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Diverging temperature response of tree stem CO_2 release under dry and wet season conditions in a tropical montane moist forest

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Abstract It is commonly presumed that plant respiratory CO_2 release increases with increasing temperature. However, we report on very contrasting stem CO_2 release (R_S)–temperature relationships of trees in a species-rich tropical montane forest of southern Ecuador under dry and wet season conditions. Rates of R_S were low and completely uncoupled from the dial temperature regime during the humid season. In contrast, during the dry season, R_S was generally higher and temperature sensitivity of R_S differed greatly in degree and even in the direction of response, indicating that temperature might not be the only determinant of R_S. In order to explain the heterogeneity of R_S, we related R_S to vapour pressure deficit, wind speed and solar radiation as important abiotic drivers influencing transpiration and photosynthesis. Stepwise multiple regression analyses with these meteorological predictors either were biased by high collinearity of the independent variables or could not enhance the ability to explain the variability of R_S. We assume maintenance respiration to dominate under humid conditions unfavourable for energy acquisition of the tree, thus explaining the pronounced uncoupling of R_S from atmospheric parameters. In contrast, the drier and hotter climate of the dry season seems to favour R_S via enhanced assimilatory substrate delivery and stem respiratory activity as well as elevated xylem sap CO_2 imports with increased transpiration. In addition, tree individual differences in the temperature responses of R_S may mirror diverging climatic adaptations of co-existing moist forest tree species which have their distribution centre either at higher or lower elevations.

Keywords Climatic adaptation · Ecuador · Stem respiration · Temperature sensitivity of respiration · Tree species richness

Introduction

Temperature has long been identified as the most important abiotic factor influencing plant respiratory activity due to its well known effect on enzymatic reactions (e.g. Amthor 1989). A strong relationship between temperature and plant tissue respiration has been exhaustively proved and verified under controlled conditions (e.g. Maier et al. 1998; Tjoelker et al. 1999, 2001; Atkin et al. 2000, 2006, 2007; Loveys et al. 2003; Armstrong et al. 2006). However, in the field, a consistent relationship is often not found (e.g. Edwards and McLaughlin 1978; Negisi 1982; Lavigne 1987; Gunderson et al. 2000; Teskey and McGuire 2002). Especially, woody tissue respiration is reported not to be exclusively related to temperature since other sources of CO_2 than the respiratory activity of living wood cells (inner bark, cambium, xylem parenchyma) alone can influence the apparent amount of CO_2 escaping through the bark. Imports of dissolved CO_2 via the transpiration stream can add substantial amounts to the stem internal carbon dioxide. The quantitative contribution of the different sources to the internal flux of CO_2 was found to vary considerably on a seasonal as well as daily basis. Consequently, stem internal CO_2 concentrations can constantly fluctuate, which in turn can affect the amount of CO_2 diffusing out of the bark (e.g. McGuire and Teskey 2004; Teskey et al. 2008; Saveyn et al. 2008a, b).

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Stem respiration usually depends on substrate availability, the demand for energy equivalents and the enzymatic activity (Amthor 1995; Lambers et al. 1998; Pruyn et al. 2002, 2005; Atkin et al. 2005). However, it is still barely understood how stem CO_2 release (R_S) is finally controlled and how internally circulating CO_2 is influencing the apparent efflux. High rates of R_S coincided with high xylem sap fluxes (Levy and Jarvis 1998; Levy et al. 1999; Horna and Zimmermann 2002). Other studies reported a negative correlation between xylem flux and radial CO_2 efflux (Negisi 1979; Edward and Hanson 1996; Teskey and McGuire 2002; Gansert and Burkdorf 2005; Teskey and McGuire 2007). All these studies suggested that R_S might be linked to canopy water use. However, removing the foliage had little effect on the dial pattern of R_S in an experiment of Maier and Clinton (2006). No relationship between sap flow and R_S was found by Ceschia (2001), Carey et al. (1996) and Edwards and Wullschleger (2000).

From a biomechanical point of view, the resistance to radial gas diffusion as controlled by xylem, cambium or the bark layers (Sorz and Hietz 2006; Lendzian 2006; Steppe et al. 2007) can significantly influence the apparent stem CO_2 release. Bark structural properties differed between species and these differences could explain much of the between-species variation in the velocity of oxygen diffusion in wood segments in a laboratory study by Sorz and Hietz (2006). Under controlled conditions, where abiotic influences could be excluded, Steppe et al. (2007) found a substantial variation in the resistance to radial CO_2 diffusion from stem and branch wood of three *Populus deltoides* clones. However, Steppe et al. (2007) used branch segments from different positions within the tree canopy known to vary considerably in their pattern of CO_2 release and the underlying cause of this variation remained unsolved.

Under natural conditions, where the influence of environmental factors cannot be excluded, the picture gets even more complicated due to the fact that co-occurring plants are responding individualistically to their specific environment and probably even more so to shifts in the environmental setting (Larigauderie and Körner 1995; Arnone and Körner 1997; Amthor 1989; Oren and Pataki 2001; Reich et al. 2003; Atkin et al. 2005; Kerkhoff et al. 2005; Enquist et al. 2007). A better understanding of the variability in R_S among different individuals in a population, different species in a stand, and different patches of the forest is therefore crucial to predict changes in the carbon dioxide exchange between tree wood and the atmosphere, in particular, in highly diverse tropical forests (Kerkhoff et al. 2005; Enquist et al. 2007).

