/clay

Site		Wayqecha	San Pedro	Tono	Tambopata
Layer	Property				
Oh	depth / cm	17	7		
	density / g cm^{-3}	0.063	0.053		
	% C	47.4	41.3		
	$\delta^{13}C$	−27.13	−29.08		
	C stock / kg m^{-2}	5.04	1.53		
	C/N	25	15		
	pH ($CaCl_2$)	2.4	3.3		
A(h/a)	depth / cm	15	7	3	1
	density / g cm^{-3}	0.36	0.39	0.17	0.410
	texture	12/72/16	13/71/16	64/31/5	66/27/5
	% C	14.5	10.5	24.9	5.7
	$\delta^{13}C$	−25.79	−27.16	−28.91	−29.39
	C stock / kg m^{-2}	7.76	2.85	1.24	0.23
	C/N	18	15	20	14
	pH ($CaCl_2$)	3	3.5	3.4	3.4
B1	depth / cm	15	15	25	25
	density / g cm^{-3}	0.52	0.39	0.44	0.69
	texture	7/79/14	69/27/4	13/68/19	44/41/10
	% C	7.9	4.8	4.9	1.3
	$\delta^{13}C$	−24.91	−25.87	−27.28	−26.83
	C stock / kg m^{-2}	6.22	3.92	4.96	2.29
	C/N	14	18	13	10
	pH ($CaCl_2$)	3.9	4	4.1	3.7
B2	depth / cm	20	28	25	25
	density / g cm^{-3}	0.6	0.45	0.62	0.84
	texture	12/52/36	31/54/15	9/66/25	49/36/15
	% C	5.5	4.0	2.0	0.8
	$\delta^{13}C$	−24.23	−24.97	−25.38	−24.96
	C stock / kg m^{-2}	6.67	4.99	2.85	1.59
	C/N	15	17	10	10
	pH ($CaCl_2$)	4	4.4	4.2	3.8

10.7 (9.4–12.1)°C, at site B it was 3.98 (±0.16) µmol m^{-2} s^{-1} and a soil temperature of 17.2 (16.5–18.6)°C, at site C it was 4.10 (±0.16) µmol m^{-2} s^{-1} and 19.6 (17.8–20.8)°C, and at the lowest site D it was 4.31 (±0.22) µmol m^{-2} s^{-1} and 23.6 (22.1–23.8)°C. The R_s values along the transect were not significantly different between the four sites (paired *t*-tests, $P > 0.27$). At all sites, R_s increased with short-term increases in soil temperature, but we did not calculate temperature sensitivity, as the number of observations for the single sites was too small to predict reliable Q_{10} values.

R_s of the translocated soil cores

All cores showed large R_s values for the first 30 days, with the CO_2 effluxes stabilizing after this initial phase independently of site temperature. Therefore, we consider that this period of 30 days is an appropriate limit to use in separating the stabilization and stabilized phases across the transect (see Discussion).

The calculated parameters for Equation 1 for sites A to D are listed in Table 3. The correlation coefficients R^2 between the model equation and the measured values were between 0.69 and 0.88 (Figure 2). To compare the climate dependence of soils from different sites, we calculated Q_{10} values for the average soil temperatures at the four sites, and for the fixed temperature range from 10 to 20°C, keeping the WC constant (Table 3). Using a fixed temperature range from 10 to 20°C, the Q_{10} values showed no trend along the transect and varied between 2.46 and 3.84. The result was different if calculated using the site-specific mean soil temperatures: in this case, Q_{10} values declined continuously with site elevation from 2.53 to 1.24.

Figure 3 illustrates the results generated by fitting measured R_s to Equation 1 for an optimal WC and the trend of the Q_{10} values from 5 to 30°C. The respiration rates grew exponentially with temperature to a point of inflection, and with decreasing rates of increase at greater temperatures. This inflection point was reached at a temperature of 13°C for sites A to C, and at 11°C for site D, and is equivalent to a drop of the Q_{10} value below 2. For all four sites, the function resulted in large Q_{10} values at low temperatures up to the inflection point, and slightly decreasing values at greater temperatures after this point.

