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Temporal variation and climate dependence of soil respiration and its components along a 3000 m altitudinal tropical forest gradient

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[1] To simulate the effect of temperature on soil respiration rates, we translocated soil cores among four sites (3030, 1500, 1000, and 200 m asl) along an altitudinal tropical forest gradient in the Peruvian Andes, traversing a difference in mean annual temperature of 13.9°C. Rates of total (R_s) and heterotrophic (R_{sh}) respiration were measured twice a month from April 2007 to March 2009 and additionally for full 24 h periods. The diurnal range in R_s increased with altitude; this variation was mainly root and litter derived, whereas R_{sh} varied only slightly over full 24 h periods. Although mean annual daytime R_s rates were not significantly different among the four sites (4.45–4.05 μmol CO$_2$ m^{-2} s^{-1}), the annual amount of respired C decreased with increasing altitude from 1639 g C m^{-2} yr^{-1} at 200 m asl to 1064 g C m^{-2} yr^{-1} at 3030 m asl. The contribution of R_{sh} to R_s was not correlated with elevation and ranged from 25% to 60%. The temperature dependence of R_s was lower at the midelevation sites (Q_{10} of 2.07 and 2.94 at 1500 and 1000 m asl, respectively) than at the highest and lowest sites of the gradient (Q_{10} of 4.33 and 6.92 at 3030 and 200 m asl, respectively). The temperature sensitivity of R_{sh} was higher for the sites at 3030 and 200 m asl and increased with time, i.e., with the loss of the most labile C pools.

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1. Introduction

[2] The rate and underlying mechanism of soil respiration is the subject of a large number of ongoing studies, because soil CO$_2$ effluxes might change considerably with predicted global warming, and substantially impact the terrestrial carbon cycle [*Kirschbaum*, 1995; *Davidson and Janssens*, 2006; *Meir et al.*, 2008]. The principal sources of soil CO$_2$ efflux comprise: microbial communities decomposing accumulated soil organic matter (SOM) (R_{sh}); respiring roots (autotrophic respiration, R_{sa}); and the decomposition of litter (R_{sl}). The amount of respired CO$_2$ is mainly controlled by temperature, soil moisture and substrate availability [*Yuste et al.*, 2007].

[3] Not all ecosystems may react to the same extent to changes in climate, as warming might accelerate SOM decomposition in cold environments more rapidly than in warmer environments [*Bekku et al.*, 2003]. Ecosystems in warmer regions, where the seasonal signal in temperature is small, generally respond most strongly to changes in seasonal precipitation patterns [*Sotta et al.*, 2004; *Meir et al.*, 2008]. Therefore, altitudinal gradients that span considerable climatic variation over short geographic distances, but that experience otherwise similar environmental conditions, are well suited to study the climate sensitivity of respiration processes [*Townsend et al.*, 1995; *Garten et al.*, 1999; *Raich et al.*, 2006]. A key focus is the behavior of the different components of R_s. It is possible that each component might react differently to climate change and to address this concern it is necessary to partition them and study their climate sensitivities individually.

[4] *Hanson et al.* [2000] and *Kuzyakov* [2006] reviewed the most commonly applied field methods to separate different CO$_2$ efflux sources in situ. Methods can be mainly distinguished into the physical separation of R_s sources and the tracking of CO$_2$ effluxes with different isotopic signatures. Physical separation involves the exclusion of single sources such as litter or roots, and the calculation of their contribution by difference with respect to total R_s [*Luo and Zhou*, 2006]. A drawback of this approach is that the intact system is disturbed physically and this may lead to errors in estimating the component contributions in short-term experiments.

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Table 1. Descriptions of the Four Sampling Sites[a]

Altitude (m asl)	Site Name	Coordinates (South/West)	Vegetation Type	MAT (°C)	MAP (mm)
3030	Wayqecha	13° 11′ 29” / 71° 35′ 24”	Montane cloud forest	12.5	1710
1500	San Pedro	13° 02′ 52” / 71° 32′ 34”	Cloud forest	18.3	2630
1000	Tono	12° 53′ 25” / 71° 33′ 17”	Highland rain forest	21.3	3090
200	Tambopata	12° 49′ 50” / 69° 16′ 11”	Lowland rain forest	26.4	2730

[a] Mean annual temperature (MAT) and precipitation (MAP) for the study period from 2007 to 2008 are from *Girardin et al.* [2010].

[5] As well as exhibiting variation in temperature sensitivity, rates of each component of R_s can vary over time [*Rayment and Jarvis*, 2000; *Xu and Qi*, 2001], and it is therefore important to consider diurnal and seasonal variations in these components if an accurate estimate of the total amount of respired C is required. Short-term variations in R_s are mainly caused through diurnal differences in temperature, photosynthetically active radiation and rainfall events [*Tang et al.*, 2005; *Liu et al.*, 2006] and R_s can decline by up to 61% during the night [*Zimmermann et al.*, 2009a]. Respiration measurements taken manually with closed chamber systems during the day must therefore be corrected for diurnal variations if reliable annual totals of R_s are to be calculated.

[6] Another topic of debate is the temperature sensitivity of the different compounds that comprise SOM. Whether labile or recalcitrant SOM pools have inherently higher temperature sensitivities has been widely discussed. *Liski et al.* [1999] and *Giardina and Ryan* [2000] reported that the decomposition of recalcitrant SOM was insensitive to temperature, whereas *Knorr et al.* [2005] and *Leifeld and Fuhrer* [2005] found higher temperature sensitivities for recalcitrant SOM pools than for labile pools. Other studies have concluded that labile and recalcitrant SOM pools have similar temperature sensitivities [*Fang et al.*, 2005; *Conen et al.*, 2006].

[7] The key questions we address here are (1) which is the temperature sensitivity of R_s along an altitudinal gradient? (2) how do the different CO_2 efflux sources vary along this gradient? (3) how large are the variations in annual and diurnal respiration rates? and (4) will the temperature sensitivity of R_{sh} change with ongoing substrate decomposition? For this, we measured R_s and R_{sh} for 2 years along a tropical forest transect in the Peruvian Andes spanning almost 3000 m in elevation. We used soil cores in plastic tubes to quantify R_{sh} and calculated the combined litter and root contribution (R_{sal}) to R_s by difference. In addition, we translocated soil cores among 4 elevations spanning the full 3000 m in altitude in order to quantify the temperature sensitivity of R_{sh} under natural climatic conditions.

2. Methods

2.1. Translocation Experiment

[8] Soil cores were excavated and translocated outside of 1 ha permanent study plots (http://www.andesconservation.org) along the eastern flank of the Peruvian Andes as described by *Zimmermann et al.* [2009b]. In brief, intact mineral soil cores were taken at 3030, 1500, 1000, and 200 m asl along a continuous tropical forest gradient, ranging from lowland rain forest to upper montane cloud forest with a difference in mean annual temperature of 13.9°C (Table 1). Dominant tree families shifted from Clusiaceae and Cunoniceae at 3030 m asl to Clethraceae at 1500 m asl, to Elaeocarpaceae, Moraceae and Fabaceae at the lower rain forest sites. Soils were classified (after FAO) as histic Lithosol at 3030 m asl, umbric Gleysol at 1500 m asl, fluvic Gleysol at 1000 m asl and haplic Ferralsol at 200 m asl. Soils were shallower at higher elevations, and the soil profile at 3030 m asl consisted of a 17 cm thick organic layer and 50 cm of mineral soil. To translocate the same mineral soil volumes from the four sites, 50 cm long intact mineral soil cores were collected in plastic tubes of 10 cm diameter. Litter was completely removed, and the organic-rich topsoil layers collected separately. At each site, 12 cores were excavated and equipped with a soil moisture probe in the top 10 cm of the mineral horizon (Echo EC-10, Decagon, Pullman, Washington, United States). Soil compaction was minimal (<5%), as the sites were very wet during the sampling period at the end of the wet season in March 2007. Three cores were then reinstalled at the same site as controls, and the other cores translocated to the three other elevations. To reinstall the soil cores, holes were drilled with a large-diameter hand auger, the bottom of the soil core tubes covered with a 63 μm nylon mesh, and the separately collected organic topsoils refilled into the tubes above the mineral soil. CO_2 effluxes of these soil cores represent R_{sh}. The translocated tubes were capped with collars or funnels to maintain the same rainfall amount per m^2 as at the site of their origin, as we aimed to manipulate the temperature but not the soil moisture of the translocated soil cores. A summary of the soil properties, including C concentrations and C stocks, is given in Table 2.