In this paper, we report on in situ-measurements of the diurnal rates of R_S of representative tree species in a tropical montane moist forest in southern Ecuador during two hydrologically contrasting seasons of the year. Under the prevailing moist conditions, mean annual temperature is relatively low and diurnal temperature amplitudes are small. In contrast, the short dry season climate is characterised by exceptionally high day-time and low night-time temperatures. Trees of this ecosystem have to cope with constantly low temperatures, compared to lowland forests, while being exposed to unpredictable short-term microclimatic shifts. The objectives of this study were (a) to analyse the temperature-response of R_S of adapted moist forest tree species during two contrasting seasons, i.e. sunny-dry versus cloudy-moist weather conditions, and (b) to compare patterns of R_S of eight co-existing tree species from seven families for quantifying variability between trees. Linear regression analyses and stepwise multiple regressions with selected meteorological factors (vapour pressure deficit, wind speed, solar radiation) were used to take account of abiotic drivers controlling transpiration and photosynthesis, which may affect R_S under contrasting climatic conditions. We hypothesise that plant inherent factors and external variables apart from temperature are playing an important role in determining the apparent R_S at the level of individual trees.

Materials and methods

Study area and tree selection

The study was conducted in the Reserva San Francisco (RSF) adjacent to the Podocarpus National Park (PNP) on the eastern slopes of the southern Ecuadorian Andes. The study site (03°58′345″S/79°04′648″W) is located at 1,890 m elevation and covered by a species-rich montane forest of about 12 m in height. Forest structure and species composition are described in more detail by Röderstein et al. (2005) and Leuschner et al. (2007). The soils of the region developed from metamorphic shale, quartzite, and sandstone bedrock; they are characterised by low fertility (Schrumpf et al. 2001).

Within the stand, we selected 20 mature canopy trees representing abundant families and comprising a broad range of stem diameters. Further details on tree selection are given in Zach et al. (2008).

For the exemplary study on the impacts of the dry climate conditions on stem respiratory activity, we restricted analysis to 10 out of the 20 mature canopy trees sampled (Table 1). These trees had been measured under pronounced dry season conditions as characterised by high ambient temperature, relatively high vapour pressure deficits (D) and declining soil water availability (Fig. 1). The remaining 10 trees were measured 1 week earlier, when

Table 1 Daily mean stem CO_2 release rate (R_S, μmol CO_2 m^{-2} s^{-1}) of individual trees at the study site at 1,890 m elevation as measured during the dry (R_S dry) and during the humid (R_S wet) season of the year

Abbreviations	Species	Family	*d*	*h*	R_S dry	R_S wet	Stem diameter increment
Cr	*Clethra revoluta*	Clethraceae	23.45	12.69	0.99 (0.10)	0.41 (0.09)	0.68
Eo	*Endlicheria oreocola*	Lauraceae	20.80	10.00	0.87 (0.24)	0.14 (0.07)	0.05
Ge	*Graffenrieda emarginata*	Melastomataceae	26.11	16.54	0.61 (0.18)	0.07 (0.10)	0
Hm	*Hyeronima moritziana*	Euphorbiaceae	9.52	13.70	0.39 (0.13)	0.22 (0.07)	1.17
Ia	*Ilex amboroica*	Aquifoliaceae	9.63	7.50	0.18 (0.11)	0.33 (0.07)	–
Lo	*Ladenbergia cf oblongifolia*	Rubiaceae	9.48	7.92	0.28 (0.08)	0.19 (0.08)	–
Mi1	*Matayba inelegans*	Sapindaceae	8.17	8.30	0.85 (0.22)	0.40 (0.11)	0.98
Mi2	*Matayba inelegans*	Sapindaceae	10.53	12.70	1.04 (0.34)	0.64 (0.18)	–
Mp1	*Miconia punctata*	Melastomataceae	10.62	14.05	1.34 (0.26)	0.52 (0.07)	–
Mp2	*Miconia punctata*	Melastomataceae	12.00	7.06	0.57 (0.11)	0.64 (0.11)	0

Relative stem diameter increment (in %) as determined between September 2005 and April 2006. SD in parentheses. Missing values due to dendrometer defects

d stem diameter (cm), *h* stem height (m)

some rain fell, which did not allow for an appropriate comparison of wet and dry season respiratory patterns. The tree selection comprised climax species of seven families (Table 1). Most of the tree species were represented by only one individual, except *Miconia punctata* and *Matayba inelegans* of which each two individuals of similar size were sampled (Table 1). Trees were equipped with dendrometer bands for stem increment measurements. However, due to dendrometer defects, we could not determine stem increment rates for all tree individuals.

Rates of stem CO_2 release (R_S) of the selected tree individuals were measured during 4 days in the dry period in November 2005 (DOY 324–327; Fig. 1) and 4 days during the humid season in April 2006 (DOY 117-120). For each tree, we conducted one 24-h-course of R_S with rates being logged half-hourly. The diurnal half-hour-values were averaged to calculate the mean daily rate of R_S of each tree (Table 1), while the entire dataset was used for regression analysis (Table 2; Fig. 2). R_S was monitored at breast height (1.3 m) using the mobile 6-chamber respiration system ANARESY 2 (Walz, Effeltrich, Germany) and an integrated LI-7000 infrared gas analyzer for CO_2 and H_2O (Li-Cor, Inc., Lincoln, NE, USA) running in differential mode. Details of the technical equipment are provided by Zach et al. (2008). Air temperature (T_A) and relative air humidity at 2 m height inside the stand were monitored synchronously using a Rotronic sensor (Rotronic AG, Bassersdorf, Switzerland) connected to the data logger of the ANARESY system (CR 10, Campbell Scientific, Logan, UT, USA).

