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

Citation for published version:

Digital Object Identifier (DOI):
10.1029/2010GB003787

Link:
Link to publication record in Edinburgh Research Explorer

Document Version:
Publisher's PDF, also known as Version of record

Published In:
Global Biogeochemical Cycles

Publisher Rights Statement:
Published in Global Biogeochemical Cycles. Copyright (2010) American Geophysical Union.

General rights
Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy
The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact openaccess@ed.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.
Temporal variation and climate dependence of soil respiration and its components along a 3000 m altitudinal tropical forest gradient

Michael Zimmermann,1,2 Patrick Meir,2 Michael I. Bird,1 Yadvinder Malhi,3 and Adan J. Q. Ccahuana4

Received 19 January 2010; revised 7 July 2010; accepted 13 July 2010; published 5 November 2010.

[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 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 temperature dependence of $R_{sh}$ to $R_s$ was not correlated with elevation and ranged from 25% to 60%. The temperature sensitivity of $R_s$ was lower at the mid-elevation 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 3.33 and 6.92 at 3030 and 200 m asl, respectively).


1. Introduction

[2] The rate and underlying mechanism of soil respiration is the subject of a large number of ongoing studies, because soil CO₂ 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 CO₂ 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 CO₂ 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 CO₂ efflux sources in situ. Methods can be mainly distinguished into the physical separation of $R_s$ sources and the tracking of CO₂ 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.
[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 m² 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” \( R_{sh} \) 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 soil cores 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 cm². Measurements were made twice a month from
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 (Tₐ) outside the tubes, WC in the tubes and air temperature (Tₑ) within the measurement chamber. Before the Rₛₑ 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 Rₛₑ as well as Rₛ₀ of the control cores was measured once at 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 Rₛₑ, a Lloyd and Taylor [1994] function

$$Rₛₑ = a \times e^{\frac{Q₁₀}{Tₛ−T₀}}$$  (1)

as given by Davidson et al. [2006] was fitted to the measured respiration rates, where a, E₀, and T₀ are fitted parameters, and Tₛ 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 Tₛ than the standard Arrhenius function [Fang and Moncrieff, 2001]. Although this function might not be valid if T₀ equals Tₛₑ this was of no concern at our study sites.

[13] Temperature sensitivities as expressed by Q₁₀ values were then calculated comparing respiration rates at 5°C above and below the site specific mean annual Tₛₑ:

$$Q₁₀ = \frac{Rₚₑ⁰₅}{Rₚₑ⁻⁰₅}.$$  (2)

Q₁₀ values for Rₛₑ were calculated following the approach by Conant et al. [2008a], which takes into account the decline of Rₛₑ 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 (tₚₑ₃⁰₃₀) with the time required to decompose the same fraction of the SOC stock from the corresponding soil cores installed at 1000 m asl (tₚₑ₁₀₀₀), as these two sites have a difference in Tₛₑ of ~10°C:

$$Q₁₀ = tₚₑ₃⁰₃₀/tₚₑ₁₀₀₀$$  (3)

SOC losses with time were calculated by applying the averaged Rₛₑ 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 Rₛₑ 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, Rₛₑ at 3030 and 1500 m asl was higher during the wetter season from October to April (t test, p < 0.03), whereas Rₛₑ at 1000 and 200 m asl did not change.
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 \( R_s \) \((\pm SE)\) for the four sites were between 4.45 \((\pm 0.11)\) and 4.05 \((\pm 0.09)\) \(\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}\) \(\text{ (Table 3)}\), but did not vary significantly \((\text{ANOVA, } p = 0.16)\) 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.

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

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 \( R_s \). 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).

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

<table>
<thead>
<tr>
<th>Altitude (m asl)</th>
<th>( R_s ) (( \mu \text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1} ))</th>
<th>( R_{sh} ) (( \mu \text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1} ))</th>
<th>( R_{sal} ) (( \mu \text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1} ))</th>
<th>( T_s ) (°C)</th>
<th>( T_a ) (°C)</th>
<th>WC (m³ m⁻³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>3030</td>
<td>4.45 (0.70) a</td>
<td>1.61 (0.59) a</td>
<td>2.83 (0.85) a</td>
<td>10.58 a</td>
<td>12.61 a</td>
<td>0.174 a</td>
</tr>
<tr>
<td>1500</td>
<td>4.33 (0.56) a</td>
<td>1.83 (0.74) ab</td>
<td>2.50 (0.85) a</td>
<td>17.81 b</td>
<td>20.06 b</td>
<td>0.375 b</td>
</tr>
<tr>
<td>1000</td>
<td>4.05 (0.60) a</td>
<td>2.66 (0.84) b</td>
<td>1.64 (0.75) b</td>
<td>19.85 c</td>
<td>21.73 c</td>
<td>0.367 b</td>
</tr>
<tr>
<td>200</td>
<td>4.45 (0.64) a</td>
<td>1.11 (0.23) a</td>
<td>3.34 (0.72) a</td>
<td>23.57 d</td>
<td>25.24 d</td>
<td>0.175 a</td>
</tr>
</tbody>
</table>

\( R_{sh} \) 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, \( p = 0.05 \)).

\[ \text{Soils from 3030 m asl} \]

\[ \text{Soils from 1500 m asl} \]

\[ \text{Soils from 1000 m asl} \]

\[ \text{Soils from 200 m asl} \]

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

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

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.

