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Elevational change in woody tissue CO_2 efflux in a tropical mountain rain forest in southern Ecuador

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Summary Much uncertainty exists about the magnitude of woody tissue respiration and its environmental control in highly diverse tropical moist forests. In a tropical mountain rain forest in southern Ecuador, we measured the apparent diurnal gas exchange of stems and coarse roots (diameter 1–4 cm) of trees from representative families along an elevational transect with plots at 1050, 1890 and 3050 m a.s.l. Mean air temperatures were 20.8, 17.2 and 10.6 °C, respectively. Stem and root CO_2 efflux of 13 to 21 trees per stand from dominant families were investigated with an open gas exchange system while stand microclimate was continuously monitored. Substantial variation in respiratory activity among and within species was found at all sites. Mean daily CO_2 release rates from stems declined 6.6-fold from 1.38 µmol m^{-2} s^{-1} at 1050 m to 0.21 µmol m^{-2} s^{-1} at 3050 m. Mean daily CO_2 release from coarse roots decreased from 0.35 to 0.20 µmol m^{-2} s^{-1} with altitude, but the differences were not significant. There was, thus, a remarkable shift from a high ratio of stem to coarse root respiration rates at the lowest elevation to an apparent equivalence of stem and coarse root CO_2 efflux rates at the highest elevation. We conclude that stem respiration, but not root respiration, greatly decreases with elevation in this transect, coinciding with a substantial decrease in relative stem diameter increment and a large increase in fine and coarse root biomass production with elevation.

Keywords: altitudinal transect, coarse root respiration, infrared gas analysis, stem respiration, temperature dependence.

Introduction

Plant tissue respiratory activity is thought to consume 30–80% of daily assimilated carbon (Amthor 2000), constituting one of the main sources of CO_2 released to the atmosphere (Trumbore 2006). Although the carbon balance of forests is the focus of current global change research, the respiration of stems, branches and coarse roots remains one of the least studied processes (Sprugel and Benecke 1991). Knowledge of tropical forest respiration is particularly sparse, despite the acknowledged importance of tropical forests in the global carbon balance (Meir and Grace 2002, Chambers et al. 2004). For reliable modeling of the carbon sink strength of tropical forests in a changing climate, a detailed knowledge of plant respiration is needed, particularly its variability among forest types, and its dependence on the environment. The few in situ measurements of respiration of tropical forest trees indicate that woody tissue respiration accounted for 10–13% of gross photosynthesis (Ryan et al. 1994, Meir and Grace 2002). Earlier studies in tropical forests based on observations of CO_2 release from excised plant organs yielded values between 23 and 50% (Müller and Nielson 1965, Yoda 1967, Whitmore 1984).

To our knowledge, only one gas exchange study has been conducted in tropical high-elevation forests: Cavieres et al. (2000) measured leaf gas exchange of two tree species in the Venezuelan Andes. Studies quantifying woody tissue respiration along altitudinal transects in tropical mountain forests are lacking. Information from such studies would help to predict effects of global temperature change on plant respiration in tropical ecosystems. Woody tissue CO_2 release rates can vary enormously, not only among forest types (Lavigne et al. 1996, Ryan et al. 1997), but also among species within a stand and among individuals of the same species (Meir and Grace 2002). Information on the spatial variability of woody tissue respiration is indispensable when extrapolating gas flux data from tree to stand. This information is particularly important in tropical forests with their high species richness and large structural variability across environmental gradients (Meir and Grace 2002, Chambers et al. 2004).

The current study was undertaken to: (1) quantify species-specific differences in woody tissue respiration in tropical mountain forests; (2) compare the respiratory activity of stems and coarse roots; and (3) analyze changes in stem and root respiration along an altitudinal span of 2000 m in a tropical mountain rain forest in southern Ecuador.

Materials and methods

Study sites

The study was carried out in Podocarpus National Park (PNP) in the surroundings of Loja on the eastern slopes of the southern Ecuadorian Andes. We chose three forest stands along an

altitudinal gradient ranging from 1050 to 3050 m a.s.l. The maximum distance between stands was about 30 km. The low-elevation stand (1050 m, 04°06′54″ S, 78°58′02″ W) is located in the northeastern part of PNP (Bombuscaro section) in the Province of Zamora-Chinchipe. The mid-elevation stand (1890 m, 03°58′345″ S, 79°04′648″ W) is close to the Estacion Cientifica San Francisco (ECSF), 30 km from Loja on the road to Zamora, Province of Zamora-Chinchipe. The high-elevation stand (3050 m, 04°06′711″ S, 79°10′581″ W) is in the Cajanuma area in the northwestern part of PNP, Province of Loja. All stands were selected on gentle slopes (26–31°) facing northeast to northwest, covering an area of 20 × 20 m.

