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Spatial and temporal variation in soil CO_2 efflux in an old-growth neotropical rain forest, La Selva, Costa Rica

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Abstract. Our objectives were to quantify and compare soil CO_2 efflux of two dominant soil types in an old-growth neotropical rain forest in the Atlantic zone of Costa Rica, and to evaluate the control of environmental factors on CO_2 release. We measured soil CO_2 efflux from eight permanent soil chambers on six Oxisol sites. Three sites were developed on old river terraces ('old alluvium') and the other three were developed on old lava flows ('residual'). At the same time we measured soil CO_2 concentrations, soil water content and soil temperature at various depths in 6 soil shafts (3 m deep). Between 'old alluvium' sites, the two-year average CO_2 flux rates ranged from 117.3 to 128.9 mg C m^{-2} h^{-1}. Significantly higher soil CO_2 flux occurred on the 'residual' sites (141.1 to 184.2 mg C m^{-2} h^{-1}). Spatial differences in CO_2 efflux were related to fine root biomass, soil carbon and phosphorus concentration but also to soil water content. Spatial variability in CO_2 storage was high and the amount of CO_2 stored in the upper and lower soil profile was different between 'old alluvial' and 'residual' sites. The major factor identified for explaining temporal variations in soil CO_2 efflux was soil water content. During periods of high soil water content CO_2 emission decreased, probably due to lower diffusion and CO_2 production rates. During the 2-year study period inter-annual variation in soil CO_2 efflux was not detected.

Introduction

Tropical forests play an important role in the global carbon budget. Tropical evergreen forests account for ~35% of the world's potential net primary production on land (Melillo et al. 1993; Field et al. 1998). In the past, old growth tropical rain forests were often considered as steady-state systems, but some evidence suggests that tropical rain forests may act as carbon sinks (Grace et al. 1995; Mahli et al. 1998). Other studies predict large carbon losses from tropical forests if temperature increases due to climate change (Cox et al. 2000; White et al. 2000). It is therefore

critical to understand how the carbon budget of tropical forests will react to changes in environmental conditions. For this reason "CARBONO", a long-term, landscape-scale project was set up at La Selva Biological Station in Costa Rica. Its major goal is to assess the major carbon stocks and fluxes and to investigate the effects of climatic factors on ecosystem carbon dynamics.

To characterize the carbon exchange in forest ecosystems, an assessment of the dynamics of soil CO_2 efflux is important as soil respiration is a major CO_2 flux in the carbon cycle, second in magnitude to gross canopy photosynthesis (Raich and Schlesinger 1992).

CO_2 in the soil is produced by root respiration and by decomposition of litter and soil organic matter. Efflux of CO_2 from the soil to the atmosphere is controlled by diffusion and therefore related to the concentration of CO_2 in the soil atmosphere and soil textural and soil structural properties that control the diffusivity of CO_2 in the soil (De Jong and Schappert 1972). Although multiple factors influence the biological and physical processes controlling soil CO_2 release, many studies have shown that soil temperature and soil moisture are the most important factors regulating soil CO_2 efflux (Singh and Gupta 1977; Howard and Howard 1993; Kicklighter et al. 1994). A complication is that soil temperature and soil water content often covary, which makes it difficult to separate their effects (Reiners 1968; Dörr and Münnich 1987; Davidson et al. 1998).

In this study our first objective was to quantify and compare the soil CO_2 efflux rates of two different soil types in an old-growth neotropical rain forest in Costa Rica. Our second objective was to evaluate how environmental factors control the efflux of CO_2 from the soil surface.

Materials and methods

Study sites

Our study was carried out in old-growth forest at the La Selva Biological Station. La Selva is located in northeastern Costa Rica (10°20′ N, 83°50′ W) between the Atlantic coastal plain and the foothills of the Central Cordillera at an elevation of 35 – 150 m. La Selva is classified in the Holdridge Life Zone System as Tropical Wet Forest (Hartshorn and Hammel 1994). The long-term average annual precipitation at La Selva is 4200 mm; average monthly air temperature is 26 °C, with little temperature difference between months (Sanford et al. 1994). In this study we distinguished two seasons based on the actual monthly rainfall measured during the study period. Months with more than 400 mm rainfall were defined as wet season and the drier season are those periods of at least two consecutive months with less than 400 mm rainfall.

For this study we selected three 0.5 ha plots on each of the two dominant soil types of La Selva: 'old alluvium' (plot A2, A3, A4) and 'residual' (plot L4, L5, L6) soils. For more details on site selection see Clark et al. (1998) and Clark and Clark

Table 1. Characteristics of the investigated soil types. Data are means per soil type (n = 3) for the upper (0 – 1 m) and lower (1 – 3 m) soil profile.

Depth of sampling (m)	Clay content (%)	Bulk density (g cm^{-3})	Soil air space (cm^3 cm^{-3})	Total C (%)	Total N (%)	Total P (mg kg^{-1})	pH (KCl)
'old alluvium'							
0 – 1	70.7	0.81	0.12	2.02	0.19	0.96	3.97
1 – 3	52.5	1.01	0.02	0.74	0.07	0.95	4.00
'residual'							
0 – 1	76.3	0.79	0.20	2.80	0.24	0.62	4.11
1 – 3	65.2	1.01	0.03	0.61	0.05	0.48	4.52

(2000). The 'old alluvium' soil is formed on old river terraces and has previously been classified as an Inceptisol. The strongly weathered 'residual' soils originate from andesitic lava flows and were classified as Ultisols (Sollins et al. 1994). Only 'residual' sites which were located on relatively flat ridges were studied. Kleber et al. (submitted) recently reclassified these soils. Both soil types meet the rationale for the classification as Oxisols: low silica:sesquioxide ratio, low base exchange capacity, low acitivity of clays, and low content of weatherable minerals. Considering the perudic moisture regime both soils were classified as Typic Haploperox (Kleber et al. (submitted)).