[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 <
3.4. Temperature Dependency of Total Soil Respiration

\[ R = \beta \cdot \exp(\alpha \cdot T) \]

The fitted exponential regression functions at 1000 m asl and 2.94 at 1000 m asl. 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.

3.5. Temperature Dependency of Heterotrophic Soil Respiration

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

<table>
<thead>
<tr>
<th>Time Period</th>
<th>3030 m asl</th>
<th>1500 m asl</th>
<th>1000 m asl</th>
<th>200 m asl</th>
</tr>
</thead>
<tbody>
<tr>
<td>( R_s ) (( \mu \text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1} ))</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>day</td>
<td>3.21 (1.21)</td>
<td>a</td>
<td>3.46 (0.09)</td>
<td>a</td>
</tr>
<tr>
<td>night</td>
<td>5.08 (0.09)</td>
<td>b</td>
<td>4.22 (0.04)</td>
<td>b</td>
</tr>
<tr>
<td>( R_{sh} ) (( \mu \text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1} ))</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>day</td>
<td>1.99 (0.06)</td>
<td>a</td>
<td>3.04 (0.03)</td>
<td>c</td>
</tr>
<tr>
<td>night</td>
<td>2.01 (0.04)</td>
<td>b</td>
<td>1.98 (0.01)</td>
<td>b</td>
</tr>
</tbody>
</table>

\[ Q_{10} = \frac{Q_{101}}{Q_{102}} \]

**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 (\( T_a \)) ±5°C.
to unrepresentative CO₂ 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 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.
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 \( R_{aw} \) 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, \( R_{aw} \) 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 \( T_a \) 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 \( \mu \)mol 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 \( \mu \)mol CO\(_2\) m\(^{-2}\) s\(^{-1}\), but mean
annual $T_v$ in these study sites were between 23°C and 26°C [Sotta et al., 2007]. The uniformity in $R_e$ along the transect is even more striking considering the different soil C stocks, which were correlated highly significantly with $T_v$ ($R = -0.99, p < 0.01$), and experienced different average annual WC (ranging from 17.4% to 37.5%), different dominant vegetation characteristics and different $R_{sal}$ contributions to $R_e$.

[28] However, if we correct measured daytime $R_e$ 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 $R_e$ 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 $R_e$ was very similar across our study sites, the sensitivity of $R_e$ 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 Lenten and Huntingford [2003].

[30] The correlations between $R_e$ 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 $R_e$, which led to steeper increases in $R_e$ under warmer and wetter conditions, resulting in higher $Q_{10}$ values. However, the application of combined temperature and moisture model functions to fit $R_e$ 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 $R_e$ [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 $R_e$ was not correlated with elevation and ranged from 25% to 60% of $R_e$. 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 $R_e$ declined with increasing $R_e$, but this was not the case for our altitudinal gradient, as daytime $R_e$ 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 $R_e$ 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 $R_e$ 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 $R_e$ during the daytime, which means that root respiration at 3030 m asl comprised about 9% of $R_e$. 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 $R_e$ 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 $R_e$ 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 $R_e$ 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 $R_e$ 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 $R_e$ 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].
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

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 \( Q_{10-\vartheta} \) values of the soil cores from 200 m asl were the largest, followed in respective declining order by the \( Q_{10-\vartheta} \) values for soils from 3030, 1000, and 1500 m asl.

The trend in \( Q_{10-\vartheta} \) values was consistent with \( Q_{10} \) values calculated for total \( R_s \) (see Figure 4). The results also indicate that the \( Q_{10-\vartheta} \) 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 \( Q_{10-\vartheta} \) 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).

### 5. Conclusions

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.

Auxiliary materials are available with the HTML. doi:10.1029/2010GB003787.
References


---

M. I. Bird and M. Zimmermann, School of Earth and Environmental Science, James Cook University, Townsville, Qld 4811, Australia. (michael.zimmermann@jcu.edu.au)
A. J. Q. Ccahuana, Department of Biology, Universidad San Antonio Abad, Av. de la Cultura, Nro. 733, Cusco, Peru.
Y. Malhi, Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, OX1 3QY, UK.
P. Meir, School of Geosciences, University of Edinburgh, Edinburgh, EH9 3XP, UK.