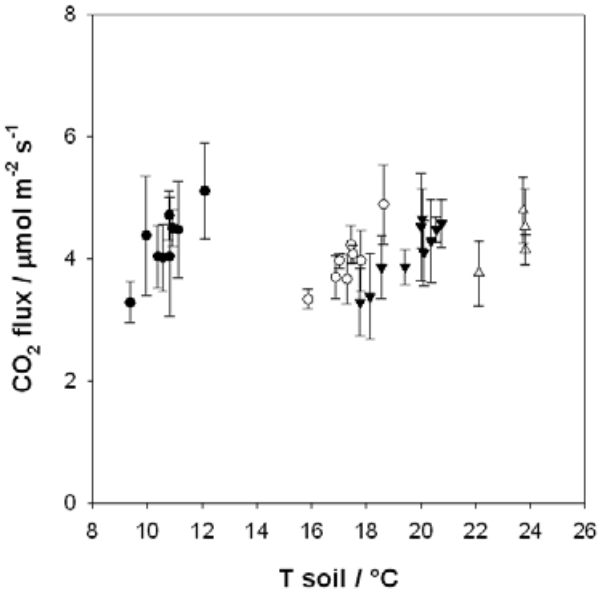

Figure 1 Total 'native' R_s from undisturbed soil collars along a 3000 m altitudinal transect in tropical forest during the dry season of 2007. Values are means from three soil collars, measured twice, with their standard deviations (• = site A 3030 m above sea level, ◦ = site B 1500 m above sea level, ▼ = site C 1000 m above sea level, Δ = site D 200 m above sea level).

Water contents

The soil moisture contents as recorded with the data loggers were averaged for each day and are given together with the means of the WC for the translocated cores in Figure 4. The native soil moisture content at site A varied between 5 and 15%, at site B between 8 and 17%, at site C between 22 and 42% and at site D from 8 to 19%, although these measures of soil WC are not directly comparable with the data from the soil cores as the sensors were installed in the organic layer rather than the mineral layer (see Methods). The dataset recorded from site C is incomplete, as the data logger was attacked by termites.

The soil cores installed at a single site but with different provenances (i.e. different original sites) showed large variations in their WC, caused by differences in the textures of the different soils, and differences in the sizes of the partial covers placed on the tops of the soil tubes. However, variations in WC were much smaller when cores taken from the same site were compared with each other. All cores taken from sites A, B, C and D had WCs of 18 to 32%, 23 to 35%, 33 to 46% and 25 to 34%, respectively.

On the basis of the calculated best fit model after Equation 1, the optimal WC for all four sites was between 25 and 32% (Table 4). The theoretical lower WC limit for R_s for all four soils was 0% as determined by the model assumptions. However, the upper limit was defined by the measured WC, at which the soils are saturated, and varied from 48 to 63%. To compare moisture sensitivities of different soils, we here define the range of WC, in which the quadratic part of Equation 1 has a slope between −1 and 1, as a theoretically ideal WC for R_s. Thus slopes of ±1 are arbitrary, but the relative sensitivities would not change when considering any other constant slopes.

Discussion

Changes in C stocks with altitude

The amount of SOC stored in the organic topsoils plus 50-cm depth of mineral soil showed a strong correlation with altitude, as reported elsewhere in studies of tropical forest transects (Townsend *et al*., 1995; Graefe *et al*., 2008). Altitude thus integrates changes in the various conditions that determine soil C storage, including temperature, soil moisture, atmospheric pressure, radiation, litter input, and soil weathering, amongst others (Körner, 2007).

The large SOC contents in the Oh layers of 47.4 and 41.3% at sites A and B, respectively, are close to the SOC inputs of litter and root (Aerts, 1997), and indicate that the organic

Table 3 Calculated equation parameters for the best fit functions after Lloyd & Taylor (1994) and a modified third order polynomial fit in combination with a quadratic soil moisture function with the corresponding Q_{10} values as calculated for site-specific mean soil temperatures (Tsm) and for the temperature range from 10° to 20°C

Origin	Calculated best fit parameters	R^2	Q_{10} (Tsm)	$Q_{10(10-20°C)}$
	Lloyd & Taylor			
Site A	$R_s = 8.49*\exp(-24.99/(T_s + 1.64))*(13.87*WC - 27.65*WC^2)$	0.88	2.53	2.7
Site B	$R_s = 5.32*\exp(-17.53/(T_s - 1.7))*(7.82*WC - 12.32*WC^2)$	0.69	1.55	3.17
Site C	$R_s = 3.83*\exp(-14.54/(T_s - 1.34))*(6.65*WC - 13.58*WC^2)$	0.87	1.45	3.84
Site D	$R_s = 4.57*\exp(-14.68/(T_s - 3.41))*(15.87*WC - 28.91*WC^2)$	0.74	1.24	2.46
	Third order polynomial			
Site A	$R_s = (-4.57*T_s^2 + 0.01*T_s^3) * (-0.04*WC + 0.08*WC^2)$	0.89	2.56	2.71
Site B	$R_s = (6.05*T_s^2 + 0.14*T_s^3)*(-0.01*WC - 0.02*WC^2)$	0.71	1.57	2.84
Site C	$R_s = (-4.61*T_s^2 + 0.10*T_s^3)*(-0.03*WC + 0.05*WC^2)$	0.85	1.53	2.95
Site D	$R_s = (0.13 * T_s^2 + 0.003*T_s^3) * (0.52*WC - 1.08*WC^2)$	0.74	0.63	2.52