In August 1997 we took soil samples at 0.05, 0.20, 0.40, 0.75, 1.50 and 2.50 m depth from one soil pit of each 0.5 ha plot. Bulk density was determined by taking undisturbed soil samples (300 cm^3), which were subsequently dried at 105 °C for 48 h. Total pore space (cm^3 cm^{-3}) was calculated from measurements of bulk density and an assumed particle density of 2.65 g cm^{-3}. Soil air space (cm^3 cm^{-3}) was estimated by subtracting volumetric soil water content (θ_v) from total pore space. To measure the particle size distribution, air-dried and sieved (2 mm) soil samples were treated with H_2O_2 to remove organic matter and then dispersed with pyrophosphate. The particle fractions were determined using the pipette method. Soil pH was measured with a combined electrode in potassium chloride (1 M) at a soil:solution ratio of 1:2.5. To determine total carbon, nitrogen and phosphorus subsamples were dried (40 °C) and pulverized. An elemental analyzer (Elementar analysator CNS, Vario EL, elementar, Hanau, Germany) was used to estimate total carbon and nitrogen. To determine total P, the ground samples were digested with HNO_3^-. The P content was measured with an ICP (Spectro Analytical Instruments, Kleve, Germany). Main physical and chemical characteristics of the upper (0 – 1 m) and lower soil profile (1 – 3 m) of the investigated soils are given in Table 1.

Soil CO_2 efflux

We used dynamic, closed chambers for measurement of soil CO_2 efflux (Parkinson 1981; Norman et al. 1992). Eight chambers were deployed randomly along four parallel transects at each site. Transects were 15 m long and spaced 5 m apart. In August 1997, aluminum rings (0.20 m in diameter, 0.15 m tall) were inserted to a depth of about 0.02 m into the soil. Once inserted, the rings were left in place throughout the time investigated, except for two chambers which had to be replaced due to tree fall. The chambers were kept free of seedlings throughout the whole study period. Each of the six sites was sampled bi-weekly from April 1998 to April 2000. It took 2 days to measure the six sites; three sites per day were measured in a randomly chosen order. All measurements were conducted between 8 AM to 2 PM local time. Preliminary studies did not reveal a detectable diurnal pattern of CO_2 efflux.

Flux chambers were closed with an aluminum cover (0.15 m tall) for about 5 minutes. Air was circulated at a flow rate of 0.6 l min^{-1} between an infrared CO_2 gas analyzer (April 1998 to January 2000: LI-6251, since February 2000: LI-800; LI-COR, Inc., Lincoln, Nebraska, USA) and the flux chambers. To prevent pressure differences between the chamber and atmosphere, the chamber was vented to the atmosphere through a 0.25 m long stainless steel tube (3.2 mm outer diameter). CO_2 concentrations were recorded at 5 second intervals with a datalogger (April 1998 to January 2000: Campbell CR 10X, since February 2000: Campbell CR 510X; Campbell Scientific, Inc., Logan, Utah, USA). CO_2 flux was calculated from linear regression of increasing CO_2 concentration within the chamber versus time, usually between 2 and 4 min after placing the cover over the ring. The coefficient of determination (r^2) of the simple linear regression was typically better than 0.99. The infrared gas analyzer was calibrated in the lab using nitrogen as zero standard and a secondary CO_2 standard (450 ppm). Secondary standards were calibrated against primary standards supplied by Scott-Marin, Inc. (Riverside, CA, USA).

For each of the six sites the average CO_2 efflux rate was calculated from the eight chamber flux measurements on a sampling day. Daily mean soil efflux for each site was calculated by linear interpolation between sampling dates. Daily CO_2 flux rates were then cumulated to estimate annual flux rates. Due to equipment failure or heavy rainfall we lost approximately 1% of the data. Where there were missing data the average of the previous and following sampling date was used.

Soil CO_2 profile concentration and CO_2 storage

At each of the six selected sites a soil shaft (about 0.75 by 2 m with 3 to 4 m depth) was installed. In August 1997, stainless steel tubing (3.2 mm outer diameter) was inserted horizontally at 0.05, 0.20, 0.40, 0.75, 1.50 and 2.50 m depth. These tubes had holes at one end and a septum holder with septum at the other end to allow sampling of soil gases. The tubes at depths of 0.05 – 0.75 m were 0.90 m long; tubes at greater depth were 1.80 m long. Thermocouples and soil moisture sensors (Campbell CS 615) were installed at the same depths as the gas sampling

tubes. The 'pit wall effect' on CO_2 concentration was tested. At 1.50 m depth tubes of 0.45, 0.90, 1.35, 1.80 and 2.70 m length were inserted horizontally. The horizontal CO_2 concentration gradient was measured several times and a fit of the data revealed that the CO_2 concentration, measured at 1.80 m from the pit wall, was around 95 % of the CO_2 concentration at the estimated asymptode.