[9] To measure the total “native” R_s, including soil organic matter, litter and root respiration, three additional soil collars were installed at each site close (within 5 m) to the soil core sampling locations. These plastic collars of 7 cm height were gently pushed 3 cm into the ground, taking care not to cut too many fine roots, but enabling all sources of soil CO_2 efflux from the soil to be captured.

[10] At each elevation, an additional soil moisture probe was installed at 10 cm depth to record volumetric water contents (WC) in undisturbed soils.

2.2. Soil Respiration Measurements

[11] CO_2 effluxes from the soil translocation tubes and the collars were measured using a Li-8100 (Li-Cor, Nebraska, United States) portable infrared gas analyzer equipped with a proprietary 10 cm survey chamber with a volume of 835 cm^3. Measurements were made twice a month from

Table 2. Soil Properties of the Organic Soil Horizons (Where Present) Plus the Top 50 cm of Mineral Soil Beneath, Along the Transect[a]

Horizon	Property	3030 m asl	1500 m asl	1000 m asl	200 m asl
O	depth (cm)	17	7	3	1
	C stock (kg m^{-2})	5.04	1.53	1.24	0.23
	C/N ratio	25	15	20	14
	pH ($CaCl_2$)	2.4	3.3	3.4	3.4
Ah	depth (cm)	15	7	0	0
	texture (% sand/silt/clay)	12/72/16	13/71/16		
	C stock (kg m^{-2})	7.76	2.85		
	C/N ratio	17	14		
	pH ($CaCl_2$)	3	3.5		
B1	depth (cm)	15	15	25	25
	texture (% sand/silt/clay)	7/79/14	69/27/4	13/68/19	44/41/10
	C stock (kg m^{-2})	6.22	3.92	4.96	2.29
	C/N ratio	14	18	13	9
	pH ($CaCl_2$)	3.9	4	4.1	3.7
B2	depth (cm)	20	28	25	25
	texture (% sand/silt/clay)	12/52/36	31/54/15	9/66/25	49/36/15
	C stock (kg m^{-2})	6.67	4.99	2.85	1.59
	C/N ratio	13	17	11	11
	pH ($CaCl_2$)	4	4.4	4.2	3.8
	Total C stock (kg m^{-2})	*25.69*	*13.29*	*9.05*	*4.11*

[a] Detailed sampling procedures and analytical methods are given by *Zimmermann et al.* [2009b].

April 2007 to March 2009 with fewer measurements at 200 m asl, as site access was limited. Every collar was measured twice on each occasion with a time interval of about 30 min together with the soil temperature at 10 cm depth (T_s) outside the tubes, WC in the tubes and air temperature (T_a) within the measurement chamber. Before the R_{sh} of the soil cores was measured, any new litter accumulated between measurement occasions was carefully removed from the tubes. In addition to the bimonthly measurements, each of the native R_s as well as R_{sh} of the control cores was measured once at half-hourly intervals for full 24 h periods on various days distributed throughout the dry and wet season in 2007.

2.3. Calculation of Temperature Sensitivity

[12] To calculate the temperature dependence of R_s, a *Lloyd and Taylor* [1994] function

$$R_s = a \times \mathrm{e}^{-E0/(TS-T0)} \qquad (1)$$

as given by *Davidson et al.* [2006] was fitted to the measured respiration rates, where a, E_0, and T_0 are fitted parameters, and T_s is the measured soil temperature at 10 cm depth. This temperature function has been suggested to give a better and unbiased relation between respiration and T_s than the standard Arrhenius function [*Fang and Moncrieff*, 2001]. Although this function might not be valid if T_0 equals T_s, this was of no concern at our study sites.

[13] Temperature sensitivities as expressed by Q_{10} values were then calculated comparing respiration rates at 5°C above and below the site specific mean annual T_s:

$$Q_{10} = R_{Ts+5}/R_{Ts-5}. \qquad (2)$$

Q_{10} values for R_{sh} were calculated following the approach by *Conant et al.* [2008a], which takes into account the decline of R_{sh} rates in incubation experiments with time [*Hartley and Ineson*, 2008]. In this method, the temperature dependence of SOC decomposition is calculated by comparing the time elapsed during the decomposition of a defined amount of C at different temperatures. We modified this idea slightly and compared the elapsed time in which each 0.1% portion of the SOC stock was respired from the soil cores installed at 3030 m asl (t_{3030}) with the time required to decompose the same fraction of the SOC stock from the corresponding soil cores installed at 1000 m asl (t_{1000}), as these two sites have a difference in T_s of ~10°C:

$$Q_{10-q} = t_{3030}/t_{1000} \qquad (3)$$

SOC losses with time were calculated by applying the averaged R_{sh} rates, corrected for diurnal variations, between two field measurement occasions to all days between the measurements. To calculate continuous losses with time, double exponential regression functions were fitted to the accumulated proportions of respired SOC.

2.4. Statistics

[14] Average values for each set of three replicates (twice measured) are given with standard errors (SE), and were tested for significant differences with one-way ANOVA, t test, or Mann-Whitney rank sum test (p = 0.05). Correlations among parameters were calculated with Pearsons product moment correlation (R) test using SIGMAPLOT 11. Measured R_s were fitted to equation (1) by minimizing the least square regressions, using the software package STATISTICA 6.0.

3. Results

3.1. Annual Respiration Rates

[15] As shown in Figure 1, R_s at 3030 and 1500 m asl was higher during the wetter season from October to April (t test, $p < 0.03$), whereas R_s at 1000 and 200 m asl did not change