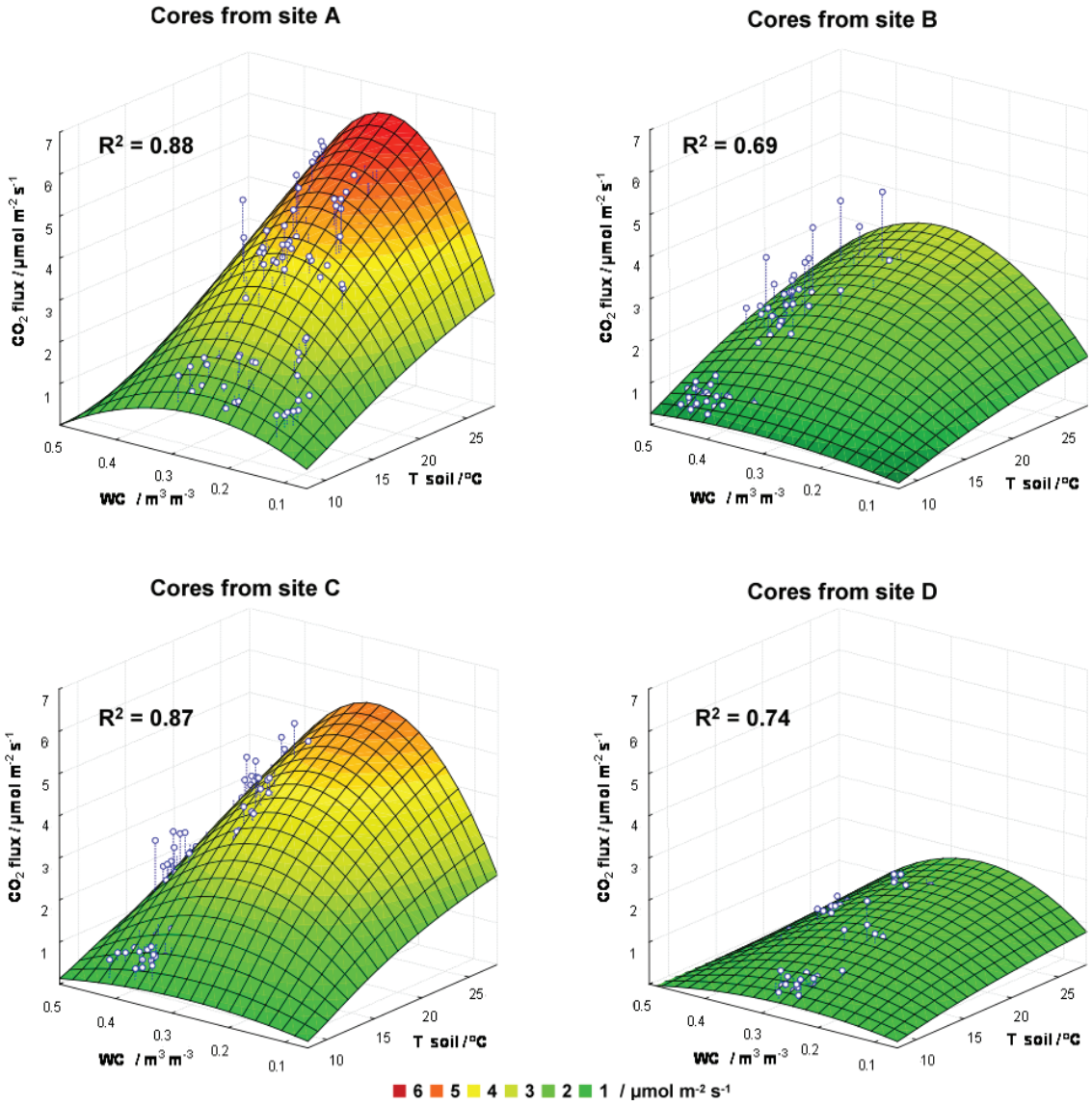

Figure 2 Measured heterotrophic soil respiration (R_s) values (◦, average of two measurements) of translocated soil cores along a 3000 m altitudinal transect in tropical forest showing the dependence of R_s on the soil temperature (T_{soil}) and water content (WC), with the best fit model (surface) for the function $R_s = a \times \exp(b/(T_{soil} - c)) \times (d \times WC + e \times WC^2)$, whereas a, b, c, d and e are fitted parameters.