The measured tree individuals were not equipped with thermocouple elements for stem tissue temperature (T_T) monitoring. Therefore, we used data deriving from tissue temperature measurements conducted later in the year in the study site. In July 2006, thermocouples (diameter 3 mm, length 20 mm, Siemens, Munich, Germany) were installed at breast height (depth 10 mm) at two arbitrarily chosen tree stems (DBH 15 and 20 cm) for the continuous measurements for stem tissue temperature. We used data from July/August 2006 and November 2006 to establish relationships between the continuously recorded air temperature and tissue temperature:

$$\text{wet season: } T_T = 19.74\left(1 - \exp^{(-0.0888T_A)}\right) \times \left(\text{adj } r^2 = 0.83,\ p < 0.0001\right) \quad (1)$$

$$\text{dry season: } T_T = 23.13\left(1 - \exp^{(-0.0736T_A)}\right) \times \left(\text{adj } r^2 = 0.87,\ p < 0.0001\right), \quad (2)$$

where T_A is the air temperature measured inside the stand. These equations were used to calculate tissue temperature from air temperature in our two measurement periods in 2005 where tissue temperature was not recorded directly.

Climate conditions of the study periods

In general, the climate of the study area is humid throughout the year. However, an extremely wet period (April–July) is followed by several months with less frequent rainfall (September–December) (Bendix et al. 2006). Mean annual precipitation at 1,960 m a.s.l. is ca. 2,200 mm (Emck 2007). At the study site, annual mean air temperature is 15.7°C and relative humidity 90.7% (Moser et al. 2008).

During November 2005, foehn winds caused an exceptionally dry and sunny period throughout the study area. Fires occurred frequently throughout the wider region during this period. Only 90 mm of rainfall were recorded in

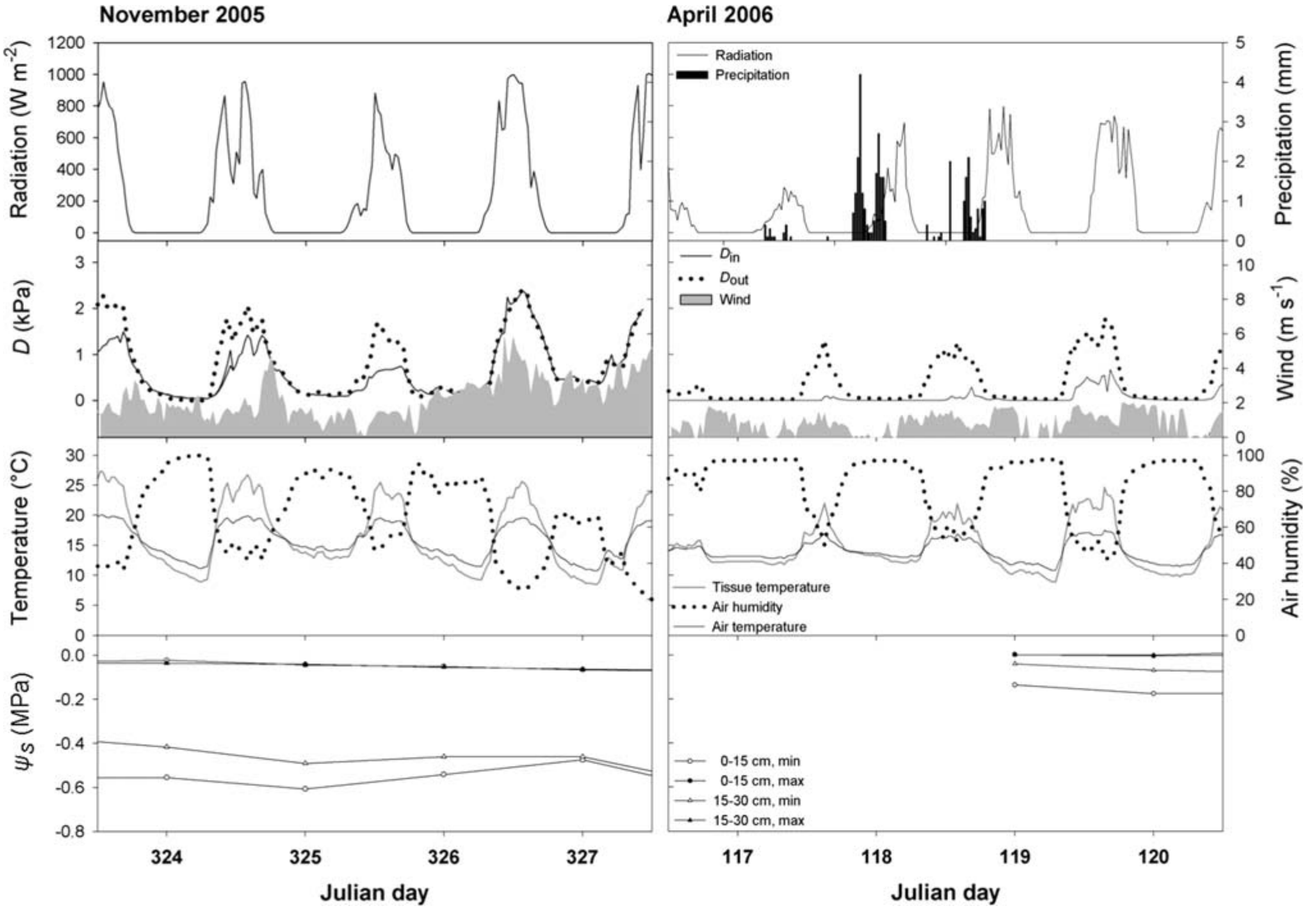


Fig. 1 Climate data for the measurement periods in November 2005 (dry season) and April 2006 (wet season) as recorded at a nearby climate station at 2,000 m a.s.l. (M. Richter, unpublished data). Vapour pressure deficit was calculated from the climate station data (D_{out}) and from climate data recorded inside the forest site at 2 m above ground (D_{in}). Soil matric potential (ψ_S) was measured at adjacent forest sites at 2,000 m (S. Engelhard, unpublished data). Tissue temperature was calculated from air temperature with Eqs. 1 and 2