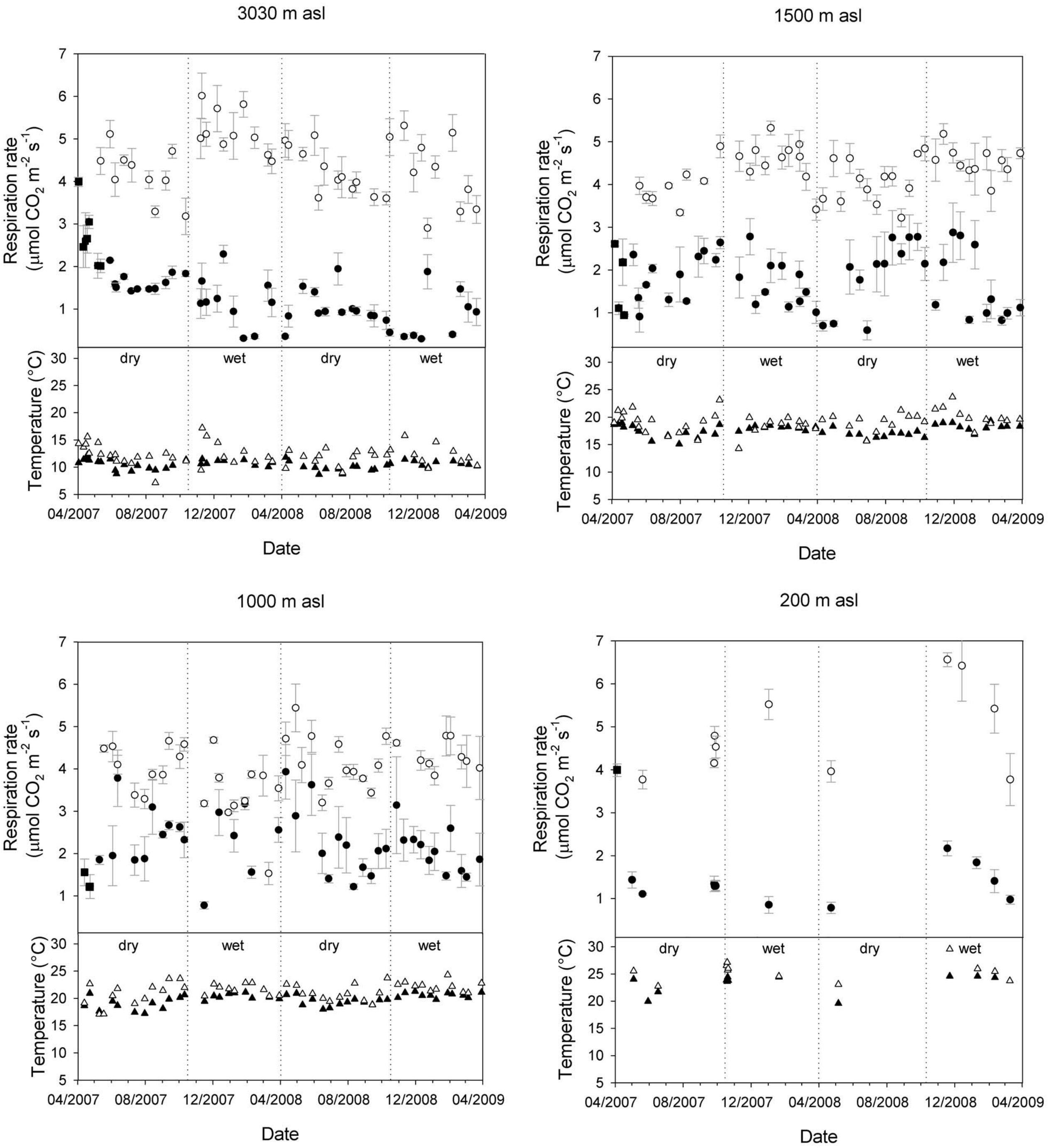

Figure 1. Variations in total (open circles) and heterotrophic (solid circles) soil respiration (with standard errors) along the gradient together with soil (solid triangles) and air (open triangles) temperatures throughout the dry and wet seasons from April 2007 to March 2009. Heterotrophic respiration rates from the first month (solid squares) were not considered in any further calculations.

significantly over the annual cycle. R_s rates were significantly ($p < 0.05$) positively correlated with T_s at all four sites, whereas WC was significantly correlated with R_s only at 3030 m asl ($R = 0.47$, $p = 0.04$). On an annual basis calculated for the year 2008, average daytime R_s (±SE) for the four sites were between 4.45 (±0.11) and 4.05 (±0.09) μmol CO_2 $m^{-2}s^{-1}$ (Table 3), but did not vary significantly (ANOVA, $p = 0.16$) across the full transect, spanning nearly 3000 m in elevation. Both T_a and T_s declined with increases in altitude from 23.6°C at 200 m asl to 10.6°C

Table 3. Average Annual Rates (With Standard Errors) of Total Soil Respiration R_s (Not Corrected for Diurnal Variations), Heterotrophic Respiration R_{sh}, Calculated Combined Root and Litter Respiration R_{sal}, Soil (10 cm, T_s) and Air (Soil Surface, T_a) Temperatures, and Volumetric Moisture Contents (in 10 cm Depth, WC) as Measured During Daytimes in 2008[a]

Altitude (m asl)	R_s (μmol CO$_2$ m^{-2} s^{-1})	R_{sh} (μmol CO$_2$ m^{-2} s^{-1})	R_{sal} (μmol CO$_2$ m^{-2} s^{-1})	T_s (°C)	T_a (°C)	WC (m^3 m^{-3})
3030	4.45 (0.70) a	1.61 (0.59) a	2.83 (0.85) a	10.58 a	12.61 a	0.174 a
1500	4.33 (0.56) a	1.83 (0.74) ab	2.50 (0.85) a	17.81 b	20.06 b	0.375 b
1000	4.05 (0.60) a	2.66 (0.84) b	1.64 (0.75) b	19.85 c	21.73 c	0.367 b
200	4.45 (0.64) a	1.11 (0.23) a	3.34 (0.72) a	23.57 d	25.24 d	0.175 a

[a] R_{sh} for 3030 m asl was corrected for decreasing respiration rates with time (see section 3.1). Letters indicate significant differences among the sites (one-way ANOVA, $p = 0.05$).

at 3030 m asl, but notably, this decline in temperature was not reflected in concomitant declines in R_s.

[16] Only at 3030 m asl, R_{sh} of the control cores decreased exponentially with time following the start of the sampling ($R_{sh} = 1.98 \times \exp(-0.0016 \times \text{days})$, $R^2 = 0.42$, $p < 0.01$) (Figure 1). Therefore, the inverse function was applied to correct R_{sh} values to calculate the contribution of R_{sh} to R_{sh}. Average daytime R_{sh} of the control cores was significantly higher (ANOVA, $p < 0.01$) at the two midelevation sites than at the upper and lower sites (Table 3).

[17] Knowing the total and heterotrophic respiration rates enables the contribution of R_{sal} to R_s to be calculated by