Soil gas samples were collected with a needle and polypropylene syringes with a three-way stopcock mounted to the tip. When sampling, first the 'dead' volume in the tubes was discarded. Then 30 ml gas was withdrawn from each gas sampling tube. Within 6 hours the gas samples were analyzed in the lab for CO_2 concentration using a Shimadzu GC-8 gas chromatograph with a thermal conductivity detector. Gas samples passed through an anhydrous $CaSO_4$ (Drierite) trap to remove water vapor followed by a sample loop of about 1 ml. Samples were injected on a Porapak Q (80/100 mesh) packed stainless steel column (2.0 m × 3.2 mm) using a 6-port manually actuated valve (Valco Instruments). Oven temperature was maintained at 40 °C. Helium carrier gas flowed at approximately 30 ml min^{-1}. The retention time for CO_2 was about 1.1 minutes. Soil air CO_2 concentration was calculated by comparison of integrated peak areas of samples with standard gases (0.045% and 4.93% CO_2), which were used to make a two point calibration. Storage tests indicated that on average 1 to 2% (maximal 5%) CO_2 were lost between time of sampling and analyses.

The soil profile was divided into six layers (0 – 0.10 m, 0.10 – 0.30 m, 0.30 – 0.50 m, 0.50 – 1.00 m, 1.00 – 2.00 m and 2.00 – 3.00 m). Soil CO_2 storage of the different soil layers was calculated as follows (Equation 1):

$$\text{Soil } CO_2 \text{ storage per soil layer} = \text{Soil air } CO_2 \text{ concentration} \times \text{soil air space} \times \text{soil volume per soil layer} \times \text{factor} \times 1000$$

With:
Soil CO_2-C storage of the different soil layers (mg C m^{-2})
Soil CO_2 concentration measured in the soil air space per soil layer (volume %)
Soil air space (m^3 m^{-3}) = Total pore space (m^3 m^{-3}) – Soil water content (m^3 m^{-3})
Soil volume per soil layer (m^3) = 1 m^2 × vertical extension of the respective soil layer (m)

$$\text{Factor} = \frac{\text{Molecular weight of carbon } (12\,g\ mol^{-1})}{\text{Volume of a mole of gas } (0.0224\,mol\ m^{-3})}$$

Soil CO_2 storage calculated for each of the six soil layers was then added up for the upper part of the soil profile (0 – 1 m), the lower part of the soil profile (1 – 3 m) and for the whole profile (0 – 3 m).

Environmental parameters

Soil temperature was measured adjacent to each flux chamber at approx. 0.05 m depth and within the soil shaft with a thermocouple T-probe and a thermometer reader (OMEGA HH 64).

Soil water content was determined using frequency domain reflectometry (FDR). The probe (Campbell CS 615) consisted of 0.30 m long stainless steel rods that were placed horizontally into the soil (O'Brien and Oberbauer 2001). The sensor output was converted to estimates of volumetric soil water content (θ_v) using the calibration curve developed by Veldkamp and O'Brien (2000).

For two study sites ('old alluvium' site A4 and 'residual' site L6) the volumetric water content (from 0.05 m depth) was converted to matric potential using water retention curves generated from pressure plate analyses of intact cores. Volumetric water contents (θ_v) were measured at 0, 0.25, 5.6, 10, 33, 100, 300 and 1500 kPa tension. Based on these data the following exponential functions were calculated (Papendick and Campbell 1981):

'old alluvium': matric potential $(MPa) = 843.4e^{-0.224 \times \theta_v}$

'residual': matric potential $(MPa) = 320.5e^{-0.209 \times \theta_v}$

Statistical analyses

Prior to statistical analyses the parameters were tested for normality. One-way analysis of variance was used to determine spatial and temporal differences. Linear and nonlinear regression analyses were used to examine relationships between soil CO_2 efflux, soil water content, soil temperature and other factors. Significant effects were determined at $P < 0.05$. All our statistical analyses were carried out using the STATISTICA 5.5 software package (StatSoft Inc., Tulsa, Oklahoma, USA).

Results

Spatial and temporal variation in soil CO_2 efflux

Within-site spatial variation among soil chambers was large. The coefficient of variation (CV) within a site at each date was on average about 35% of the mean for 'old alluvium' sites and 45% for 'residual' sites and ranged typically from 15 to 70%.

Soil CO_2 efflux rates also varied between sites. The two-year average CO_2 flux rates between 'old alluvium' sites ranged from 117.3 to 128.9 mg C m^{-2} h^{-1}. Efflux of CO_2 was higher on the 'residual' sites ($P < 0.05$), ranging from 141.1 to 184.2 mg C m^{-2} h^{-1} (Table 2a).

Table 2a. Average (mg C m^{-2} h^{-1}) and cumulative soil CO_2 efflux (Mg C ha^{-1} yr^{-1}) measured in Year 1 (April 14, 1998 to April 9, 1999) and Year 2 (April 23, 1999 to April 20, 2000).

	'old alluvium'			'residual'		
	A2	A3	A4	L4	L5	L6
Year 1	137.3	113.6	114.1	182.7	179.4	146.1
Cumulative		*10.7*[a]			*14.8*[b]	
Year 2	120.4	121.1	121.7	171.6	189.0	136.1
Cumulative		*10.6*[a]			*14.5*[b]	

[a]Different letters indicate within-year differences between soil types, at $P < 0.05$ (ANOVA)

Besides the spatial variability, soil atmosphere CO_2 efflux also varied in time. There was a progressive decrease in soil CO_2 efflux during the wet season. Minimum CO_2 flux values were always measured at the end of the wet season when the soil volumetric water content was highest. Soil CO_2 release started to increase again at the onset of the drier season. Although there were seasonal changes in soil CO_2 efflux, the magnitude of soil CO_2 efflux between the wet and drier season was not different ($P > 0.05$). Seasonal trends were similar for both soil types; however, the variation in CO_2 efflux seemed to be more pronounced at the 'old alluvium' sites (Figure 1).