The climate of the area is mainly influenced by easterly winds that bring frequent rainfall throughout the year with peaks from May to July. During our study, conducted from October to December 2005, westerly winds strongly influenced the local weather causing a relatively dry and sunny period in the study area.

The soils in the area developed either from granodiorite (low-elevation stand) or metamorphic shale, quartzite and sandstone bedrock (mid- and high-elevation stands). Throughout the study region, the soils are relatively infertile (Schrumpf et al. 2001).

Forest structure and selection of tree individuals

The stands were selected to: (1) be representative of the vegetation type at each elevation; (2) have a closed canopy within a surrounding area of 100 × 100 m; and (3) be free of recent anthropogenic influence or landslide disturbance. The low-elevation stand (1050 m) represents the transitional zone between tropical lowland and lower montane rain forest. The mid-elevation stand (1890 m) is a typical montane rain forest, and the high-elevation stand (3050 m) is located close to the timberline and represents a typical elfin forest characterized by stunted trees with warped stem forms. Further details on forest structure are given in Table 1. All plots have been previously studied and described by Röderstein et al. (2005), Leuschner et al. (2007) and Moser et al. (2008).

In each stand, a minimum of 80 canopy trees were identified at the species level. As long as they reached the canopy, trees smaller than 5 cm DBH (diameter at breast height) were included in the samples. To measure CO_2 release rates of woody organs, 13 to 21 trees per stand were selected. We required that trees belong to abundant families in the particular stand and comprise a broad range of DBH classes in order to represent the floristic composition and size heterogeneity of the stand. Thus, each sample consisted of trees from 10–11 families. In the mid- and low-elevation stands, we included more trees (n = 20 and 21, respectively) to account for the wider diameter range than in the high-elevation stand (n = 13). Diameters of the selected trees ranged from 8.70 to 43.85 cm at 1050 m, from 3.02 to 26.47 cm at 1890 m and from 2.48 to 17.67 cm at 3050 m. We measured 4–8 coarse roots (1–4 cm diameter) at each site depending on accessibility.

Gas exchange measurements

Woody tissue CO_2 release rates were measured in situ between October and December 2005, which corresponds to the drier season of the year, although each month received at least 80 mm of rain. In each stand, the measurements were made over a 10-day period, during which continuous measurements were made of CO_2 efflux from woody organs (stems and coarse roots). Stem CO_2 release was monitored at breast height (1.3 m) using transparent Plexiglas chambers (95.1 cm^3 volume) tightly fitted onto the bark surface. When necessary, mosses and lichens were gently removed from the measured stem segment with a soft brush. Segments of coarse roots were enclosed in transparent Plexiglas chambers of 473.8 cm^3 volume sealed around the organ with Terostat VII (Teroson, Henkel AG, Düsseldorf, Germany). The cylindrical chamber design allows for measurement of organ sections ranging in diameter from 1 to 4 cm. Both types of chambers have a relatively small volume and are designed with inlet and outlet nozzles at opposite sides to ensure adequate mixing of the incoming air. Air-tightness of the measurement chambers was controlled by electronic air flow meters.

The diameters of the stems and roots were measured in the middle of the organ section enclosed by the chamber. The surface temperature of the measured organ section was recorded with thermocouples attached on the outside of the stem surface next to the chamber. We selected coarse roots (1–4 cm diameter) growing a few centimeters beneath the soil surface and uncovered the root section to be measured with a soft brush.

Gas exchange system

Net exchange of CO_2 across stem or root surfaces was measured with a mobile 6-chamber respiration system ANARESY 2 (Walz, Effeltrich, Germany) with an integrated infrared gas analyzer for CO_2 and H_2O (LI-7000, Li-Cor, Lincoln, NE). The open gas exchange system was operated in differential mode (Ryan et al. 1995) and allows for continuous diurnal measurements of the apparent CO_2 release rate in six Plexiglas

Table 1. Climate and stand structure characteristics of the study sites at elevations of 1050, 1890 and 3050 m (data from Moser et al. 2008, means with standard deviation in parenthesis). Mean air temperature and mean relative humidity were recorded inside the stands at a height of 2 m. Rainfall data are extrapolated from measurements in gaps at about 1050, 1950 and 3170 m by P. Emck (unpublished). Abbreviations: AGB, aboveground biomass; and BGB, belowground biomass.