November, which fell during the first 2 weeks (M. Richter, unpublished data). When we started measurements in end of November, the rainless period had already lasted for 7 days. The lack of rainfall resulted in a substantial decrease of air humidity and an increase of daily temperature amplitudes compared to the wet season conditions. Vapour pressure deficit (D) continuously increased during the four consecutive measurement days in November (Fig. 1, data recorded by M. Richter at a nearby climate station, unpublished). Substantially higher wind speeds were recorded during this dry period compared to the humid days (Fig. 1). The average soil water matric potential (ψ_S) as measured in adjacent forest sites at 2,000 m progressively decreased during the four measurement days in November from −0.15 (±0.13) to −0.24 (±0.12) MPa at 15 cm depth and from −0.10 (±0.09) to −0.19 (±0.12) MPa at 30 cm (S. Engelhard, unpublished data). Minimum values of −0.60 MPa (15 cm) and −0.49 MPa (30 cm) were recorded at the end of the measurement period (Fig. 1).

The measurement campaign in the wet period was conducted at the beginning of the humid period in April 2006. During this month, precipitation was frequent. Low diurnal temperature amplitudes and a moderate vapour pressure deficit were characteristic for this season (Fig. 1). Data of the soil matric potential were only available for the last two measurement days. These data indicated that soil moisture exceeded field capacity with potential values greater than −0.1 MPa (S. Engelhard, unpublished data).

Data treatment

Rates of stem CO_2 release (R_S) were calculated as:

$$R_S = D[\mathrm{CO_2}]F/\mathrm{AC} \tag{3}$$

where R_S is the CO_2 release rate (μmol CO_2 m^{-2} s^{-1}), $D[CO_2]$ is the difference between ambient (reference gas) and chamber (sample gas) CO_2 concentration, F is the molar air flow rate (mol s^{-1}) which passes through the chamber, and AC is the surface area (m^2) of the enclosed

Table 2 Pearson's coefficients of determination (r^2) of linear regression analyses of stem CO_2 release of 10 trees on meteorological predictors

	T_{T}			D			w			*rad*	
	Day	dt	nt	Day	dt	nt	Day	dt	nt	Day	dt
Dry											
Cr	**0.38**	**0.26**	**−0.30**	**0.56**	**0.42**	0.07	**0.31**	0.09	0	**0.55**	**0.38**
Eo	**0.49**	**0.53**	**0.34**	**0.45**	**0.51**	**0.31**	**0.18**	**0.19**	**0.21**	**0.19**	**0.16**
Ge	**−0.31**	0.12	0.05	**−0.24**	0.03	0	**0.25**	**0.36**	0.18	**−0.21**	0.03
Hm	0.02	0	0.01	0.03	0	0	0.01	0.04	0	0.03	0
Ia	**−0.22**	0.14	**−0.56**	**−0.13**	0.09	**−0.49**	**−0.13**	0.10	**−0.23**	0.01	0
Lo	**0.10**	0.12	0.02	**0.11**	**0.16**	0.04	0.01	0	0.03	0.01	0
Mi1	**0.23**	**0.23**	**0.36**	0.05	0.04	0.1	**−0.35**	**−0.37**	**−0.32**	0.02	0
Mi1*			**0.80**			0.09			**−0.62**		
Mi2	**0.87**	**0.89**	**0.67**	**0.68**	**0.66**	0.05	**0.27**	0.05	0.03	**0.49**	**0.30**
Mp1	**0.49**	**0.68**	**0.55**	**0.39**	**0.65**	**0.39**	**0.38**	**0.42**	**0.39**	**0.14**	**0.26**
Mp2	**0.77**	**0.76**	**0.31**	**0.64**	**0.53**	0	**0.22**	0.02	0	**0.37**	0.11
Wet											
Cr	0	0.1	0	0.04	**−0.31**	0.02	0.03	0.02	0	0	0.02
Eo	**0.13**	**0.27**	0.13	**0.16**	**0.25**	0.11	0.03	**0.25**	**−0.23**	**0.20**	**0.29**
Ge	0	0.01	0.11	0	0.06	0	0.10	0.02	0.04	0.06	0.02
Hm	0	0.04	0.05	0.02	0.09	0.07	0.08	0.11	**−0.43**	0.03	0.15
Ia	0.03	0	0.06	0.02	0	0.01	0	0	0.09	0.01	0
Lo	0	0.02	**0.22**	0	0	0.17	**0.11**	0.01	**0.24**	0	0
Mi1	0	0.09	0.04	0	0.11	**−0.59**	0	0.08	0.21	0.01	0.08
Mi2	0.03	0.03	**0.23**	0	0.04	0.03	0.03	**−0.36**	0.07	0.09	**−0.41**
Mp1	0.08	0.04	0.15	**−0.16**	0.02	0.11	0.06	0.13	0	**−0.19**	0.08
Mp2	**0.21**	**0.28**	0.06	**0.24**	**0.42**	0.03	0	0.20	0	**0.18**	0.26