topsoils at these sites are less decomposed and mixed with mineral soil than at the two lowland sites, which had SOC concentrations of 24.9 and 5.7%. This is also confirmed by the stable C isotope signatures, which are coupled to root and litter inputs and change during the course of decomposition (Garten *et al*., 2000; Powers & Schlesinger, 2002). Garten (2006) showed that $\delta^{13}C$ enrichment factors (ε), calculated after the Rayleigh equation (Mariotti *et al*., 1981), correlate with SOC turnover times along an altitudinal forest gradient in the Appalachian Mountains, USA. For our study sites, calculated ε values tended to decrease with altitude ($R^2 = 0.61$, $P = 0.22$) from -0.451 at site D to -0.707 at site C, -0.588 at site B, and -0.750 at site A, which, consistent with Garten (2006), also indicates reduced organic matter decomposition at higher altitudes.

In relation to differences between sites in SOC stock and SOC compound composition, the C/N ratio of the organic topsoil at site B was disproportionately smaller than at the adjacent sites, A and C. This could be the result of a greater activity of the microfaunal community at site B; Gonzalez & Seastedt (2001) showed that high densities and diversities of soil fauna lead to enhanced N release from litter in some tropical forests, resulting in lower C/N ratios.

Another decisive factor controlling SOM decomposition is acidity (Leifeld *et al*., 2008). The pH values in all soil profiles were very acidic. pH became slightly less acidic with depth at each site