Parameter	1050 m	1890 m	3050 m
Air temperature (°C)	20.8 (3.3)	16.8 (4.4)	10.6 (3.1)
Relative humidity (%)	87.3 (16.1)	87.4 (21.9)	91.0 (13.0)
Precipitation (mm $year^{-1}$)	2230	1950	4500
DBH (cm)	17.3 (1.3)	12.2 (0.8)	7.2 (0.4)
Stem height (m)	15.6 (0.7)	10.1 (0.4)	5.2 (0.3)
Basal area (m^2 ha^{-1})	33.6	36.9	42.2
Stem density (ha^{-1})	968	2333	8317
LAI	6.0 (0.4)	5.7 (0.5)	2.2 (0.2)
Wood density (g cm^{-3})	0.64 (0.15)	0.60 (0.16)	0.69 (0.15)
Stand leaf mass (Mg ha^{-1})	6.82 (0.44)	9.74 (0.83)	3.64 (0.29)
AGB (Mg ha^{-1})	285.1	173.0	112.2
BGB (Mg ha^{-1})	32.1	25.8	62.7

chambers (Horna and Zimmermann 2000). Buffered incoming air was continuously passed through all six chambers at a maximum flow rate of 1 l min^{-1}. Every 6 min, the system automatically switched from one chamber to the next, thus recording about two CO_2 release values per chamber per hour. The six chambers were moved to different trees after completing a 24-hour measurement cycle. Electrical power was supplied by a generator that charged car batteries connected in series (24 V DC). The generator was placed at a distance of over 100 m from the measuring system to avoid any influence of the fumes on measurements. For every 10-day measurement interval, the entire set up was moved to the next site. The weather conditions during the measuring period from October to December 2005 were sufficiently stable to allow for a comparison of the three stands.

Calculation of respiration rates

The LI-7000 infrared gas analyzer continuously determines both the absolute CO_2 concentration ($[CO_2]$) and the difference between ambient atmospheric $[CO_2]$ and the concentration inside the chamber corrected for atmospheric pressure. Air flow rate is expressed as a molar flow rate. The woody tissue CO_2 release rate was calculated as:

$$R = [CO_2]_{diff} \frac{F}{A_c} \quad (1)$$

where R is the respiration rate in μmol CO_2 m^{-2} s^{-1}, $[CO_2]_{diff}$ is the difference between ambient (reference gas) and chamber (sample gas) $[CO_2]$, F is the air flow rate (mol s^{-1}) that passes through the chamber, and A_c is the surface area (m^2) of the enclosed organ segment.

Depending on the diameter of the measured object, CO_2 release rates of woody biomass in tropical forests have been related either to surface area (Levy and Jarvis 1998, Chambers et al. 2004), tissue volume (Ryan et al. 1994), or a combination of both (Meir and Grace 2002). Recently, Cavaleri et al. (2006) found that the unit of expression of CO_2 release by tropical woody tissue is dependent on the position within the tree, with canopy rates related to surface area, but efflux rates in the bottom 2 m of the canopy related to both volume and surface area. Nevertheless, because the volume of living tissue in stems and woody roots may differ considerably among tropical trees of different systematic classifications and ages (Meir and Grace 2002, Chambers et al. 2004), we used the surface area of the measured wood sections as the basis for calculation.

Despite evidence that dissolved CO_2 is transported in substantial quantities in the xylem sap of certain tree species (Levy and Jarvis 1998, Levy et al. 1999, Horna and Zimmermann 2000, Teskey and McGuire 2002, McGuire and Teskey 2002, Gansert and Burgdorf 2005), we ignored this flux in the current measuring program and interpreted our stem and root efflux data as woody tissue respiration rates.

Thermal regimes differed greatly along the altitudinal gradient, with little overlap in temperature between the low- and high-elevation sites. Converting respiration rates to a common temperature (e.g., 15–20 °C) would yield extrapolated release rates beyond naturally given amplitudes and would result in comparison of efflux rates at the lowest night temperatures at 1050 m with rates at the upper daytime temperature limit at 3050 m. Therefore, we decided to underpin our comparisons of mean stand respiration rates with results of individual regression analyses rather than adjusting apparent efflux rates to a common temperature.