We estimated cumulative (annual) CO_2 emissions by integrating soil CO_2 efflux over time. Annual soil CO_2 efflux of each soil-type group did not differ between Year 1 and Year 2; however, annual CO_2 efflux was higher at 'residual' than at 'old alluvium' sites ($P < 0.05$) (Table 2a).

Spatial and temporal variation in soil CO_2 storage

Soil air CO_2 concentrations varied between soil depth and soil types. In the uppermost layer (0 – 0.10 m depth) an average CO_2 concentration of 0.7% was measured in 'old alluvium' soils. At the same depth a significantly lower CO_2 concentration (0.2%) was found in 'residual' soils. In both soil types soil air CO_2 concentration increased throughout the depth profile. Between 2 and 3 m depth the average CO_2 concentration was 2.8% in 'old alluvium' and 'residual' sites.

Large spatial variations and differences in CO_2 storage between the upper and lower profile were identified for both soil types (Figure 2, Table 2b). For example, the two-year average CO_2 storage (0 – 3 m depth) between 'old alluvium' sites ranged from 719 to 1881 mg C m^{-2}. Between 1184 and 1248 mg C m^{-2} were stored in the 'residual' soil profiles (0 – 3 m depth). Although the average amount of CO_2 stored in the whole profile did not differ between 'old alluvium' (1190 mg C m^{-2}) and 'residual' sites (1198 mg C m^{-2}), a closer examination shows that the CO_2 storage in the upper and lower part of the profiles are significantly different between 'old alluvium' and 'residual' sites. With 655 mg C m^{-2} a higher amount was calculated for the upper profile of the 'old alluvium' soils than for 'residual' soils (576 mg C m^{-2}). In contrast, in the lower part of the profile (1 – 3 m depth) more

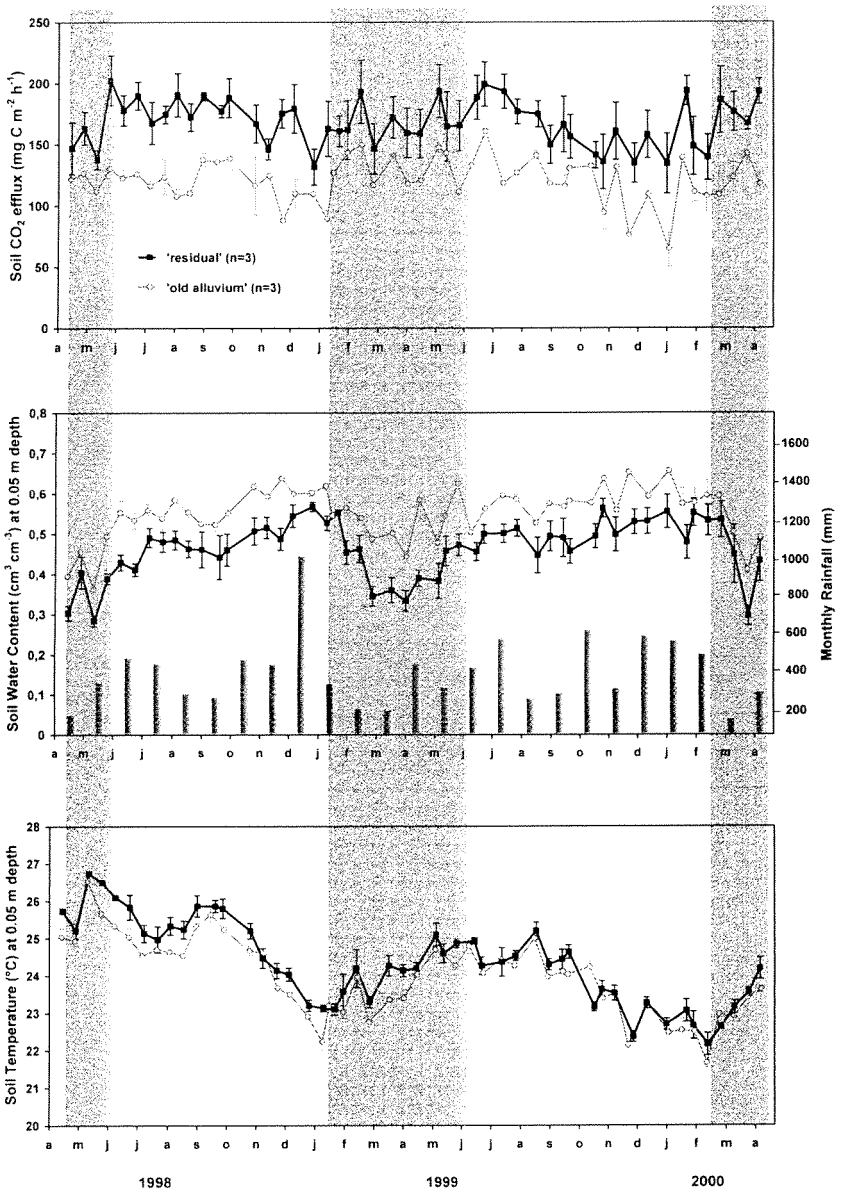

Figure 1. Bi-weekly measurements of soil CO_2 efflux, soil water content and soil temperature at 0.05 m depth. Each point is the mean of three sites (for soil respiration with 8 chamber measurements at each site). Error bars represent ± standard error of the mean. The shaded areas mark the drier season; white background is the wet season.