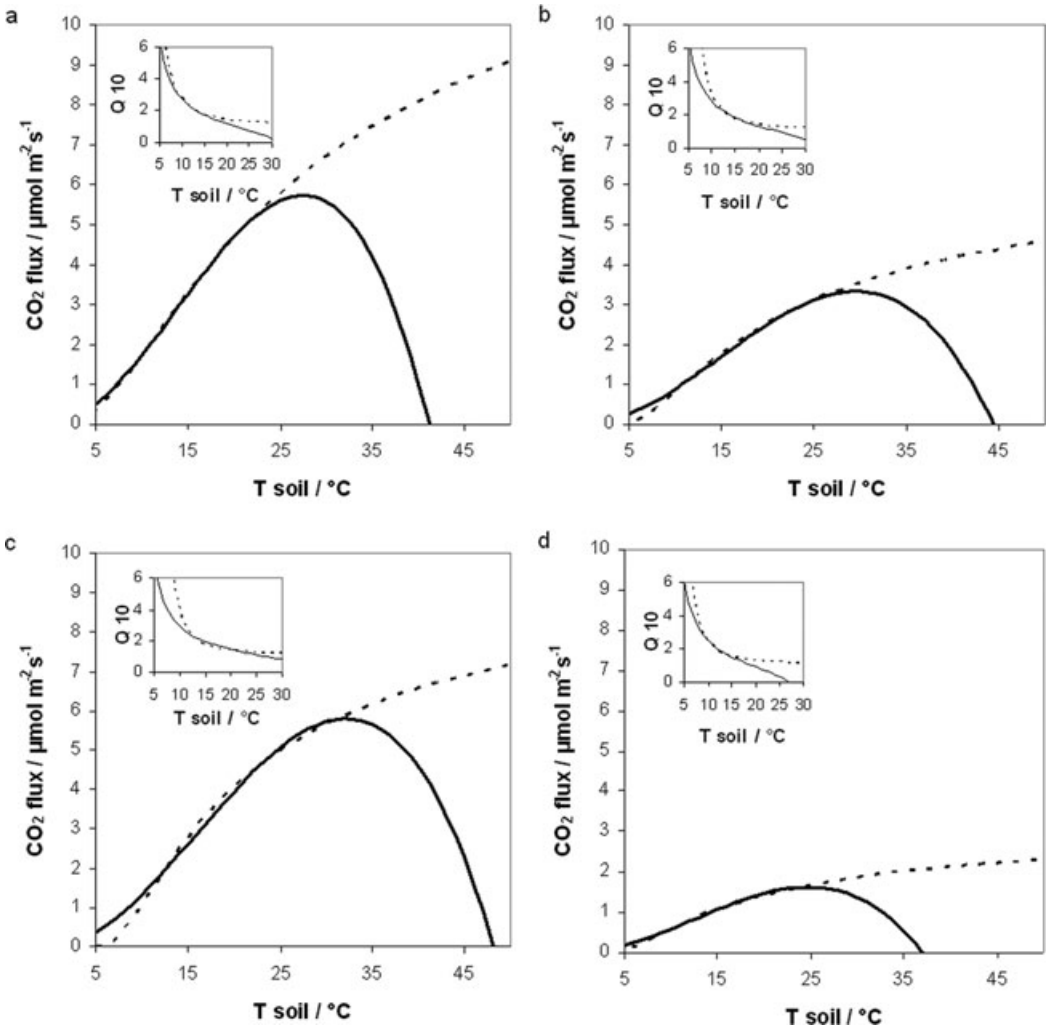

Figure 3 Heterotrophic R_s plotted against soil temperature as calculated with different functions (dotted line: Lloyd & Taylor, 1994, $R_s = (a \times e^{-E0/(TS-T0)}) \times (b \times WC + c \times WC^2)$; solid line: new modified third order polynomial fit, $R_s = (d \times T_s^2 - e \times T_s^3) \times (b \times WC + c \times WC^2)$) for optimal water contents for soil cores originating from 3030 m above sea level, 1500 m above sea level, 1000 m above sea level and 200 m above sea level. The inset graphs show the trend of the temperature sensitivities (Q_{10}) for the corresponding functions.

from the organic topsoils downwards to the mineral layers, and among sites, the pH of the organic topsoils decreased at higher altitudes. Under acidic conditions, cell-wall-degrading exoenzymatic activities can be inhibited, resulting in slow decomposition rates (Kok & van der Velde, 1991). Walse *et al*. (1998) showed that the decomposition of organic material can be considerably suppressed at pH values below 5, with the biggest negative impact on bacterial growth rates, which appear to be more pH-sensitive than fungal growth rates. The acid pH values of 2.4 and 3.0 in the Oh and Ah layers from site A might therefore be an additional factor leading to reduced decomposition rates.

A variety of processes limit the decomposition of SOM at higher altitudes. This is of special interest if we consider the minimal variation with altitude in 'native' R_s along the transect. Although biomass production and its decomposition in soils are often considered to be very temperature-dependent (Peng & Dang, 2003; Davidson & Janssens, 2006), we could not detect any differences in R_s at the four sites (mean R_s of 4.12 (±0.15) µmol m^{-2} s^{-1}, range of means from 3.98 to 4.31 µmol m^{-2} s^{-1}), over a large mean soil temperature range of 10.7–23.6°C. Taking into account the C accumulation at higher altitudes, this has implications for understanding C allocation among the different components of the ecosystem and implies that the total C input into the soils in the form of woody debris, root and leaf litter and root exudates is likely to be greater at the colder sites. Other possible modes of C export have not been measured at this site, but the loss of C by leaching of dissolved C or through landslides would be affected more on steep slopes at high altitudes than on relatively flat lowland forests and hence does not provide an explanation.