Stand microclimate

During the 10-day measurement intervals, air temperature and relative humidity at 2 m height inside the stands were monitored synchronously with a Rotronic sensor (Rotronic AG, Bassersdorf, Switzerland) connected to the data logger of the ANARESY system (CR 10, Campbell Scientific, Logan, UT). Annual means of air temperature (T_a) and relative humidity (RH) for each site were computed from daily climate data from instruments located in each stand (1.5 m above ground).

Statistical analysis

Mean stem respiration rates of individual trees were log-transformed for homogeneity of variances before analysis of variance (ANOVA) testing for significant differences between sites (Scheffé test for unbalanced data sets, $P < 0.05$). Root respiration data matched parametric assumptions without transformation.

Carbon dioxide release rates were regressed against tissue surface temperature with the 45 half-hour respiration rates (0100–2300 h) of all measured stems and roots per site. Additionally, we determined the regression coefficients for each tree and root segment and for all stems and roots per site. We ran an ANOVA based on the results of the regression analysis of the various stems and roots to test for significant differences in respiration rates at 0 °C (intercept) and responsiveness to temperature (slope) between the study sites. We used the coefficient of determination (r^2) to quantify the influence of the independent variable (temperature) on the dependent variable (CO_2 efflux).

Results

Microclimate

The study months, October to December 2005, were characterized by westerly foehn winds causing dry conditions. In this period, 20–30% less rain fell per month compared with 2004. As a consequence, RH and T_a showed considerable variation during the 10-day measurement periods at all study sites (Table 2).

Woody tissue CO_2 efflux along the altitudinal transect

Mean daily CO_2 release rates from stems (R_s) differed significantly between sites. Values decreased from 1.38 μmol m^{-2} s^{-1} at 1050 m to 0.21 μmol m^{-2} s^{-1} at 3050 m, with a mean R_s of 0.76 μmol m^{-2} s^{-1} at 1890 m (Table 3). Thus, mean stem respiration rate declined by a factor of 6.6 over an altitudinal span

of 2000 m. Parallel to R_s, mean coarse root CO_2 efflux (R_r) also decreased along the elevational transect (Table 3). Mean R_r decreased by 20% from 1050 to 1890 m and by 2% from 1890 to 3050 m, resulting in a 43% reduction across the transect, but differences were not significant.

There was considerable variation in R among trees within each stand (Figures 1–3). The overall range of R values was higher at the low- and mid-elevation stand (two orders of magnitude) than at the high-elevation stand (one order of magnitude). Coarse root respiration varied over one order of magnitude within all study sites (data not shown).

Woody tissue CO_2 efflux and dependence on temperature

Mean diurnal R_s and R_r exhibited little change with T_a over the course of the day in the stands (Figure 1). Despite contrasting diurnal T_a regimes at the low- and high-elevation sites, the slopes of the regression analyses of the integrated datasets of stems and coarse roots were similar and remarkably flat (Figure 2). An ANOVA conducted for intercept and slope of the regression lines of every individual stem (n = 13–21) and root segment measured (n = 4–8) confirmed that there were no significant differences in temperature responsiveness (slope) for stems and coarse roots between the study sites (Table 3). Parallel to the apparent respiration rates at ambient temperature, the mean y-axis intercept of the individual regression lines decreased significantly for R_s between 1050 m and 3050 m. For R_r, the intercept (i.e., respiration rate at 0 °C) also tended to decrease with elevation, but differences between sites were not significant.

Although pooling data at the stand level resulted in no major differences in temperature responsiveness between sites, regression analysis of data for individual trees and root segments showed exceptionally high variation in temperature response and respiration rates at 0 °C (intercept; data not shown) between individuals as well as within sites. Furthermore, we found remarkable discrepancies among individuals in the direction and strength of the temperature dependence of R_s and R_r. Highly significant positive as well as negative relationships were found at 1050 and 1890 m, but no overall temperature response was detected. Only in the high-elevation stand (3050 m) did the regression analysis for individual stems reveal significant positive correlations of R_s and T_a in most cases, but no negative relationships were detected. Similarly, R_r at 3050 m showed mainly a significant positive relationship with T_a. In contrast, at the two lower sites in most coarse roots, R_r showed no relationship with T_a. The direction of response was unrelated to taxonomic group (family) in any of the stands.

Table 2. Stand mean air temperature (T_a) and relative humidity (RH) during the 10-day measurement campaigns at the study sites at 1050, 1890 and 3050 m elevation. Overall ranges are given in parenthesis.