Table 2b. Soil CO_2 storage (mg C m^{-2}) measured in Year 1 (April 14, 1998 to April 9, 1999) and Year 2 (April 23, 1999 to April 20, 2000)

	'old alluvium'			'residual'		
	A2	A3	A4	L4	L5	L6
Year 1						
0 – 1 m	540	1016	441	371	672	658
1 – 3 m	405	927	359	1001	571	476
Year 2						
0 – 1 m	607	954	371	307	663	794
1 – 3 m	402	866	267	818	459	440

CO_2 was stored in the 'residual' (627 mg C m^{-2}) soils as compared to the 'old alluvium' soils (538 mg C m^{-2}) (Table 2b).

Generally, no pronounced seasonal changes in soil CO_2 storage could be observed. However, during the wet season 1998 the amount of CO_2 stored in the upper soil profile (0 – 1 m depth) of the 'old alluvium' sites tended to increase steadily. Due to extraordinary high soil air CO_2 concentrations (up to 3% in 0 – 0.10 and 0.10 – 0.30 m depth) a CO_2 storage of approx. 1000 mg C m^{-2} was calculated. At the onset and during the drier season 1999 the CO_2 storage decreased in the upper soil profile of the 'old alluvium' sites. During April and May 1998 when comparatively low soil moisture contents were measured (Figure 1), the CO_2 storage in the lower profile in all sites was unusually high (Figure 2).

Although individual sites showed differences in CO_2 storage between Year 1 and Year 2 (A4, L4, and L6), the average amount of CO_2 accumulated in the upper and lower profile did not differ between years (Table 2b). However, during Year 2 soil CO_2 storage in the 'old alluvium' and 'residual' sites varied within a greater range between sampling dates and no distinct accumulation peak was found at the end of the wet season as compared to Year 1 (Figure 2).

Effects of soil water content and soil temperature on soil CO_2 efflux and soil CO_2 storage

Combining the CO_2 efflux measurements from all dates per site showed that the relationship between soil CO_2 efflux and the volumetric water content (at 0.05 m depth) can best be described as a parabolic function. This function could be applied to both 'old alluvium' and 'residual' sites (Figure 3). However, the shape of the curves and the soil water content at which maximum CO_2 evolution occurred differed between sites and soil types. At the 'old alluvium' sites the highest soil CO_2 efflux occurred when the soil water content (at 0.05 m depth) ranged between 0.45 and 0.50 cm^3 cm^{-3}. At the 'residual' sites the highest CO_2 release from the soil was measured when the water content was between 0.35 and 0.50 cm^3 cm^{-3} (Figure 3). At the peak CO_2 emission, the soil matric potential for the 'old alluvium'

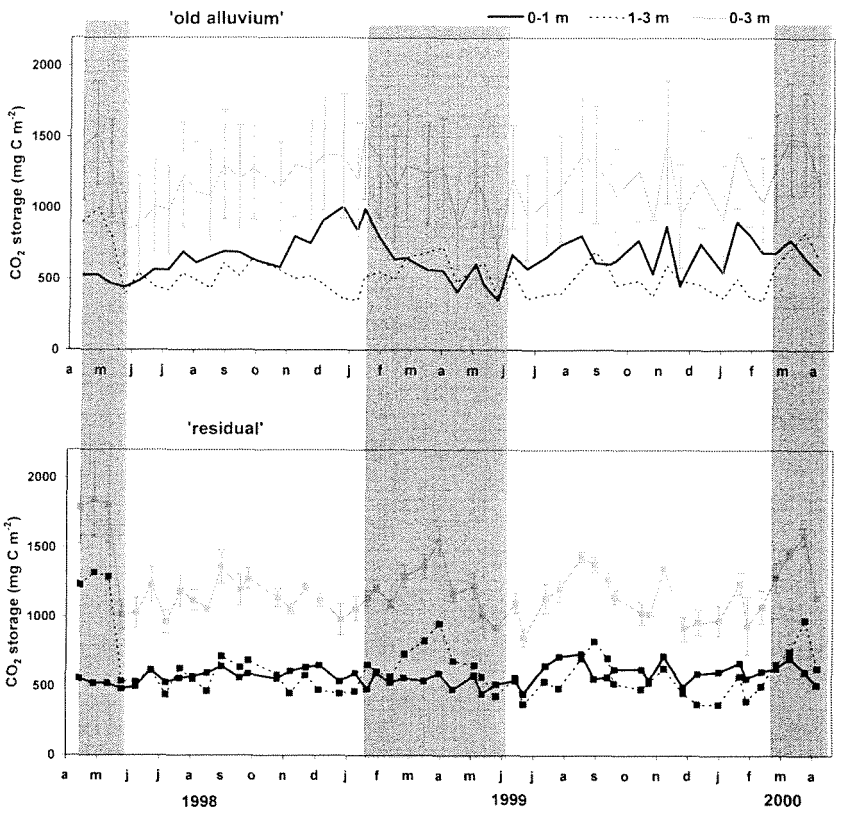

Figure 2. Bi-weekly measurements of soil CO_2 storage in 0–1 m, 1–3 m and 0–3 m depth. Means (± standard error) are given (n = 3). The shaded areas mark the drier season; white background is the wet season.

site A4 was equivalent to –0.01 MPa. For the 'residual' site L6 the highest CO_2 efflux occurred at a matric potential of –0.03 MPa.