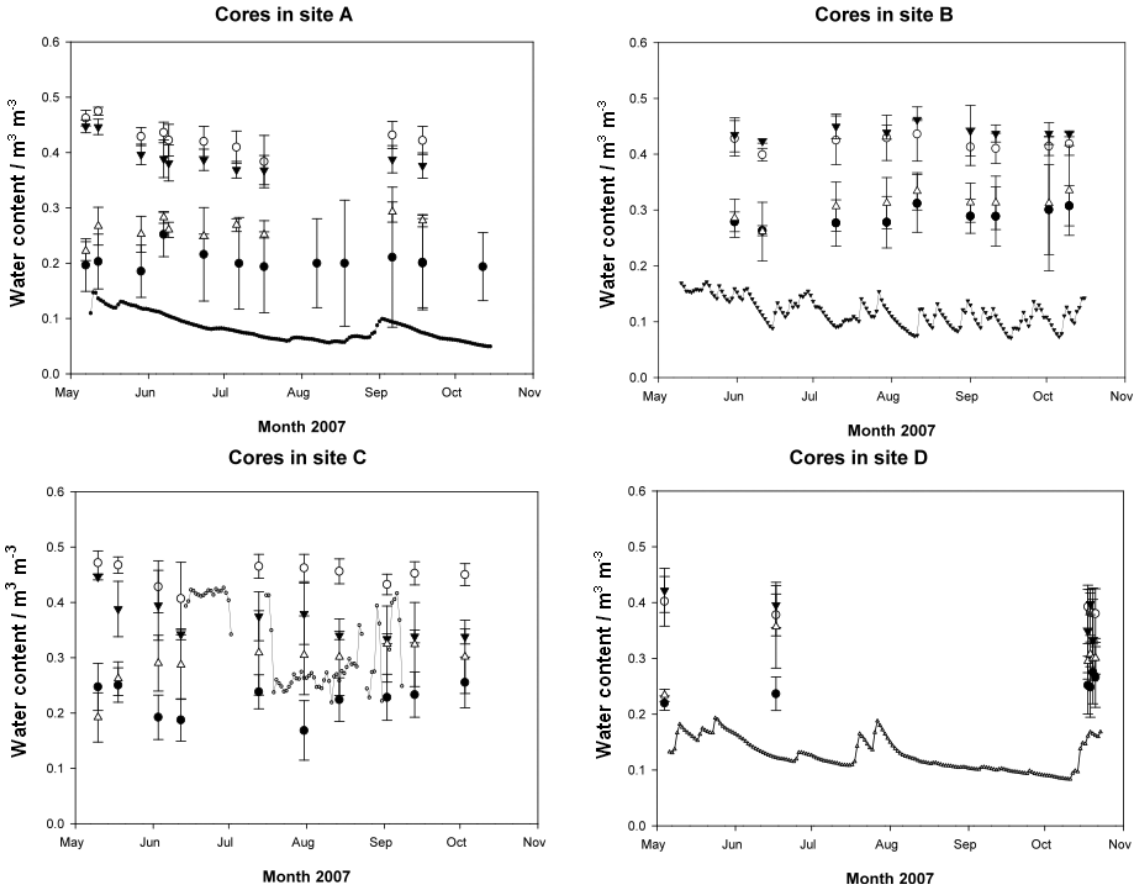

Figure 4 Soil moisture content at 5 cm depth in undisturbed soil (solid lines) and at 10 cm in soil cores from site A (●), site B (○), site C (▼) and site D (Δ) along a 3000 m altitudinal transect in tropical forest at their translocation sites during the dry season of 2007. Standard deviations are given for each set of three cores originating from the same site.

Initial stabilization phase

R_s values during the first 30 days after the translocation were greater than after this period. Possible reasons for the larger initial CO_2 effluxes are examined below.

Rapid consumption of the most labile soil C fraction is possible as soil from lower temperature sites is warmed. Most model-based studies estimate the labile SOM pool to represent 5–15% of total C (Conant *et al*., 2008; Hartley & Ineson, 2008). Here, the soil from site A, which showed the greatest temperature sensitivity, lost only 0.87% of its total C in this initial stabilization phase after being translocated to the warmest location, site D. Furthermore, this stabilization process lasted for more or less the same duration for different soils, C amounts and field temperatures. Thus, it is possible that the respired C during this initial phase might not correspond with the labile SOM pool of existing soil C models, but was released from other components of the SOM pool.

A combination of impacts on root-related processes may also be involved. The depletion of root exudates after excision of all living roots during the soil core extraction (Hanson *et al*., 2000) may cause a decline in R_s. As long as plants are photosynthetically active, roots produce exudates consisting mainly of carbohydrates, amino-acids and organic acids (Hütsch *et al*., 2002). However, as most root exudates are respired within a few days and are water soluble (Kuzyakov & Siniakina, 2001), it seems unlikely that a cessation of their production alone could support the observed large R_s rates for as long as 30 days. Increased R_s might also have been caused by the decomposition of excised and dead roots (Kuzyakov, 2006). The starch from cut, dead roots in the mineral layer and fine roots in the Oh layer could have provided additional substrate for microorganisms and thereby have enhanced CO_2 effluxes (Högberg *et al*., 2001; Bhupinderpal *et al*., 2003).

Finally, the physical disturbance of the translocation itself may explain our observations. It is useful here to distinguish between disturbance to the mineral and the organic layers. Mineral aggregates might have been broken down as a result of the sampling process, and previously physically protected SOM exposed to decomposing organisms (Sollins *et al*., 1996). The structure of the organic topsoil was completely disturbed, as we sieved the organic material and refilled a defined amount into the tubes to retain the original bulk soil material of these layers.