Given are results of regression analyses of the diurnal (day), day-time (dt) and night-time (nt) data set of each tree individual measured for the dry and the wet season. Significant correlations ($p < 0.05$) are printed in bold. Mi1*- data calculated by omitting two outlying data points measured during night-time. Tissue temperature as calculated from air temperature with Eqs. 1 and 2. For key to species' abbreviations, see Table 1

T_{T} tissue temperature (°C), D vapour pressure deficit as calculated from temperature and air humidity from a climate station at 1,960 m a.s.l. (kPa), w wind speed as recorded at a climate station outside the forest (m s^{-1}), *rad* solar radiation as recorded outside the forest (W m^{-2})

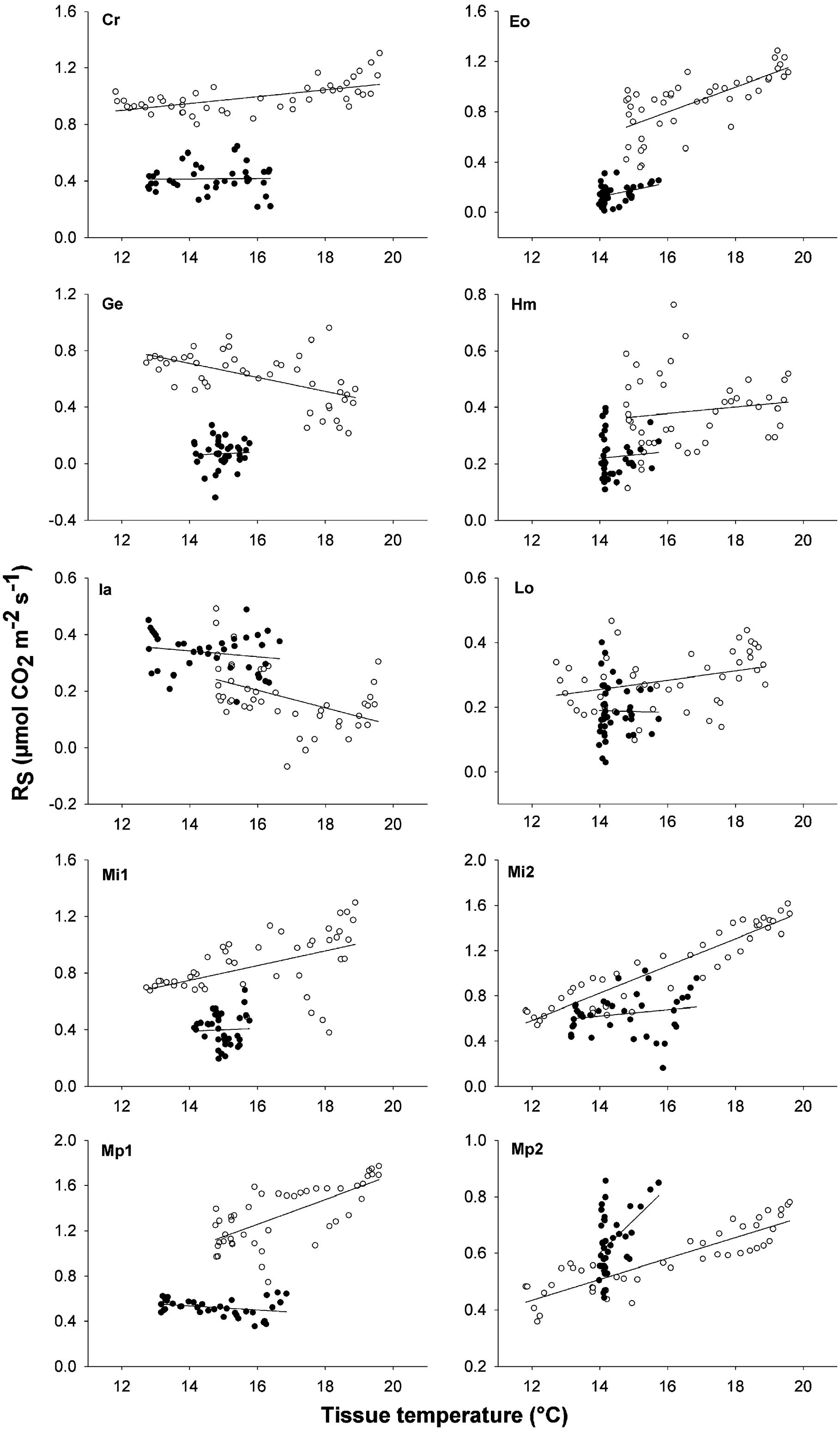
stem segment. In an earlier study (Zach et al. 2008), we found better agreement when relating the apparent CO_2 efflux rates from tropical montane forest trees of South Ecuador to stem surface area than to volume.

We chose the slope of the regression curve of R_S on temperature as a measure of the temperature sensitivity of R_S instead of the commonly used Q_{10} value. The Q_{10} of respiration (i.e. the factor expressing the proportional change in respiratory CO_2 release per 10°C rise in temperature) basically compares the CO_2 release rate at a given temperature to that at a 10°C lower temperature (Atkin et al. 2005). Plant respiration is a process influenced by various environmental factors. Consequently, neither the Arrhenius nor the Q_{10} model has been found to adequately describe the observed temperature response of respiration under field conditions. For that reason, reported measures of temperature responsiveness have to be treated with caution (Tjoelker et al. 2001; Atkin and Tjoelker 2003). In addition, there is increasing evidence that the respiratory response to temperature is neither constant nor necessarily exponential (Atkin et al. 2000, 2005; Atkin and Tjoelker 2003). Therefore, instead of focussing on few single data points on the temperature axis, we used the entire diurnal dataset of R_S for analysing the temperature dependency of R_S.