We correlated the residuals from the parabolic soil water – soil CO_2 efflux relationship with soil temperature (at 0.05 m depth) to test if we could explain any further part of CO_2 efflux with soil temperature. For one of the six sites ('residual' site L6), we found a significant positive correlation between the residuals and soil temperature. Selecting only wet season data, we found a negative linear relationship between CO_2 flux and soil water content. The median r^2 for 'old alluvium' and 'residual' sites was 0.51 and 0.21, respectively. For the wet season data a significant positive correlation between the residuals and soil temperature was found for one of the six sites ('old alluvium' site A2). Hence, for two sites soil temperature was useful as a variable explaining variance in soil CO_2 efflux.

Variations in CO_2 storage, spatial as well as temporal, were due to changes in soil air CO_2 concentration and soil water content (see Equation 1). However, the

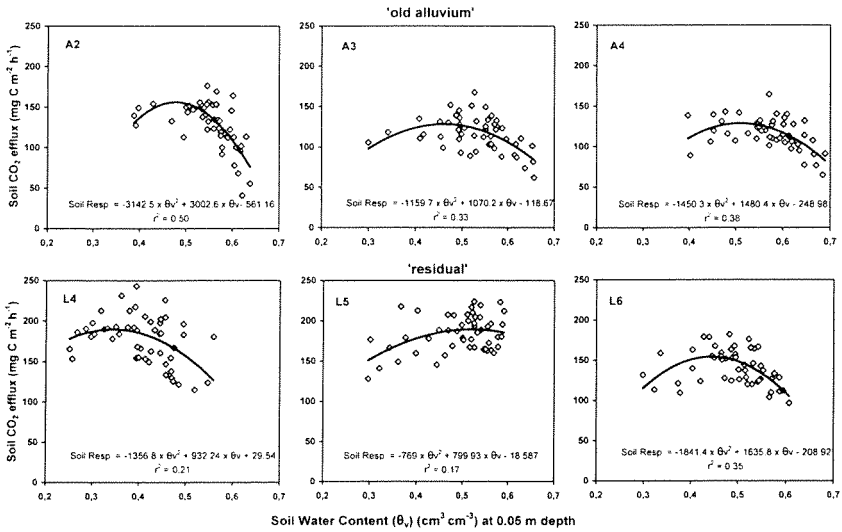

Figure 3. Relationship between soil water content and soil CO_2 efflux. Each estimate of soil CO_2 efflux is a mean of 8 chamber measurements and one soil water measurement at 0.05 m depth made on a given date.

relationship between soil air CO_2 concentration, soil water content and CO_2 storage was different for the upper and lower soil profile. In the upper profile changes in CO_2 storage were mainly due to changes in CO_2 concentration. No correlation was found between soil moisture content and CO_2 storage. In contrast, below one meter changes in CO_2 storage cannot be explained by variations in CO_2 concentration but by changes in soil air space.

The apparent effect of temperature on soil CO_2 efflux (parabolic function with an optimum at around 24 °C) is probably the result of the covariance between soil temperature and soil water content. At 'old alluvium' sites (at 0.05 m depth) soil temperature and soil water content were negatively correlated across seasons (Figure 4). The same pattern was observed for 'residual' sites (wet season and drier season $r^2 = 0.33$) although the soil (at 0.05 m depth) at these sites was significantly warmer and drier than at the 'old alluvium' sites. In general, both soil types were wetter but warmer ($P < 0.05$) during wet season (Figures 1 and 4). Exceptionally high temperatures (> 26 °C) and comparatively low soil water contents were observed in May 1998 (Figure 1). This was probably caused by the occurrence of an El Niño Southern Oscillaton (ENSO) drought cycle in 1997/1998.

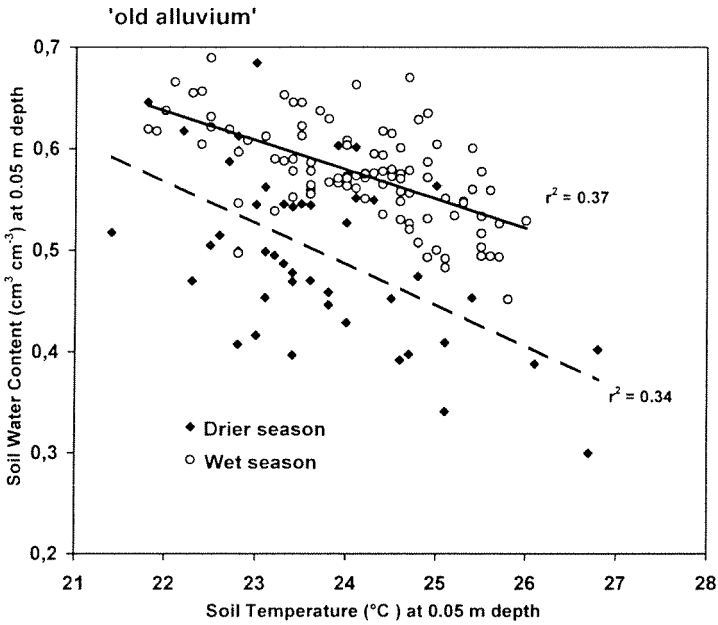

Figure 4. Covariation of soil temperature with soil water content at 0.05 m depth for 'old alluvium'. Each point represents individual soil temperature and soil water measurements made at all 'old alluvium' sites on a given date.