Elevation (m)	T_a (°C)	RH (%)
1050	20.8 (16.1–30.3)	87.1 (39.6–99.9)
1890	17.2 (9.5–25.5)	77.6 (15.1–99.9)
3050	10.6 (4.5–19.9)	91.1 (43.4–99.7)

Discussion

Elevational changes in stem and root respiration—evidence for shifts in the relative importance of root versus shoot growth with altitude

To our knowledge, our respiration data are the first reported values for tropical mountain forests. Along our elevational transect from 1050 to 3050 m, mean R_s decreased more than sixfold, whereas R_r did not decrease significantly. Because we investigated a large number of stems from different species representing the most abundant families in the three forest stands, this marked decrease in CO_2 efflux rates must be a general trend across the altitudinal transect. Moreover, the altitudinal change in R_s across the transect coincides with a pronounced shift in the aboveground:belowground biomass ratio from 9:1 at 1050 m to 2:1 (Moser et al. 2008) at 3050 m.

Table 3. Mean daily CO_2 efflux (R) of stems and coarse roots at ambient temperature at 1050, 1890 and 3050 m elevation. Analysis of variance was performed on daily mean efflux and on regression coefficients (i.e., intercept and slope of the increase in R with temperature) as determined by linear regression analysis for each individual stem and root segment. Standard deviations are given in parenthesis. Different letters indicate significant differences between sites ($P < 0.05$, Scheffé test). Data on changes in basal area (increment per existing basal area per year in %) of stems (n = 80 per site) and coarse roots (n = 20 per site) were supplied by G. Moser (University of Göttingen, Germany). Ranges in diameter at breast height (DBH) of the stems or root diameter (diam) and mean diameters of the increment studies are also given.

Elevation (m)	n	R (μmol m^{-2} s^{-1})	Intercept	Slope	Basal area change (% $year^{-1}$)	DBH/diam (cm)	
						Mean	Range
Stems							
1050	21	1.38 (0.88) a	1.29 (1.20) a	0.005 (0.046) a	2.11	17.3	5.34–69.32
1890	20	0.76 (0.52) b	0.63 (0.63) ab	0.008 (0.029) a	1.34	12.2	4.20–35.26
3050	13	0.21 (0.12) c	0.13 (0.13) b	0.008 (0.007) a	0.47	7.2	2.91–16.47
Roots							
1050	8	0.35 (0.23) a	0.35 (0.21) a	–0.003 (0.016) a	0.40	7.93	3.21–32.23
1890	7	0.28 (0.20) a	0.27 (0.40) a	0.0004 (0.026) a	1.26	7.11	4.52–10.06
3050	4	0.20 (0.15) a	0.04 (0.08) a	0.015 (0.012) a	1.92	4.56	3.57–6.77

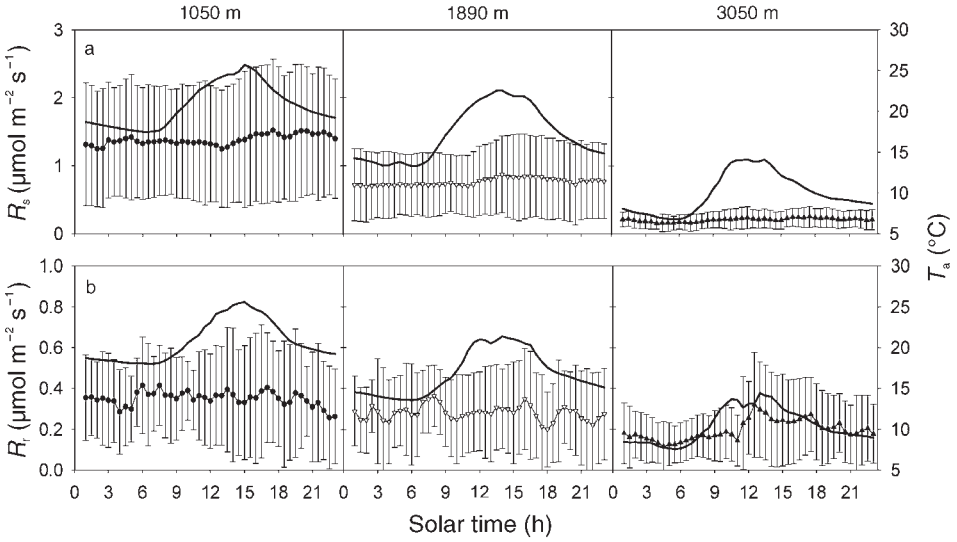

Figure 1. Diurnal course of mean (a) stem (R_s) and (b) coarse root (1–4 cm diameter; R_r) respiration and air temperature (T_a; solid line) at the study sites at 1050 m (●; n = 21 stems, n = 8 roots), 1890 m (▽; n = 20 stems, n = 7 roots) and 3050 m a.s.l. (▲; n = 13 stems, n = 4 roots). Error bars equal 1 standard deviation. Air temperature was measured at 2 m height inside the stands. Note the different scales of the y-axis in panels a and b.