Table 4 Modelled minimal, optimal and maximal water contents (WC) for R_s after the equation: $R_s = (a \times e - E^0/(T^S - T^0)) \times (b \times WC + c \times WC^2)$. The ideal WC range represents the WC range in which the slopes of the quadratic functions are ±1

Site	Minimal WC /m^3 m^{-3}	Optimal WC /m^3 m^{-3}	Maximal WC /m^3 m^{-3}	Ideal WC range /m^3 m^{-3}
A	0.00	0.25	0.50	0.23–0.27
B	0.00	0.32	0.63	0.28–0.36
C	0.00	0.28	0.55	0.21–0.28
D	0.00	0.28	0.48	0.26–0.29

The altered availability of oxygen and moisture in the newly-constructed organic topsoil could therefore also have caused large CO_2 respiration rates during the initial phase (Borken *et al*., 2003).

Summarizing, there are various possible processes that all might have led to large R_s values after the start of the translocation, but it is not possible to separately identify them. To calculate the temperature sensitivity for the different soils, we therefore excluded the CO_2 flux rates from this initial phase.

Temperature sensitivity of heterotrophic R_s

Heterotrophic R_s is controlled by substrate supply, microbial biomass and climate, and not solely by temperature (Davidson *et al*., 2006). The temperature sensitivity of R_s as represented by Q_{10} takes into account a wide range of kinetic properties involved in SOM decomposition and reflecting this complexity (Davidson & Janssens, 2006). The calculation of Q_{10} itself depends also on the equation with which it has been determined (Kirschbaum, 1995). The application of Equation 1 showed that the use of the same function for standardized temperature ranges or site-specific mean soil temperatures might lead to different conclusions, as already described by Kirschbaum (1995). The Q_{10} values as calculated for the temperature range from 10 to 20°C decreased from site C to sites B and A, with the smallest value for site D (Table 3). These Q_{10} values would thus imply that the Q_{10} value of heterotrophic R_s is independent of the temperature or the substrate amount, as it does not correlate with their regime along the transect. This is inconsistent with findings elsewhere that R_s is dependent on temperature and substrate availability (Kätterer *et al*., 1998; Davidson & Janssens, 2006; Hartley & Ineson, 2008). In contrast, if we use the site-specific average soil temperatures to calculate the temperature sensitivities, Equation 1 gives decreasing Q_{10} values from high-elevation sites to lowlands, and the Q_{10} values correlate strongly with the available substrate amount ($Q_{10} = 0.06 \times$SOC-stock$+0.9$, $R^2 = 0.96$). These Q_{10} values vary from 2.53 to 1.24 and are slightly smaller than other reported Q_{10} values from studies of tropical forests. Bekku *et al*. (2003) calculated Q_{10} values of 2.1 for tropical soils by warming them by 8°C under laboratory conditions, and Mo *et al*. (2007) found Q_{10} values between 2.3 and 2.1 for a monsoon forest in China. The Q_{10} values as calculated here show that the soil from 3030 m asl, which has the largest C-stock, had more than two-fold greater heterotrophic temperature sensitivity than the soil from 200 m asl.

Influence of soil moisture contents

The WC in the translocated soil cores was in all cases larger than that at their original site. This can be mainly explained by three factors. First, cutting the roots might have restricted plant water uptake, resulting in larger WC (Hart & Sollins, 1998). Secondly, the soil moisture probes inserted in the undisturbed soil at each site were installed at 5-cm depth and not in the mineral layers, as in the soil tubes. This means in the cases of sites A and B that the soil moisture probes were installed in the organic layers with much greater porosities than in the mineral layers of the soil tubes. Thirdly, although the soil compaction of the mineral soils during the core sampling was minimal, it could have led to a decrease of preferential flow paths, resulting in a reduced drainage and greater WC. The soil at site C is characterized by a very large content of fine silt (2–20 μm, 52%) and the site receives the largest precipitation of all four sites (3100 mm per year). This is reflected in the large WC of the undisturbed soil, as well as of the soil cores from this site. At site D, the sand content in the top 50 cm was, on average 47%, which may lead to greater drainage rates and smaller WC.