Discussion

Spatial variation and magnitude of CO_2 efflux

The two-year average CO_2 flux from 'residual' plots was about 40% higher than that from 'old alluvium' plots (Figure 1, Table 2a). These weathered 'residual' sites have a significantly higher amount of fine roots (DA Clark, unpublished data) and greater numbers of arbuscular mycorrhizal fungal spores (C Lovelock, unpublished data). This finding indicates that root respiration may explain part of the differences of soil CO_2 efflux and that root biomass gave a good reflection of root respiration. Previous research has suggested that roots/rhizosphere contribute 30 to 70% to total soil CO_2 efflux and that the release of CO_2 from the soil generally increases with increase in root/rhizosphere biomass (Epron and Badot 1997; Janssens et al. 1998; Hanson et al. 2000). Furthermore, soil CO_2 efflux and fine root biomass were negatively correlated with the soil phosphorus level (DA Clark, DB Clark, E Veldkamp, unpublished data). We suggest that more fine roots were accumulated in the 'residual' sites in order to provide enough phosphorus for tree physiological processes and that mycorrhizal associations might have the potential to increase the uptake of phosphorus at sites with low soil P levels. A positive correlation was

Table 3. Correlations of biotic and abiotic factors with soil CO_2 efflux. The analysis (Pearson product-moment correlation) is based on the data from the six study sites.

Factors	r	P
Total C (%)	0.70	ns[1]
Total N (%)	0.72	ns
Total P (mg g^{-1})	−0.60	ns
Soil water content at 0.05 m depth (cm^3 cm^{-3})	−0.81	*[2]
Soil air space (cm^3 cm^{-3})	0.67	ns
Soil temperature at 0.05 m depth (°C)	0.41	ns

[1]Not significant, $P > 0.05$
[2]Significant, $P < 0.05$

found between CO_2 efflux and soil carbon and nitrogen concentrations. In addition to these nutrient-related parameters, part of the site-specific differences in soil CO_2 efflux may also be explained by the spatial variance in soil water content. However, none of these trends was significant at $P < 0.05$, most likely because of the high variability within the relatively small data set ($n = 6$) (Table 3).

CO_2 efflux measured in this study (10.0 to 16.6 Mg C ha^{-1} yr^{-1}) were consistent with the range reported by Raich and Schlesinger (1992) for tropical moist/humid forests (8.9 to 15.2 Mg C ha^{-1} yr^{-1}). Higher CO_2 flux rates than ours were reported for an old-growth forest in eastern Amazonia where the CO_2 efflux was 20 Mg ha^{-1} yr^{-1} (Trumbore et al. 1995; Davidson et al. 2000). We didn't find a difference in the magnitude of soil CO_2 efflux between the wet and drier season. Other studies from tropical wet forest show a clear seasonal trend with lower CO_2 emission during dry hot periods (Feigl et al. 1995; Rajvanshi and Gupta 1986). The difference may be because our sites received during the time investigated more than 100 mm of precipitation each month even during the drier season. Our estimate of soil CO_2 emission was approx. 45% lower than the estimate reported by Raich (1980) for La Selva. He measured an average of 19 Mg C ha^{-1} yr^{-1} for May/July based on the soda-lime absorption technique ($n = 6$) in a mature forest site on old alluvial material. The use of a different methodology for soil CO_2 efflux, as well as the high spatial heterogeneity were most likely the reasons for this difference.

Temporal variation in soil CO_2 efflux and soil CO_2 storage

Fluctuations in CO_2 emission and CO_2 storage between sampling days, most likely due to short-term weather conditions, were overlaid by some distinctive seasonal trends. Soil CO_2 efflux rates increased at the onset of the wet season. Flushes of CO_2 following the re-wetting of soil have frequently been observed and are caused by pulses of microbial activity (Birch 1958; Orchard and Cook 1983; Kieft et al. 1987) or due to the CO_2 displacement in the soil by rain water (Singh and Gupta 1977). However, with the wet season well underway the efflux of CO_2 from the soil surface steadily decreased at all sites, reaching minimum CO_2 emission rates

at the end of the wet season. Increases in soil moisture content may decrease CO_2 production in the soil and also cause a decrease in CO_2 flux from the soil surface. Although the CO_2 concentration in the upper profile increased, the CO_2 efflux decreased. This indicates that the CO_2 exchange between soil and atmosphere was reduced due to lower diffusion rates caused by high soil water content. However, the contribution of CO_2 storage to the efflux is comparatively small. The amount of CO_2 stored in the whole soil profile (approx. 1200 mg m^{-2}) is only 7 to 10 times higher than the CO_2 efflux per hour. We also calculated the rate of CO_2 accumulation/loss (in mg m^{-2} h^{-1}) by interpolating the increase/decrease of storage which took place over a two-week period, assuming a uniform linear change between sampling dates. This rate was then compared to the observed surface flux rate on a given date. For the upper soil profile the CO_2 storage term would only account for 0.1 to 2% of the flux rate. Thus, diffusion and storage cannot solely explain the observed decline of CO_2 efflux. We suggest that CO_2 production was also reduced during the course of the wet season. The production of CO_2 from decay of organic matter could be inhibited either by oxygen limitation and/or temperature. In addition, several other factors have to be considered. Temporal changes in litterfall and root biomass may play an important role explaining seasonal variation in soil CO_2 efflux. Wofsy et al. (1988) attributed lower soil CO_2 efflux from an Amazonian forest during wet season to lower solar flux rates, which could affect photosysnthetic rates. Reduction of overall photysynthesis may also lead to lower root respiration rates. At La Selva lower solar flux rates are measured during months with higher average precipitation rates and, hence, higher persistent cloud cover (Sanford et al. 1994).