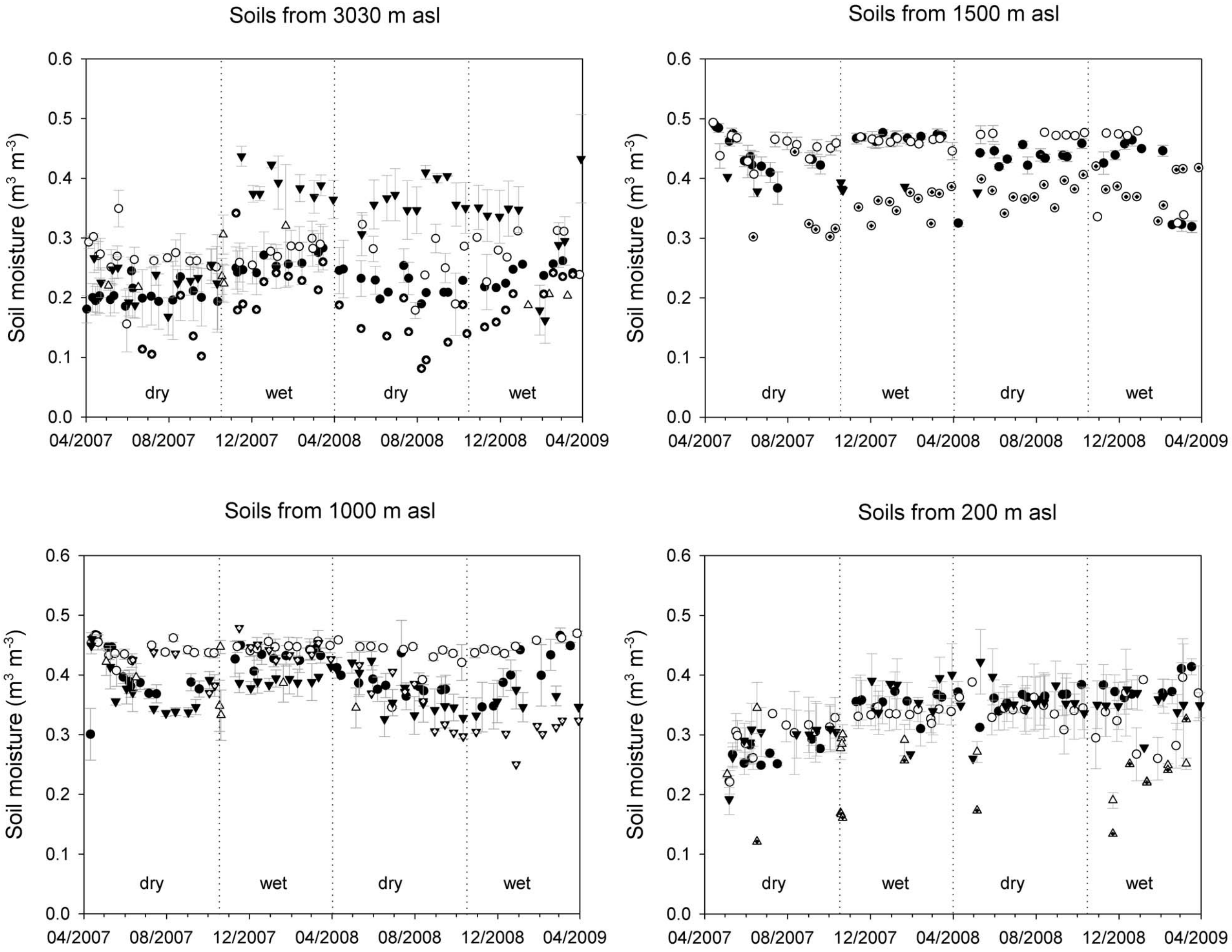

Figure 2. Soil moisture contents in soil cores as installed at 3030 m asl (solid circles), 1500 m asl (open circles), 1000 m asl (solid inverted triangles) and 200 m asl (open triangles), and in 10 cm depth in native soils (symbols with a cross) together with standard errors throughout the dry and wet seasons from April 2007 to March 2009.

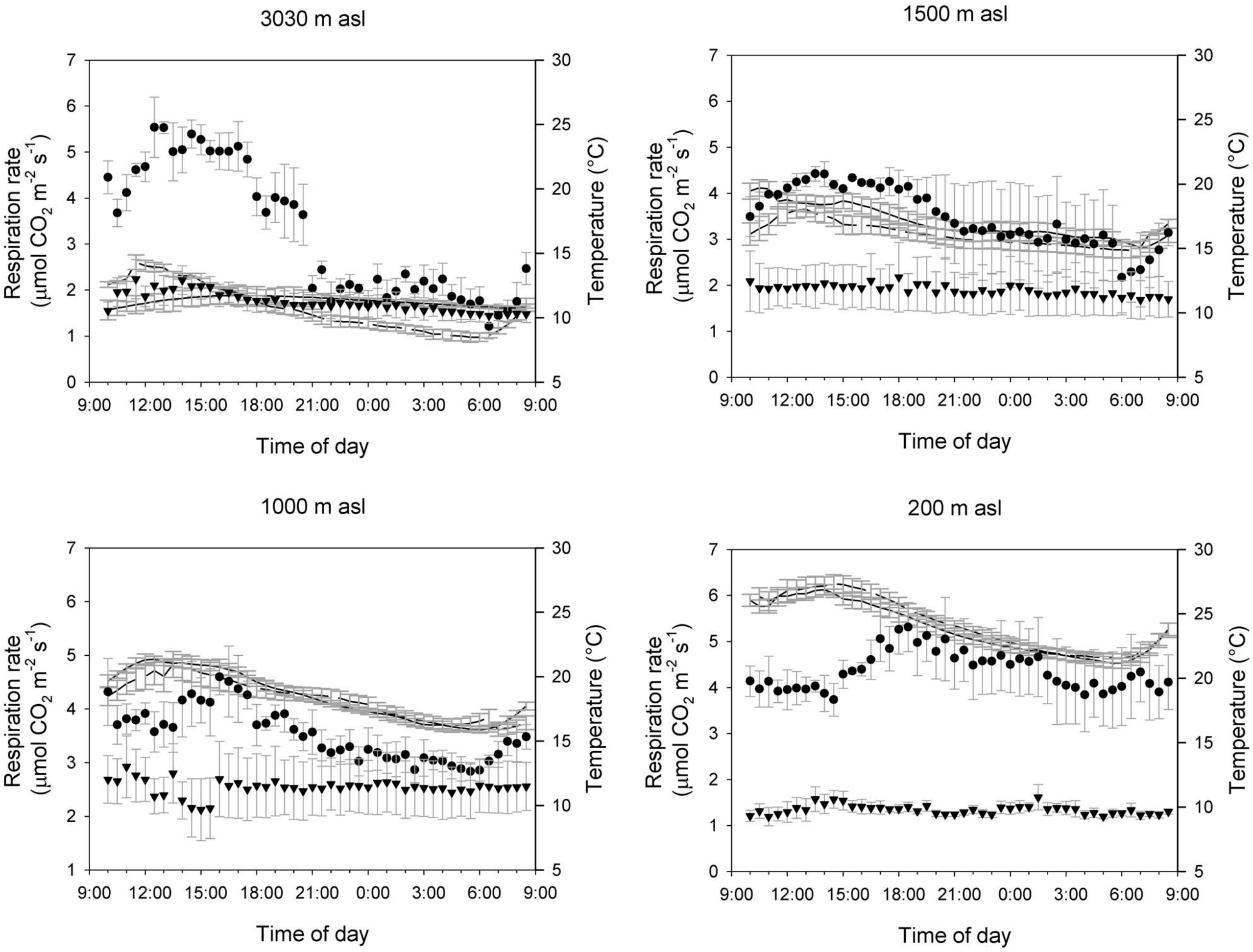

Figure 3. Diurnal variation in total (solid circles) and heterotrophic (solid inverted triangles) respiration as measured for 24 h periods throughout the seasons along the transect. Measurements were taken from soil collars (n = 3) and control soil cores (n = 3). Solid lines are air temperatures at the soil surface, and dashed lines are soil temperatures in 10 cm depth.

difference. The average R_{sal} at 1000 m asl was significantly lower than at the other sites (ANOVA, $p < 0.01$) (Table 3). As measured during daytime, R_{sal} contributed 63.9% to R_s at 3030 m asl, 57.7% at 1500 m asl, 43.0% at 1000 m asl and 75.1% at 200 m asl.

3.2. Soil Moisture

[18] Figure 2 shows the WC at 10 cm depth in the native soils as well as the measured WC in the soil cores over the 2 years. The soil core values represent the averaged WC of the three control cores per elevation. Mean annual WCs in the native soils for 2008 were 17.4 (±5.0) % at 3030 m asl, 37.5 (±2.2) % at 1500 m asl, 36.7 (±6.1) % at 1000 m asl and 20.7 (±5.3) % at 200 m asl, whereas the midelevation soils were significantly wetter than at the other two sites (ANOVA, $p < 0.05$). At 1500 m asl, the control cores were wetter than the native soil (ANOVA, $p < 0.05$), but this was not the case for the other three altitudes. Translocating the soil cores resulted for most cores in significant changes in WCs, but these were rather small (Figure 2).

3.3. Diurnal Variations in Soil Respiration

[19] High-frequency (30 min interval) respiration measurements during full 24 h periods showed clear differences in diurnal variations for R_s and R_{sh} (Figure 3). To compare daytime and nighttime respiration rates, we separated the diurnal measurement sets into two stable phases: daytime (1130–1730 LST) and nighttime effluxes (2330–0530 LST) [*Zimmermann et al.*, 2009a].