Relations between R_s and WC can be expressed by various equations (Luo & Zhou, 2006), but, in general, WC is assumed to limit R_s either through water stress at very small WC, or through very large WC, which impedes diffusion of oxygen in soils (Davidson *et al*., 1998). The relation between WC and R_s can therefore be approximated by a simple quadratic function as used by Tang & Baldocchi (2005) and Chang *et al*. (2008), even when the detailed mechanism controlling the impact of WC on R_s is not completely understood (Davidson *et al*., 2006). The concept introduced here of an ideal WC range within the quadratic function slopes ±1 does not relate to limiting soil moisture conditions, but it facilitates a comparison of the sensitivity of different soils to changing WC according to our model. This range of WC is 4% and 3% for the soils from sites A and D, respectively, and 8% and 7% for the soils from sites B and C (Table 4). The narrower range or greater vulnerability to changing moisture conditions for the soils from sites A and D can be explained by the likely large share of respired CO_2 originating from the 17-cm-thick Oh layer at site A, which has a greater porosity than the mineral layers and may react more rapidly to variations in WC, and the sandy soil texture in site D, which reduces the water holding capacity compared with the finer textured soils from sites B and C.

Theoretical optimal soil temperature

Another key component of R_s is the temperature sensitivity of the micro-organisms decomposing the SOM. The soil carbon model CENTURY (Parton *et al*., 1987) uses a function that calculates a maximal optimal temperature for R_s. Reviewing various temperature-dependent R_s functions, Fang & Moncrieff (2001)

concluded that there should be an optimal temperature for the relevant biological processes, and a maximal decomposition rate. They quoted optimal temperatures ranging from 20 to 41°C, which are dependent partly on experimental design. Pietikäinen *et al*. (2005) separated fungal and bacterial growth rates over a wide temperature regime and found that for organic soils, bacterial and fungal growth rates reached their maxima between 25 and 30°C, but respiration rates continued to increase above these temperature optima. The decoupling of growth and respiration at high temperatures was explained by enzymes continuing to function for several weeks even after the death of the micro-organisms, as observed by Ramsay & Bawden (1983). More recently, Tuomi *et al*. (2008) compared several models describing the temperature dependence of R_s using Monte Carlo simulations and concluded that an empirical Gaussian model provided the best fit to several data sets. Therefore, it seems reasonable to consider an R_s model that includes an optimal temperature, even in the absence of measurements at high temperatures. To explore this possibility empirically, we introduced a simple modified third order polynomial of the form:

$$R_s = d \times T_s^2 - e \times T_s^3, \quad (2)$$

where d and e are fitted parameters and T_s is the soil temperature in degrees Celsius. This function describes a quadratic increase of R_s to a temperature optimum, and a subsequent decrease in the efflux rate. In combination with the quadratic model for the WC, this function explained larger proportions of variance (as indicated by R^2) for three of the four sites than the Lloyd and Taylor function (Table 3). The calculated optimal temperatures were between 27 and 32°C for the soils from sites A to C (Figure 3) and are consistent with the suggested optimal microbial growth rates indicated by Pietikäinen *et al*. (2005). The lower value of 25°C, as calculated for the soil from site D, could mean that this site is already very close to its optimal temperature, but could also be an artefact of the measurement, as the soil cores from this site were transported only to higher elevation sites, and not to warmer sites.

For all four soils, the Q_{10} values calculated using Equation 2 decrease rapidly from low temperatures to approximately 13°C (the inflection point), an outcome consistent with other studies (Lloyd & Taylor, 1994; Kirschbaum, 1995; Bekku *et al*., 2003). After reaching this inflection point, the fitted functions based on our heterotrophic R_s measurements suggest a moderate decrease of the Q_{10} values to zero at the temperature optima (Figure 3). The increase of the Q_{10} values as calculated with Equation 1 also slowed down after reaching these inflection points, which were very similar for both equations. Most functions used in the literature do not take into account an optimal temperature and thus hardly any study has found Q_{10} values below one; only Davidson *et al*. (2006) have suggested that Q_{10} values could become negative at high temperatures where substrate supply becomes limiting. Our data suggest that negative Q_{10} values at temperatures above the temperature optima are possible even in the absence of significant substrate limitation.

This large temperature increase does not represent a realistic future warming scenario and may exceed the respiration optimum of a community of respiring organisms. We suggest, therefore, that calculated temperature sensitivities should not be based on 10°C increases but on more realistic warming scenarios. Cramer *et al*. (2004) predicted a warming in tropical land regions of about 4°C by the end of the century, which would lead to calculated temperature sensitivities ('Q_4') after Equation 2 of 1.66, 1.29, 1.27 and 1.0, respectively, for the four sites down the transect. Even this temperature increase may lead to R_s fluxes beyond a particular temperature optimum, but this would be in accordance with published *in situ* warming scenarios. However, these calculations do not take into account shifts in available substrate amounts over time.

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