Therefore, the apparent belowground shift in respiratory activity may reflect differences in the ratio of growth respiration versus maintenance respiration, reflecting the dominance of stem growth at lower elevations and of root growth and activity at higher elevations.

Dendrometric measurements of stem and coarse woody root growth at our study sites (G. Moser, unpublished data; Table 3) revealed a 4.5-fold decrease in relative basal area increment per year for stems from 1050 to 3050 m, counteracted by a 4.8-fold increase in annual coarse root basal area increment along the altitudinal gradient.

The reduction in stem growth and thus the decrease in stem respiratory activity with increasing elevation is most likely a consequence of decreasing nitrogen availability and reduced photosynthetic gain as a result of decreases in leaf area index and foliar nitrogen concentration at high elevations (Leuschner et al. 2007). The observed coarse root biomass increment along the gradient was paralleled by a pronounced increase in fine root biomass (Moser et al. 2008). Increasing allocations of carbon and nutrients to belowground organs is likely an adaptation to decreasing nutrient availability (Bloom et al. 1985). Soethe et al. (2006) concluded that the large investment in coarse woody root stock at the high-elevation site is an adaptation ensuring tree anchorage on waterlogged and steep slopes at 3050 m elevation.

The lower values of R_r relative to R_s that were observed at all stand elevations contrast with results commonly reported for coniferous forests. In pine forests, for example, coarse root respiration was found to exceed stem and branch CO_2 efflux two- to sevenfold (*Pinus radiata* D. Don; Ryan et al. 1996, 1997) or up to tenfold (*Pinus strobus* L.; Vose and Ryan 2002). However, these data are from different biomes. We are un-

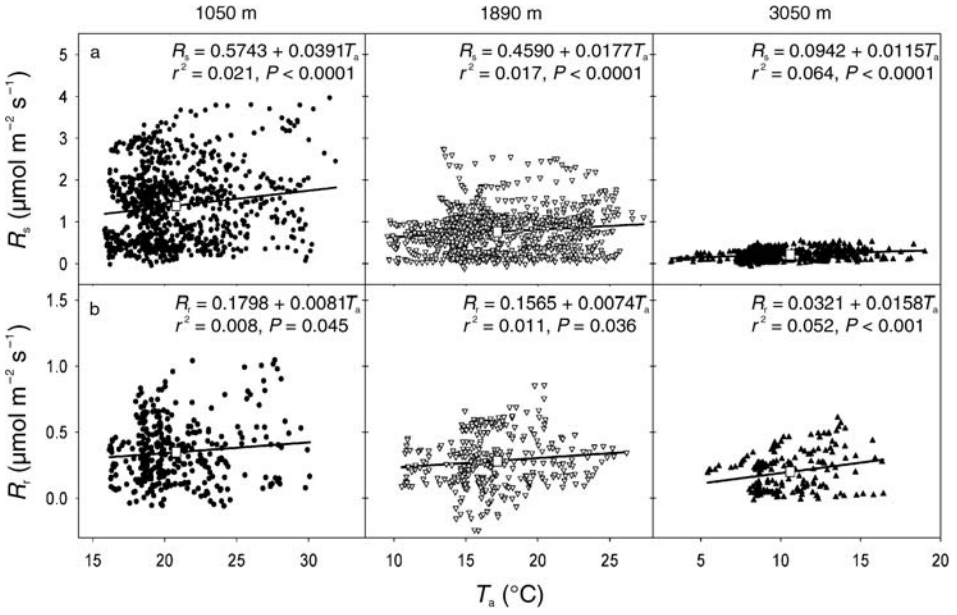

Figure 2. Dependence of the CO_2 efflux rate of all investigated (a) stems (R_s) and (b) coarse roots (R_r) on air temperature (T_a) at the three study sites (● = 1050 m, ▽ = 1890 m and ▲ = 3050 m a.s.l.). Data points are 45 half-hour values of 13–21 stems or 4–8 roots measured during a certain day at ambient temperature. The mean respiration rate at ambient temperature is marked (□) for each stand. Note the different scales of the R-axis in panels a and b.