[20] R_s rates at 3030 m asl peaked during the daytime, dropped by about 61% in the early evening (Table 4), and were strongly correlated with T_a ($R = 0.91$, $p < 0.01$). R_{sh} was also strongly correlated with T_a during the 24 h diurnal cycle ($R = 0.85$, $p < 0.01$), but showed much smaller diurnal variation and dropped only by 20% from daytime to nighttime (rank sum test, $p < 0.01$). Daytime rates of R_s were significantly higher than diurnal means (rank sum test, $p <$

Table 4. Average Respiration Rates (With Standard Errors) for 24 h Periods and Separated Into Two Stabile Phases for Day (1130–1730 LST) and Night (2330–0530 LST) for Total (R_s) and Heterotrophic (R_{sh}) Soil Respiration[a]

	Time Period	3030 m asl	1500 m asl	1000 m asl	200 m asl
R_s (μmol CO$_2$ m^{-2} s^{-1})	24 h	3.21 (1.21) a	3.46 (0.09) a	3.56 (0.09) a	4.35 (0.06) a
	day	5.08 (0.09) b	4.22 (0.04) b	4.09 (0.01) b	4.23 (0.12) a
	night	1.99 (0.06) a	3.04 (0.03) c	3.03 (0.03) c	4.25 (0.09) a
R_{sh} (μmol CO$_2$ m^{-2} s^{-1})	24 h	1.74 (0.03) a	1.89 (0.02) a	2.54 (0.02) a	1.33 (0.01) a
	day	2.01 (0.04) b	1.98 (0.01) b	2.47 (0.07) a	1.41 (0.03) a
	night	1.60 (0.02) a	1.85 (0.02) a	2.54 (0.02) a	1.36 (0.03) a

[a]Small letters indicate significant differences among 24 h, day and nighttime measurements as tested pairwise with Mann-Whitney rank sum tests (p = 0.05).

0.01) and overestimated the mean diurnal R_s by about 58%. At 1500 m asl, daytime R_s was 39% higher than nighttime R_s and 22% higher than the daily mean R_s (rank sum test, $p < 0.01$), which was correlated with T_a ($R = 0.79$, $p < 0.01$). R_{sh} effluxes measured during daytime overestimated the average diurnal R_{sh} rates by only 5% (rank sum test, $p = 0.01$). Diurnal variation in R_s was much smaller at 1000 m asl, but daytime measurements still overestimated daily averages by about 15% (rank sum test, $p = 0.01$). Over 24 h, CO$_2$ effluxes followed T_a closely ($R = 0.85$, $p < 0.01$), but this was not the case for R_{sh} ($R = -0.12$, $p = 0.41$). R_{sh} rates at 1000 m asl were not significantly different during day and nighttime (rank sum test, p = 0.68). At 200 m asl, diurnal variation in R_s and R_{sh} were not significantly different during day and nighttime (Table 4). Here, R_s showed the poorest correlation with T_a of all four elevations ($R = 0.53$, $p < 0.01$) and was not correlated with T_s ($R = -0.01$, $p = 0.99$), whereas R_{sh} was correlated with T_s ($R = 0.34$, $p = 0.04$).

[21] Correcting the mean annual R_s rates of the four sites using the few measured patterns in diurnal variation and error propagation resulted in total annual respired C amounts of 1064 (±59) g C m^{-2} yr^{-1} at 3030 m asl, 1344 (±384) g C m^{-2} yr^{-1} at 1500 m asl, 1291 (±74) g C m^{-2} yr^{-1} at 1000 m asl and 1639 (±194) g C m^{-2} yr^{-1} at 200 m asl, which were correlated with altitude ($R = 0.92$, $p = 0.08$).

3.4. Temperature Dependency of Total Soil Respiration

[22] For each elevation, the relation between R_s and T_s was calculated by fitting equation (1) to R_s measurements taken in 2008. The best fit equations were $R_s = 0.527 \times 10^{-3} \times e^{-553.6/(TS-71.96)}$ for 3030 m asl, $R_s = 0.196 \times 10^{-5} \times e^{-2925.8/(TS-218.25)}$ for 1500 m asl, $R_s = 0.0135 \times e^{-301.9/(TS-72.87)}$ for 1000 m asl and $R_s = 0.244 \times 10^{-7} \times e^{-1397.4/(TS-96.84)}$ for 200 m asl, and explained 32% to 52% of the variance in R_s (Figure 4). The temperature sensitivity of R_s (Q_{10}) varied between 2.07 and 6.92, with larger Q_{10} values at the lowest and highest elevations (4.33 at 3030 m asl and 6.92 at 200 m asl) than at the midelevation sites, which gave Q_{10} values of 2.07 at 1500 m asl and 2.94 at 1000 m asl.

3.5. Temperature Dependency of Heterotrophic Soil Respiration

[23] Figure 5 shows the relative C losses of the soil cores after 2 years and the fitted exponential regression functions for the soil cores installed at 3030 and 1000 m asl. Comparing the different soil cores installed at 3030 m asl, respiration-induced losses were between 4% and 5% of the total SOC in the cores. In contrast, the relative amounts of respired C from the soil cores installed at the warmest site at 200 m asl revealed larger differences, ranging from 15% C lost from the soil cores originating from 3030 m asl to 28% C lost from the soil cores originating from 1000 m asl. Notably, the soil cores originating from 200 m asl respired more C at 1000 m asl than at 200 m asl.

[24] Comparing the time periods needed to respire 0.1% portions of SOC at 3030 and 1000 m asl reveals the change in temperature sensitivity (Q_{10-q}) with progressing SOC depletion (Figure 6). Standard error areas were calculated based on error propagation of standard errors of measured R_{sh} rates. The first 0.2% of respired C was not considered, as disturbance effects and additional dead root material at the beginning of the experiment might have led

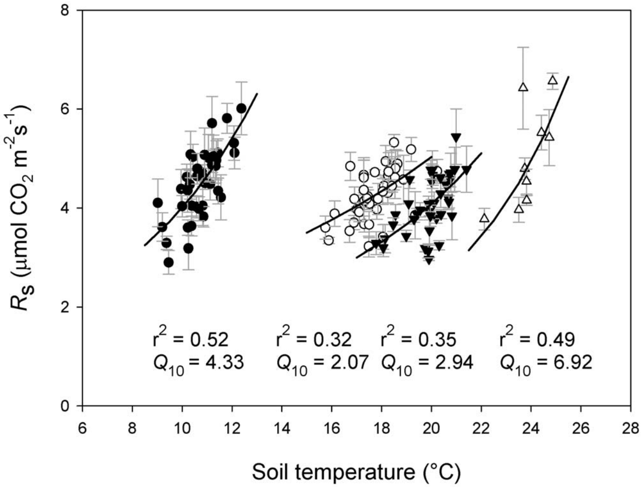

Figure 4. Temperature dependence of total soil respiration (with standard errors) at 3030 m asl (solid circles), 1500 m asl (open circles), 1000 m asl (solid inverted triangles), and 200 m asl (open triangles) for the year 2008 together with fitted *Lloyd and Taylor* [1994] functions and Q_{10} values as calculated for site specific mean annual temperatures (T_s) ±5°C.