One important source of variation in diurnal and seasonal R_S is the internal transport of dissolved CO_2 in the transpiration stream influencing the apparent CO_2 release through the bark (Edward and Hanson 1996; Levy and Jarvis 1998; Teskey and McGuire 2002, 2007; Gansert and Burkdorf 2005; Teskey et al. 2008). Because we did not measure xylem sap flow directly, we used D, wind speed and solar radiation as major determinants of transpiration in our regression analysis in the attempt to explain the large heterogeneity of R_S.

We are aware of possible impacts of tissue resistance to the stem radial CO_2 diffusion. However, we could not investigate the properties of biomechanical barriers to CO_2 diffusion in our trees. Given the relationship between

Fig. 2 Rates of stem CO_2 release (RS) of 10 tree individuals at 1,890 m elevation plotted against tissue temperature. Tissue temperature was calculated from air temperature with Eqs. 1 and 2. Separate regression lines are given for the dry season (November 2005, *open circle*) and the humid season (April 2006, *filled circle*) for each tree individual. Coefficients of determination are given in Table 2. For key to species' abbreviations, see Table 1



xylem flux and stem CO_2 release and the good coupling found between climatic conditions and transpiration in the study area (Motzer et al. 2005), we assume that environmental conditions may superimpose mechanical effects of tissue resistance to CO_2.

By means of linear regression, we analysed the temperature responsiveness of R_S for each tree individual during the dry and the humid season. For each tree, rates of R_S were plotted against the respective courses of T_T and T_A using either the diurnal dataset, or by considering only day-time or night-time values. To improve the explanatory power of the regression equation, we conducted linear regression analyses with the three additional meteorological predictor variables (D, wind speed, solar radiation). Using Pearson's correlation coefficient, we quantified the influence of these four variables on R_S by their r^2. If more than one predictor showed significant effects, we conducted stepwise multiple regression analyses ($\alpha = 0.05$ for tolerance; collinearity $|\zeta| < 0.6$) to determine main causes of diurnal, day-time and night-time variability in R_S. Subsequently, multiple regression analyses were repeatedly applied by removing factors with no significant influence ($p < 0.05$) until each individual tree model reached maximum likelihood (F test, p value).

Results

Stem CO_2 release and its temperature responsiveness under dry and humid conditions

Mean daily R_S was highly variable and ranged from 0.18 to 1.34 μmol m^{-2} s^{-1} during the dry, and between 0.07 and 0.64 μmol m^{-2} s^{-1} during the humid period (Table 1). Mean daily T_T ranged between 15.7 and 16.8°C during the dry (minimum 10.1°C, maximum 19.9°C), and between 14.5 and 14.9°C during the humid season (minimum 10.8°C, maximum 17.5°C). In most cases, R_S was higher during the dry period than under cooler and more humid conditions. Between September 2005 and April 2006, stem diameter increment differed among trees (Table 1).

Among regression models, we found linear regression to give the most appropriate fit for the relationship between R_S and temperature for both periods (Fig. 2). The respective correlation between R_S and T_T or T_A did not differ (not shown). Under dry season conditions, the response of R_S to T_T was highly divergent and showed strong discrepancies in the direction of response between different tree individuals. Moreover, the eight measured species showed contrasting patterns in their temperature response of R_S. Besides the commonly expected positive relationship, R_S was significantly negative correlated with temperature or completely uncoupled from changes in temperature in certain cases (Fig. 2). In the dry season, the temperature responsiveness of R_S differed between day-time and night-time periods. Here, we found better correlations with data separated into day-time and night-time values than with the diurnal datasets in most of the cases. Most of the trees showed higher day-time than night-time rates of stem CO_2 release parallel to higher day-time than night-time temperatures.

While most of the tree stems were more responsive to temperature during day-time hours, we found three tree species showing a higher temperature coupling during the night (Ia, Mi1, Cr; Table 2). The two trees showing significant negative temperature coupling under dry season conditions (Ge and Ia; see Fig. 2) showed also higher night-time than day-time rates of stem CO_2 release.

The general temperature responsiveness of R_S was unexpectedly low. For most of the tree individuals, plotting diurnal R_S against T_T yielded r^2 values of less than 0.5. In two of the ten measured tree species, T_T could explain more than 70% of the variability in the diurnal R_S. One tree of the species, *Hyeronima moritziana* (Hm) showed no significant relation to T_T under dry season conditions neither during the day nor the night (Table 2).

In the humid season, R_S was mostly uncoupled from temperature; only in some cases, a very weak correlation was observed (Table 2). Two trees showed significant relationships in the diurnal dataset ($r^2 = 0.13$ and 0.23). Two other trees were weakly, though significantly, correlated with T_T during night-time only ($r^2 = 0.22$ and 0.23). For the remainder species, no differences in the temperature sensitivity of R_S between day- and night-time were apparent in the humid season. Here, diurnal rates of stem CO_2 release did not differ considerably between day and night.

Dependence of stem CO_2 release on other meteorological predictors under dry and humid conditions

R_S was linearly related to all four selected meteorological parameters (not shown). Nevertheless, neither D nor wind speed or solar radiation improved the explanatory power of the regressions with respect to R_S variability under dry or humid conditions. Trees showing a significant relationship to T_T also yielded comparable correlations to the other climatological parameters, most likely because of tight intercorrelation between the parameters. In most cases, stepwise multiple regression analysis was not applicable due to the high collinearity of the meteorological variables ($\zeta > 0.6$). An exception was wind speed, which was generally less correlated to T_T, D or solar radiation ($\zeta < 0.5$).