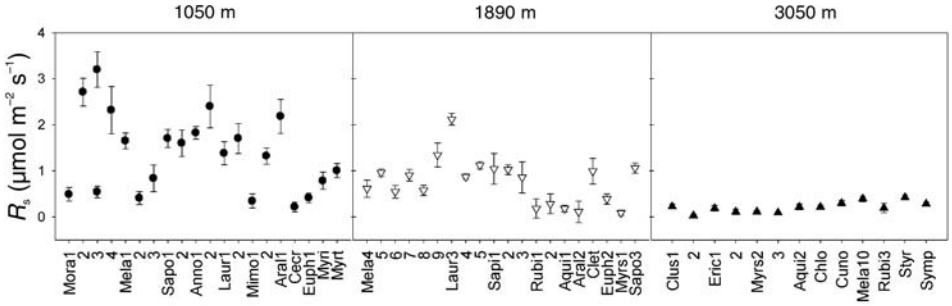

Figure 3. Stem CO_2 efflux rate (R_s) of individuals from various families in the stands at (a) 1050, (b) 1890 and (c) 3050 m elevation. Data are daily means of R_s from all measured trees, each consisting of 45 half-hourly values during one day. Error bars equal 1 standard deviation. The families included are those with the greatest number of individuals at the particular site. Abbreviations: Mora1–4 = *Ficus sp*; Mela1, 2 = *Miconia punctata*; Mela3 = indet.; Sapo1 = *Chrysophyllum sp*; Sapo2 = *Pouteria cf*; Anno1, 2 = indet.; Laur1, 2 = indet.; Mimo1 = *Inga sp*; Mimo2 = indet.; Aral1 = *Schefflera sp*; Cecr = *Pourouma cf*; Euph1 = *Alchornea sp*; Myri = *Virola cf*; Myrt = indet.; Mela4–6 = *Graffenrieda emarginata*; Mela7–9 = *Miconia punctata*; Laur3 = *Nectandra sp*; Laur4 = *Endlicheria oreocola*; Laur5 = *Ocotea aciphylla*; Sapi1–3 = *Matayba inelegans*; Rubi1 = *Palicaurea sp*; Rubi2 = *Ladenbergia cf oblongifolia*; Aqui1 = *Ilex cf amboroica*; Aral2 = *Schefflera sp*; Clet = *Clethra revoluta cf*; Euph2 = *Hyeronima morisiana*; Myrs1 = *Myrsine coriacea*; Sapo3 = *Micropholis guyanensis*; Clus1 = *Clusia sp* 1; Clus2 = *Clusia sp* 2; Eric1 = *Cerotostema cf*; Eric2 = indet.; Myrs2 = *Myrsine sp*; Myrs3 = indet.; Aqui2 = *Ilex weberlingii*; Chlo = *Hedyosmum sp*; Cuno = *Weinmannia loxensis*; Mela10 = *Axinea sp*; Rubi3 = *Faramea sp*; Styr = *Styrax foveolaria*; and Symp = *Symplocos sp*.

aware of a study on stem or root respiration of trees along altitudinal transects in the Tropics with which our data can be compared.

Mean R_s was four times higher than R_r at 1050 m, 2.7 times greater at 1890 m, but about equal at 3050 m: a result of a decrease in R_s with elevation while R_r remained almost constant. The similarity in respiration rates of plants growing across a thermal gradient (Körner and Larcher 1988) has been attributed to acclimation (Amthor 1994) or thermal homeostasis (Larigauderie and Körner 1995). Such adaptation allows plants to meet their energy requirements even when temperatures are low. However, the relative constancy of coarse root respiratory activity, which we observed with increasing altitude, despite a marked decline in stem CO_2 release, is most likely the result of a shift in resource allocation reflecting the changing environmental conditions. Even though the number of roots measured was quite low, our results closely mirrored the dendrometric studies of Moser et al. (2008) at the same sites, showing an increase in coarse root growth with increasing altitude.

Temperature sensitivity of respiration in tropical mountain forests

By measuring CO_2 efflux in 13–21 tree stems and 4–8 roots per stand, we demonstrated a substantial within-plot variation in respiratory activity (Figure 3). The coefficient of variation in R_s remained constant across the gradient, whereas only the overall range in respiratory release decreased with elevation by two orders of magnitude from 1050 to 1890 m and by one order of magnitude from 1890 to 3050 m.