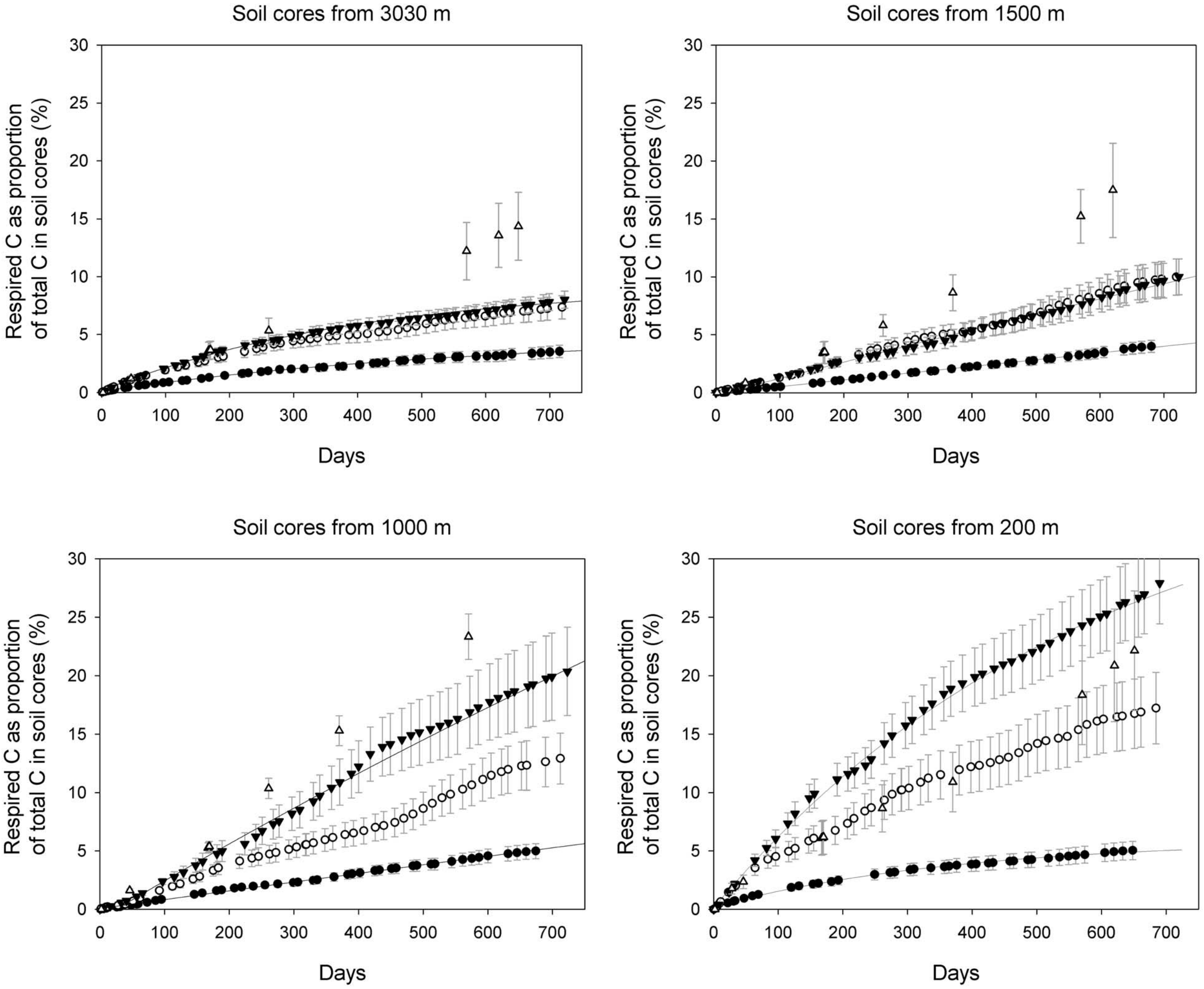

Figure 5. Percentages of heterotrophic-respired C per total C in soil cores over translocation time. Symbols indicate measured accumulated C fractions for each measurement occasion (solid circles for cores installed at 3030 m asl, open circles for cores installed at 1500 m asl, solid inverted triangles for cores installed at 1000 m asl and open triangles for cores installed at 200 m asl), and lines are the best fit regressions for cores being installed at the sites at 3030 or 1000 m asl, which have a difference in mean annual soil temperatures of ~10°C.

to unrepresentative CO_2 efflux rates [*Zimmermann et al.*, 2009b]. Soil cores originating from 3030 m asl showed decreasing Q_{10-q} values for the first 1.3% of respired SOC, and then increased up to 4.3 at 4% lost SOC. Q_{10-q} values as calculated for the soils from 1500 m asl rapidly increased to 2.0 at 0.9% of respired SOC and slightly increased afterward to 2.4 at 4% SOC loss. The Q_{10-q} values for the soil cores from 1000 m asl rapidly increased to 2.8 for first the 1.8% of respired SOC, and then more slowly up to 3.5 at 4% lost SOC. As calculated with this method, the soils from 200 m asl had the highest Q_{10-q} values which increased to 3.7 for the first 0.7% of respired C and continued to rise up to 6.7 at 4% lost SOC. Overall, Q_{10-q} values for all the soils tended to increase as the proportion of respired SOC increased over time, up to a maximum loss of 4%, as measured during the 2 years of field incubation.

4. Discussion

4.1. Temporal Patterns of Respiration Rates Varied Along the Transect

[25] The main environmental controls on R_s are temperature, moisture and substrate availability [*Davidson et al.*, 1998; *Kirschbaum*, 2004; *Tuomi et al.*, 2008]. As T_s varied significantly throughout the year at all four sites, one would expect a similar seasonal response of R_s at each site. But a seasonal trend in R_s could only be observed at 3030 and 1500 m asl. Various studies in tropical forests have demonstrated dry season declines in R_s [*Kiese and*