Wind speed and radiation were the main determinants of the diurnal variation in R_S of *Graffenrieda emarginata* (Ge) during the dry season, explaining half of the variability (model adj. $r^2 = 0.497$, $F = 23.25$, $p < 0.0001$); the correlation with radiation was a negative one (Table 2). Wind speed alone was the most important factor controlling the diurnal variation in R_S of *Matayba inelegans* (Mi1) during the dry season (model adj. $r^2 = 0.337$, $F = 24.45$, $p < 0.0001$); again, the relation was a negative one. Wind speed improved the regression model by explaining further

10.2% of the diurnal variation in R_S in *Miconia punctata* (Mp1). Together with T_T, both parameters could explain 57.7% of the variability in diurnal R_S in the dry period ($F = 31.07$, $p < 0.0001$). For the remaining tree species, multiple regression analysis either was not appropriate or could not improve the explanatory power of the model in comparison to a single-factor model with T_T alone (Table 2).

Under humid conditions, the variability of R_S could not be explained by any of the meteorological parameters. A few tree species showed significant, yet very weak, correlations to some of the predictors (Table 2). An exception was the night-time variability in R_S in *Matayba inelegans* (Mi1), which was strong and negatively related to D ($r^2 = 0.59$).

Discussion

Sources of variation in humid season stem CO_2 release

During the humid measurement period, R_S was independent of T_T (Fig. 2), and also seemed to be unaffected by any of the other investigated meteorological parameters (Table 2). Plant respiratory activity is thought to be determined by three processes, substrate supply, demand for respiratory products and potential enzyme capacity (Amthor 1995; Lambers et al. 1998; Atkin et al. 2005). Limited light availability due to cloud cover is known to strongly reduce net carbon gain of tropical forests on a seasonal as well as daily basis (Hollinger et al. 1994; Chen et al. 1999; Graham et al. 2003). In the humid season with frequent cloudiness and rainfall in the Ecuadorian Andes, assimilation rates must have been impeded, thus restricting carbohydrate supply. Porometric measurements conducted on mature canopy trees at nearby forest sites in the Podocarpus National Park showed that leaf transpiration and xylem sap flow of the tropical montane trees were substantially repressed during cloudy days and under high atmospheric humidity (Motzer et al. 2005). This may reduce the transport of dissolved CO_2 with xylem water from the roots to the stem. However, amount and concentration of xylem sap CO_2 mainly depend on the respiratory activity of the root system involved, while smaller amounts of CO_2 may also be taken up with the soil water. Differences in fine root respiration among the measured tree individuals remain unknown as well as the quantitative contribution of root respiratory CO_2 release to the transpiration stream, which might finally lower or raise rates of CO_2 release through the bark.

Sorz and Hietz (2006) found higher stem water content under conditions of sufficient soil water supply to coincide with low internal oxygen contents suppressing rates of gas efflux through the bark. However, we found trees with higher (Ia, Mp2; Fig. 2) or very similar CO_2 efflux patterns (Lo) under wet compared to the dry season conditions.

We assume that several factors have contributed to a slowed down R_S and a low temperature sensitivity of R_S, among which reduced substrate supply from photosynthesis, less demand for respiratory products under somewhat cooler temperatures, and a probably lower contribution of CO_2 from the transpiration stream are the most likely.

Sources of variation in dry season stem CO_2 release

The dry-season R_S exceeded the wet-season rates in most of the measured trees (Fig. 2). Overall higher rates of R_S in the dry season may in part be explained by an assumed higher photosynthetic carbon gain accompanied by a higher carbon investment under the sunnier and hotter conditions of the dry period. However, in the Ecuadorian montane forest, annual wood production was generally low (Moser et al. 2008) and distinct stem growth periodicities were not visible (Homeier 2004), implying that pronounced differences in growth related respiratory activity between dry and wet season were unlikely.

Temperature coupling was stronger during the dry season, though considerable scatter in the data was also evident (Fig. 2). Although the diurnal amplitude of T_T and T_A differed between the dry compared to the humid season (Fig. 1), the temperature response of R_S to variations in T_T and T_A did not differ within periods (data not shown). Hence, thermal differences between T_T and T_A could not account for the observed discrepancies in the temperature response of R_S between the two seasons. However, the actual T_T of our tree stems could differ from the calculated T_T values, since the continuous measurements of T_T on the two stems used for the extrapolation started later in the year. Higher actual values of T_T than the modelled ones could be one reason for the better temperature coupling of R_S in the dry season.

Attempts to explain deviations from the common temperature–respiration relationship or high between-tree variations in stem CO_2 release mainly focussed on four physiological phenomenon: (1) on time lags between temperature variation and CO_2 release (Ryan 1990; Lavigne 1996; Stockfors and Linder 1998), (2) the significance of stem photosynthetic activity (Sprugel and Benecke 1991; Gansert 1995; Pfanz 1999; Strobel 2004), (3) the CO_2 transport with xylem sap flux (Edward and Hanson 1996; Levy and Jarvis 1998; Teskey and McGuire 2002; Gansert and Burkdorf 2005) and/or (4) on differences in the diffusion resistance to gas by xylem, cambium and the bark (Sorz and Hietz 2006, Lendzian 2006, Steppe et al. 2007). In three of our trees (Cr, Ge, Hm; Table 1), the correlation coefficients between diurnal T_T and R_S were higher when a time lag of 1.5–2 h was considered in the analysis (data not shown). At least in two of the stems (Cr, Ge), R_S might indeed show a delayed temperature response, which should be related to the bigger tree size prolonging the radial diffusion pathway of CO_2 (Lavigne 1996) or a higher bark resistance to gas diffusion (Sorz and Hietz 2006; Lendzian 2006; Steppe et al. 2007). In the smaller stem, a lowered thermal conductivity could be the reason for the observed time delay (Hm) (Gries 2004). Bark photosynthetic activity as a significant factor could be excluded in our tree sample by comparative measurements of R_S in shaded and unshaded chambers (data not shown).