The increase in CO_2 flux and the decline of soil air CO_2 concentration and CO_2 storage in the upper profile at the onset of the drier season were probably due to soil drying which opens soil macropores and thus enhanced release of CO_2 that was accumulated in the soil during wet season. Increases in CO_2 efflux at the onset of the dry season could not be attributed to the emission of CO_2 stored in deeper layers as the amount of CO_2 stored below one meter was low during the wet season and at the onset of the drier season.

Effects of soil temperature and soil water content on soil CO_2 efflux

The relationship between soil CO_2 efflux, soil temperature and soil water content involves complex interactions depending on the relative limitation of temperature and moisture to both microbial and root activity as well gas diffusion. However, the importance of each factor varies among ecosystems and different environments. Temperature has been found to explain much of the variance in soil CO_2 efflux in temperate or boreal environments. The strong relationship between fluxes of CO_2 and temperature is not unexpected in these ecosystems since soil CO_2 efflux reflects heterotrophic and autotrophic activities and variations in temperature are high. In contrast, soil moisture is the major controlling variable during periods of very wet/dry conditions or in regions where soil temperatures are high and relatively invariable (Schlesinger 1977; Rout and Gupta 1989; Holt et al. 1990; Davidson et

al. 2000). Soil temperature of the La Selva sites are isothermic (Sanchez 1976); thus, its average monthly changes may be too small to be detected in the soil CO_2 efflux signal. Furthermore, the influence of temperature on temporal variation in CO_2 efflux was masked by the effect of soil water, which may have led to a weaker relationship between soil CO_2 release and soil temperature. Hence, it is not surprising that on both investigated soil types temporal variation in soil CO_2 efflux was primarily controlled by soil water content. A parabolic function has also been used by others to describe the relationship between soil CO_2 efflux and soil moisture (Ino and Monsi 1969; Edwards 1975; Londo et al. 1999). This reflects the general observation that CO_2 flux declines in both saturated and in very dry soils. Matric potential can be used as an indicator of water availability to plant roots and soil microorganisms (Skopp et al. 1990). We found a decrease in CO_2 efflux when the matric potential fell below –0.01 MPa ('old alluvium' site A4) and –0.03 MPa ('residual' site L6), respectively. In April and May 1998, at the end of the El Niño Southern Oscillaton (ENSO) drought cycle 1997/1998, matric potential exceeded –0.25 ('old alluvium' site A4) and –0.93 MPa ('residual' site L6). The constraints on soil CO_2 efflux may have resulted from reduced microbial activity owing to low soil moisture. According to Wong and Griffin (1976) bacterial activity declines sharply as water potential falls (–0.05 to –0.3 MPa) and is negligible at –1.5 MPa as bacterial movement is largely restricted to water films in soil and bacteria can only remain active while nutrients are able to diffuse toward and waste products away from them. But not only microbial activity is controlling CO_2 production rates and soil CO_2 efflux. Root respiration has been estimated to account for 10 – 90% of total CO_2 emission (Medina et al. 1980; Behera et al. 1990; Hanson et al. 2000). Water limitation can inhibit root growth and affects root metabolism (Sandford and Cuevas 1996; Mulkey and Wright 1996). At all study sites a peak in dead fine root biomass was found during the El Niño Southern Oscillation (ENSO) drought cycle (DA Clark, unpublished data). Fine root mortality may also contribute to a decrease in root respiration during extraordinary dry periods. However, without direct studies on root and microbial moisture responses and estimates on the contribution of soil microbial and root respiration to total soil CO_2 efflux, it is impossible to make solid conclusions about the differing soil moisture responses across sites from our data alone. Although CO_2 efflux showed an optimum soil water content on all sites (except one site, L5), the water content and matric potential at which maximum CO_2 evolution occurred differed between 'old alluvium' and 'residual' sites. This could probably be due to site-specific soil characteristics which caused differences in porosity and tortuosity, influencing gas diffusion. For example, the upper profile (0 – 1 m depth) of the 'residual' sites had a significantly higher soil air space volume as compared to the 'old alluvium' sites (Table 1). Our sites at La Selva receive a considerably amount of rain and as a result the volumetric water content can reach levels where diffusion is inhibited due to water-filled pores, even though the soil is well aggregated and has a high porosity and infiltration rates (Sollins and Radulovich 1988). Whereas at other study sites very high or low soil water contents are restricted to a short period of time, at La Selva soil water resided at > –0.008 MPa for many weeks due to the perudic moisture regime.

Our CO_2 flux data represent an integrated measure of root and heterotrophic respiration as well as gas diffusion. All these processes may respond differently to biotic and abiotic factors. Thus, it is difficult to obtain a strong correlation between soil CO_2 efflux and a single factor. As expected, our study showed that in this wet tropical environment, soil water content explained a considerable amount of the seasonal variation in soil CO_2 efflux rates despite the fact that our sampling occurred across a large area with substantial spatial variation. During periods of high soil water content CO_2 efflux rates decreased, probably due to a lower diffusion rate. But diffusion and CO_2 storage cannot fully explain the observed pattern in CO_2 efflux. CO_2 production seemed also to be reduced during the course of the wet season.

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