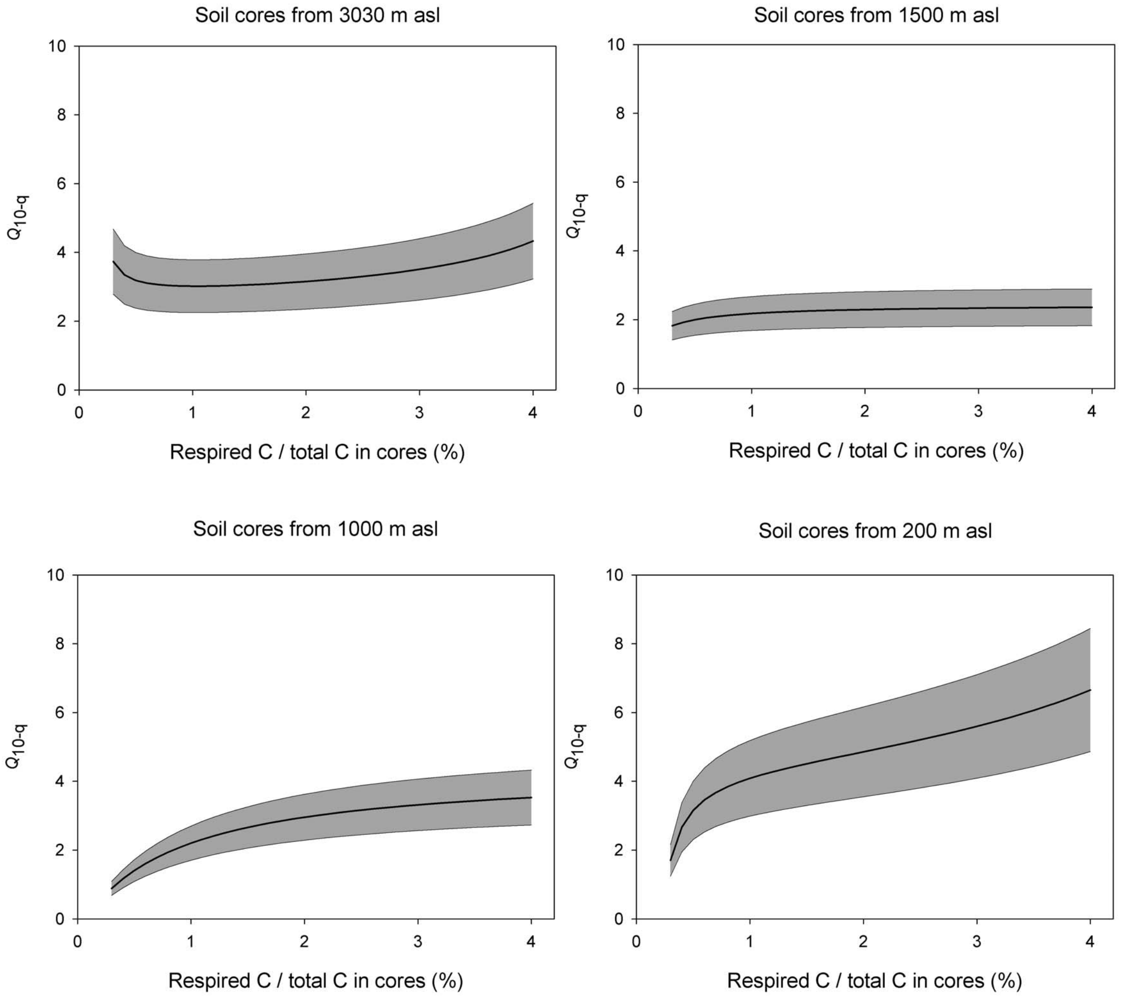

Figure 6. Evolution of Q_{10-q} values over the course of the translocation period (solid lines) with standard error areas. Values were calculated based on accumulated proportions of respired C for soil cores being installed at 3030 and 1000 m asl with a mean annual soil temperature difference of ~10°C, based on the best fit regression functions of Figure 5. The quotient between the time periods it took to respire each 0.1% fraction of soil C at 1000 and 3030 m asl is the Q_{10-q} value for this particular 0.1% C fraction.

Butterbach-Bahl, 2002; *Yi et al.*, 2007; *Sotta et al.*, 2007], but distinguishing between temperature and moisture effects is challenging in tropical forests like at our study sites, because both low temperatures and reduced precipitation occur in the same season, both decreasing respiration rates [*Ohashi et al.*, 2007].

[26] In tropical ecosystems, diurnal variation in temperature is typically larger than annual variation [*Gerold*, 2008] and therefore, diurnal variation in R_s can be larger than variation throughout the year. As differences in R_s between the day and the night were much larger at higher elevations and diurnal differences in R_{sh} were much smaller than in R_s, the change in the diurnal range in R_s along the transect is likely to be root- and litter-derived. Because of the shown correlations between respiration and temperature, R_{sal} seem to have different responses to diurnal T_a changes at the different elevations. This outcome is consistent with other studies. *Gonzalez and Seastedt* [2001] highlighted the importance of soil fauna on the decomposition of plant residues in tropical ecosystems, and *Zhang et al.* [2008] highlighted the influence of climatic conditions on litter decomposition rates, both of which change with altitude. Furthermore, it is likely that root biomass increases significantly with altitude, as found for a tropical montane forest gradient in Ecuador [*Leuschner et al.*, 2007; *Gräfe et al.*, 2008].

4.2. Total Soil Respiration: Same Rates, but Different Temperature Sensitivities

[27] The mean difference in T_s along the transect was 13°C, but daytime R_s rates were not significantly different among the four spots. Average R_s rates of 4.05–4.45 μmol CO_2 $m^{-2}s^{-1}$ correspond to flux rates reported elsewhere for tropical forests: for example, daytime R_s in different lowland rain forests in Brazil measured with similar methods to those used here ranged from 3.8 to 6.4 μmol CO_2 $m^{-2}s^{-1}$, but mean

annual T_s in these study sites were between 23°C and 26°C [*Sotta et al.*, 2007]. The uniformity in R_s along the transect is even more striking considering the different soil C stocks, which were correlated highly significantly with T_s ($R = -0.99$, $p < 0.01$), and experienced different average annual WC (ranging from 17.4% to 37.5%), different dominant vegetation characteristics and different R_{sal} contributions to R_s.

[28] However, if we correct measured daytime R_s for the diurnal variation at each site, the annual total of respired C decreased linearly with altitude from 1639 g C yr^{-1} at 200 m asl to 1064 g C m^{-2} yr^{-1} at 3030 m asl. As temperature increased also linearly with altitude, but rainfall showed no trend along the transect, temperature seems to be the more important driver for R_s rates than moisture along this altitudinal gradient. The annual respiration values are similar to the measured 1221 g C m^{-2} yr^{-1} respired in a cloud forest in Colombia [*Cavelier and Penuela*, 1990], even though the values given here were quantified for single spots and might not be representative for larger areas. *Adachi et al.* [2006] reviewed respiration rates of tropical lowland forest and reported respired C totals of 516 g to 2265 g C m^{-2} yr^{-1}, indicating that variation in the respired C totals from different tropical lowland forests can be much larger than along the much greater climate and vegetation gradient of our transect, depending on soil texture, nutrient availability and rainfall rates.

[29] Although R_s was very similar across our study sites, the sensitivity of R_s to temperature was more variable. The highest Q_{10} values of 6.92 and 4.33 were calculated for the sites at 200 and 3030 m asl, followed by lower Q_{10} values of 2.07 and 2.94 at 1500 and 1000 m asl, respectively. These temperature sensitivities did not follow a decline at higher temperatures as reported by *Lloyd and Taylor* [1994] or *Zheng et al.* [2009] and are in the upper range of globally reviewed Q_{10} values by *Lenton and Huntingford* [2003].

[30] The correlations between R_s and WC were hardly significant, but the two sites with the significantly lower average WC gave the higher temperature sensitivities. We hypothesize that the low WC at 3030 and 200 m asl during the cooler season could have limited R_s, which led to steeper increases in R_s under warmer and wetter conditions, resulting in higher Q_{10} values. However, the application of combined temperature and moisture model functions to fit R_s rates as given by *Martin and Bolstad* [2005] or *Zimmermann et al.* [2009b] did not result in satisfying correlations (data not shown).

4.3. Component Contributions to Total CO_2 Effluxes Along the Transect

[31] Various approaches like trenching, girdling, clipping etc. can be applied to quantify root-free R_s [*Hanson et al.*, 2000; *Kuzyakov*, 2006; *Subke et al.*, 2006]. The control soil cores taken and reinstalled at the same sites along the transect correspond to the trenching method. By sampling the soil cores in plastic tubes, all roots were cut and ingrowth at the bottom of the tubes was obstructed by the mesh sealing the base. Cutting the roots might have enhanced R_{sh} temporarily through the decomposition of excised and dead roots [*Högberg et al.*, 2001; *Kuzyakov*, 2006]. Therefore, we did not consider R_{sh} data from the first month in any calculations involving R_{sh}, as R_{sh} rates were higher in this period then afterward (data not shown). No fresh SOM entered the cores over the experiment period, and this will lead to a decline in R_{sh} as result of C depletion [*Reichstein et al.*, 2000; *Conant et al.*, 2008a]. But a decrease over time in R_{sh} was only observed in the control cores at 3030 m asl and consequently we used these corrected R_{sh} data for the calculations of mean annual values. The reason for this decrease is probably due to the high amount of labile C in the thicker O horizon at 3030 m asl, which was cut and disturbed considerably at the study start.