Taking account of a possible influence of xylem sap CO_2 to explain the large heterogeneity in R_S, we related R_S to D, wind speed ,and solar radiation. These parameters affect stomatal conductance and transpiration and thus the xylem sap flow with its assumed CO_2 transport capacity. Motzer et al. (2005) measured leaf transpiration and xylem sap flow in mature trees nearby and found high stomatal sensitivities to D and strong stomatal control of sap flux in these trees. Even on short time scales (i.e. passing clouds), a sudden decline in leaf transpiration could be detected. Thus, the measurements of Motzer et al. (2005) evidenced a great diurnal and seasonal variation in sap flux rates which could well have resulted in large differences of CO_2 transport in the xylem sap. This could explain why D, radiation, and wind speed indeed showed a significant effect on R_S in a number of tree species, in particular in the dry season (Table 2). Xylem sap effects could also account for the high release rates despite low temperature sensitivities evident for most of the tree individuals.

Several authors have argued that reduced cell turgor in the stem of droughted trees could cause a transient reduction in the respiratory activity of the living tissue (e.g. Saveyn et al. 2007). This effect would offer an explanation for the apparent day-time depression of R_S in *Graffenrieda emerginata* and *Ilex amboroica* (Ge, Ia; Fig. 2) during the dry season.

However, eight of the ten tree individuals showed higher, and not lower, rates of R_S during the sunny/hot period. Although higher rates of R_S could not be directly related to growth in case of the measured trees, the enhanced R_S very likely indicated that the dry season climate principally favoured photosynthetic carbon gain and xylem sap flow, hence the delivery of substrate for plant respiratory activity as well as of dissolved CO_2 from the transpiration stream, and thereby enhancing stem CO_2 release.

Atmospheric uncoupling of stem respiration versus temporal efficiency in energy acquisition—evidence for climate-sensitive and climate-tolerant tree species?

Differences in rates of R_S and temperature sensitivity of R_S between the measured trees were much more pronounced in the dry than in the wet season (Table 1) indicating a diverging response of the trees to hotter weather conditions in this species-rich montane forest. The RSF forest with its high species diversity consists of a mixture of different tree functional types and includes typical climax and pioneer tree species co-occurring in the same stand (Homeier 2004). Moreover, our study site at 1,890 m may represent a melting point of tree species which usually occur predominantly at higher or lower elevations, thus representing different climatic adaptations. This assumed variety in tree physiological types may offer an additional explanation for the large differences in patterns of R_S. For example, *Ilex amboroica* and *Graffenrieda emarginata*, the two individuals with a significant negative R_S–temperature response, are mostly recorded above 2,000 m elevation in neotropical montane forests (http://www.mobot.org/mobot/Research/ecuador/search.shtml; Missouri Botanical Garden Database; Jorgensen and Yánez 1999) and thus are growing at their lower distribution limit in the RSF (J. Homeier, personal communication). Distribution preferences towards cooler and more humid climates at higher elevations would account for a stress-induced adverse reaction to the dry season conditions at RSF (Table 2; Fig. 2). In contrast, *Clethra revoluta* is most abundant between 1,500 and 3,500 m a.s.l. in Ecuador (Jorgensen and Yánez 1999). This species seemed to be well adapted to the local climate variability, if the strong positive temperature response during the dry season is used as a criterion to assess performance under varying thermal regimes (Fig. 2). *Miconia punctata* and *Matayba inelegans* are usually occurring in tropical lowland forests below 500 and 1,000 m elevation, respectively (http://www.mobot.org/mobot/Research/ecuador/search.shtml; Missouri Botanical Garden Database; Jorgensen and Yánez 1999). Thus, they are growing at their upper distribution limit in a rather cold environment in the RSF. These species from hotter environments responded to the dry season by a relatively large increase in R_S with increasing temperature, probably revealing a better adaptation to warmer climates. In contrast, *Ladenbergia oblongifolia*, one of the more abundant tree species between 1,800 and 1,900 m a.s.l. in the RSF (Homeier 2004), is mainly recorded below 1,000 m elevation in the Neotropics (http://www.mobot.org/mobot/Research/ecuador/search.shtml; Missouri Botanical Garden Database). This tree individual showed a very weak R_S response to increasing temperature (Table 2).

Conclusion

Our study reports on the substantial variability in stem CO_2 release between seasons and among tree individuals in a species-rich tropical montane forest. Xylem sap flow effects, species-specific differences in respiratory activity or the sensitivity of R_S to atmospheric factors could be influential. The plastic response in R_S of adapted moist forest tree species to a drier climate could help to gain insights into the acclimation potential of a mega-diverse plant community to cope with the expected climate warming. In this context, tropical montane forests are of increasing relevance, since the predicted warming by 2–4 K during this century will most likely force mesic lowland taxa to migrate upwards (Mahli and Phillips 2004; Mayle et al. 2004). Understanding and monitoring of the present forest community composition and the species-specific responses to environmental changes are a crucial basis for conservation options and will provide clues for reliable future projections.

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