Similarly, Chambers et al. (2004) reported a variation of two orders of magnitude (0.03 to 3.64 μmol m^{-2} s^{-1}) within a stand. However, they focused on ecosystem exchange rates without differentiating between tree families or species. Ryan et al. (1994) found that stem CO_2 release rates varied sevenfold between two tree species. In forest stands in central Cameroon and the Brazilian Amazon, stem CO_2 release rates from 14 and 13 tree families ranged from 0.2 to 5.2 μmol m^{-2} s^{-1} and from 0.1 to 3.3 μmol m^{-2} s^{-1}, respectively (Meir and Grace 2002). Cavaleri et al. (2006) monitored plant functional groups in a tropical lowland rain forest in Costa Rica and found substantial differences in the CO_2 efflux of stems and branches of dicotyledonous tree species, lianas and palms. The comparable variation among families in stem respiration along our altitudinal transect suggests that there is no decrease in tree functional diversity toward the harsher environment close to the tree line.

Homogeneity among sites in the slopes of the respiratory response to temperature indicates that temperature sensitivity did not differ across elevations. Furthermore, the small slopes suggest that temperature responsiveness is low in the trees of this tropical mountain rain forest. By contrast, regressions for individual trees revealed highly variable response patterns within and between sites. The variability in response and the occurrence of inverse temperature responses among coexisting trees could not be explained by taxonomic status (family) or tree size (authors' unpublished observations). Negative respiration–temperature relationships as found at 1050 and 1890 m may be attributable to climatic effects on xylem sap flow which, in turn, affected the amount of CO_2 released through the bark (Gansert and Burgdorf 2005). It is also possible that the exceptionally dry hot weather during the measurement periods induced changes in respiratory activity. The capacity to acclimate to short- (hours) or medium-term (days) changes, or both, in temperature can vary greatly among plant species (Larigauderie and Körner 1995, Atkin et al. 2005). Additionally, plants or organs able to acclimate rapidly to short-term weather fluctuations may show continuously changing temperature responsiveness as found by Atkin et al. (2000) for leaf dark respiration of *Eucalyptus pauciflora* Sieb. ex Spreng.

Based on absolute values, the mean slopes of the stem and coarse root responses to temperature were steeper at the high-elevation site, indicating a more pronounced thermal sensitivity of cold-grown plants. Higher Q_{10} values in plants grown in cold environments compared with warm-grown plants were

found by Tjoelker et al. (2001), whereas Larigauderie and Körner (1995) found that the variability in leaf Q_{10} was unrelated to plant origin. Atkin et al. (2005) concluded that systematic variation in Q_{10} values does not exist and that differences among contrasting biomes are relative and thus do not reflect an inherent variable temperature responsiveness of characteristic plant species. However, our results showed that the mean temperature sensitivity of stems and coarse roots was similar among the contrasting thermal environments along the gradient, whereas the analyses of individual plant responses showed that large differences in temperature responsiveness exist within the three study sites.

Given the homogeneity of mean slopes across the differing growth environments, any differences in CO_2 release rates across our gradient resulted from differences in the *y*-axis intercept or respiration rate at 0 °C. Removing temperature as a confounding factor still yielded a marked decrease in stem CO_2 efflux along the transect from 1050 to 3050 m, indicating that temperature may not be the primary controlling factor as underpinned by the low temperature sensitivity found along the altitudinal gradient.

Our measurements along a tropical mountain transect indicate a shift from high respiratory activity of stems compared with coarse roots at lower elevation (1050 m) to an apparent equivalence of stem and coarse root CO_2 efflux rates at 3050 m. The observed decrease in the ratio of stem to root efflux rates with altitude may be explained by the substantial decrease in stem growth, while coarse root growth increased with increasing elevation. We found that responses of CO_2 release rates of woody tissue to changes in temperature differed greatly between study sites, as well as among species and plant organs, with the underlying mechanisms remaining unclear. The remarkable variation in respiratory activity and, most importantly, in temperature response of respiration, suggests that predictions at the community level or even estimates for entire ecosystems on the basis of a few point measurements of selected plant species must be interpreted cautiously. Because there was great variation in acclimation pattern among plants and between sites, questions about the response of plant community CO_2 efflux to climate change will need to be answered at the community level (Larigauderie and Körner 1995).

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