[32] The contribution of R_{sh} to R_s was not correlated with elevation and ranged from 25% to 60% of R_s. This is in the reported range of 27% to 76% for deciduous tropical forest [*Subke et al.*, 2006]. These authors found that the contribution of R_{sh} to R_s declined with increasing R_s, but this was not the case for our altitudinal gradient, as daytime R_s did not alter significantly along the transect. The large difference in the contribution from R_{sh} between the two lowland forests (1000 and 220 m asl) is a striking result because they have the most similar vegetation among the four sites. However, the two sites experienced very different WC values during the measurement period. Although rainfall differences will have contributed to the observed differences in WC, it seems most likely that the principal cause of differences in WC was soil texture: the site at 1000 m asl had a much finer soil texture than the site at 220 m asl, which was situated on an ancient sandy river terrace. Differences in the contribution to R_s from different components of soil respiration have also been reported by *Silver et al.* [2005] for tropical forests with similar vegetation, but grown on soils with different textures.

[33] The contribution of R_{sal} to R_s at the sampling spots was calculated by difference. *Zimmermann et al.* [2009a] previously showed for the site at 3030 m asl that litter alone contributed 55% to total R_s during the daytime, which means that root respiration at 3030 m asl comprised about 9% of R_s. We do not have separated data for root and litter contributions for the other sites along the transect. But most published measurements of root contributions to R_s in tropical lowland forest are in the range of 35% to 75% [*Silver et al.*, 2005; *Subke et al.*, 2006; *Metcalfe et al.*, 2007], substantially larger than the value of 9% calculated here for the 3030 m asl site. The root contribution to R_s may well increase downward the gradient, even though root biomass was shown to increase with elevation in a similar tropical montane forest in Ecuador [*Leuschner et al.*, 2007]. *Metcalfe et al.* [2007] reported furthermore a litter contribution of 8% to R_s for a lowland tropical rain forest in Brazil with similar climatic conditions, soil C stock and texture as found at the 200 m asl site. *Vasconcelos et al.* [2004] quantified the litter contribution to be 28% of R_s in a tropical forest in northeastern Brazil, and *Sayer et al.* [2007] 20% in a tropical rain forest in Panama, suggesting an increase in litter contribution to R_s with increasing altitude. However, this trend might well be caused by a combination of C allocation and litter quality together with climate, rather than being a simple consequence of the prevailing soil temperature or moisture regime [*Zhang et al.*, 2008].

[34] Overall, our data show that the contributions of SOM, litter and roots to R_s vary as much along the 3000 m transect reported here, as they do among sites classified as part of the geographically much larger biome of lowland tropical rain forests. We suggest that these differences are more likely to be driven by site specific parameters, including soil texture and the dominant vegetation type, in combination with climate, than simply by temperature or soil moisture alone.

4.4. Heterotrophic Respiration: Labile SOM Has Lower Temperature Sensitivity

[35] The soil translocation experiment enabled analysis of the temperature sensitivity of R_{sh} over a wider range of temperatures than is experienced under the natural climate of the individual sites. The approach by *Conant et al.* [2008a, 2008b] takes into account the potential decline in R_{sh} rates with time by comparing the elapsed times during the decomposition of the same fraction of C at two different temperatures. We took advantage of the fact that the elevations at 3030 and 1000 m asl have a difference in mean annual T_s of about 10°C and compared the cumulative respired C of the soil cores. The Q_{10-q} values of the soil cores from 200 m asl were the largest, followed in respective declining order by the Q_{10-q} values for soils from 3030, 1000, and 1500 m asl.

[36] The trend in Q_{10-q} values was consistent with Q_{10} values calculated for total R_s (see Figure 4). The results also indicate that the Q_{10-q} values increased quickly during the decomposition of the most labile C components, and increased more slowly afterward. Soil cores from 3030 m asl showed a different Q_{10-q} evolution for the first 0.5% of respired C, which might have been caused by a longer disturbance effect immediately following the translocation event, as this soil had a much thicker O horizon and probably needed a longer time to stabilize than the other soils. Furthermore, the decomposition of dead roots could have taken longer than 1 month (Figure S1).[1] Q_{10-q} values were calculated only for the first 4% of decomposed C, because this was the maximum amount respired by the different soils installed at 3030 m asl. These findings support the general kinetic theory [*Fierer et al.*, 2006; *Davidson and Janssens*, 2006] that temperature sensitivity of SOM decomposition increases with more stabile SOM of higher quality, and are consistent with recent studies of northern temperate ecosystems [*Hartley and Ineson*, 2008; *Conant et al.*, 2008a].

4.5. Influence of Soil Moisture on Respiration Rates

[37] Moisture can limit soil respiration at very high and low WC, because water saturation limits oxygen diffusion, and low WC restricts microbial metabolism through desiccation and reduced substrate access or diffusion [*Davidson et al.*, 1998; *Liu et al.*, 2002; *Xu et al.*, 2004]. Several models of soil respiration take into account as well soil moisture as temperature to calculate respiration rates [*Luo and Zhou*, 2006]. However, we were not able to fit such a model function satisfyingly to our data. As the soil cores from 1500 and 1000 m asl had relatively high WCs (45–50%), CO_2 efflux could have been inhibited. But R_{sh} and R_s rates were not higher under drier conditions during the year and T_s might have been the more important driving factor at these two sites. The low WCs in the undisturbed soil at the 200 m asl site were similar to the WC values observed for the control soil cores which had been taken and reinstalled at this site. When soil cores from 200 m asl were translocated to 1000 m asl, the soil moisture increased by 7%, and R_{sh} at the cooler site was higher than at 200 m asl (Figure 5). These were the only soil cores that lost more C at a cooler site than at the site of their origin. Therefore, low WC was probably limiting R_s and R_{sh} at 200 m asl. Supporting this conclusion is the fact that the lowest R_s value of 3.8 μmol CO_2 $m^{-2}s^{-1}$ at 200 m asl was measured at 22.1°C and a WC of 12%, whereas the highest R_s value of 6.5 μmol CO_2 $m^{-2}s^{-1}$ at the same site was quantified at a WC content of 25% but at a just 2.8°C higher T_s. Whether low WC also suppressed R_{sh} at 3030 m asl, which had similarly low native WC as the site at 200 m asl, is not distinguishable from temperature effects, as the cores were not translocated to a cooler site.

5. Conclusions

[38] An altitudinal gradient offers the unique possibility to study the effect of climate on soil respiration and its components under otherwise similar conditions in situ. Our data showed that although the large differences in soil and air temperatures, seasonality and soil C stocks along the transect, daytime R_s rates did not differ significantly among the four sampling sites. A combination of climate, soil texture, and C allocation patterns probably led to different contributions of litter, roots, and SOM to total R_s, with consequent effects on the different diurnal ranges in R_s observed among the different sites. Daytime R_s measurements can overestimate the mean diurnal value for R_s, and this effect is magnified considerably at higher elevations; after correcting for the diurnal patterns in R_s at each site, mean annual totals for respired C increased with increasing temperature and decreasing altitude.

[39] Q_{10} values of R_s and Q_{10-q}values of R_{sh} revealed the same trends with elevation, with lower temperature sensitivities for wetter soils. Therefore, we do not assume the R_{sal} component of R_s to have a different pattern, although root and litter respiration separately might still have opposite temperature sensitivities along the transect. A future attempt should focus on the separation of root and litter respiration and its contribution to R_s on an annual and diurnal basis.

[40] Temperature sensitivities of R_{sh} were lower for the most labile C compounds, and increased with ongoing respiration. At the sites with the drier soils at 3030 and 200 m asl, temperature sensitivities were higher as well for R_s as for R_{sh}, but temperature and moisture effects could not be distinguished. Furthermore, R_{sh} contributions were larger for wetter soils which let us assume that microbial respiration might stronger depend on soil moisture than the combined root and litter respiration does.

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[1] Auxiliary materials are available with the HTML. doi:10.1029/2010GB003787.

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