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To cite this version:

Stahl, Burban, Goret, Bonal. Seasonal variations in stem CO2 efflux in the Neotropical rainforest of French Guiana. Annals of Forest Science, 2011, 68 (4), pp.771-782. 10.1007/s13595-011-0074-2 . hal-00930807

HAL Id: hal-00930807

https://hal.science/hal-00930807v1

Submitted on 11 May 2020

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Annals of Forest Science (2011) 68:771–782
DOI 10.1007/s13595-011-0074-2

ORIGINAL PAPER

Seasonal variations in stem CO_2 efflux in the Neotropical rainforest of French Guiana

Clément Stahl · Benoit Burban · Jean-Yves Goret · Damien Bonal

Received: 29 September 2010 / Accepted: 4 January 2011 / Published online: 27 May 2011
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Abstract
• ***Introduction*** Stem CO_2 efflux (E_s) is a significant component of total ecosystem respiration, but there is only scant information on seasonal variations in E_s in tropical rainforests and on the main factors explaining these variations.
• ***Methods*** We conducted a comprehensive 18-month study in French Guiana to try to better understand which environmental factors contribute to seasonal variations in E_s in two habitats differing in soil water conditions.
• ***Results*** In both habitats, large seasonal variations in E_s were observed for most trees. The main variations occurred during climatic transition periods and were consistent with seasonal variations in soil and total ecosystem respiration.
• ***Discussion*** Seasonal variations in atmospheric conditions, including air temperature, did not explain seasonal variations in E_s. In contrast, seasonal variations in surface soil water content clearly induced seasonal variations in E_s in each habitat. Both soil drought and flooded conditions induced a decrease in E_s.
• ***Conclusion*** Our results emphasize the need to integrate the influence of soil water content on E_s into global models that simulate the response of forest ecosystem fluxes to climate changes.

Handling Editor: Michael Tausz

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Keywords Tropical rainforest · Stem CO_2 efflux · Soil water content · *Terra Firme* forest · Seasonally flooded forest

1 Introduction

Tree stems are the largest component of living aboveground biomass responsible for carbon storage. Through secondary growth, carbon is stored in stems, but the stem surface also releases large amounts of carbon into the atmosphere through stem CO_2 efflux (E_s). Stem and branch respiration account for up to 37% of the total annual ecosystem respiration in temperate forests (Janssens et al. 2001), 10% in dry Mediterranean forests (Maseyk et al. 2008), and about 13% in Neotropical rainforests (Cavaleri et al. 2008; Chambers et al. 2004).

In Neotropical rainforests, large seasonal variations in total ecosystem respiration (R_{eco}, the sum of all the autotrophic and heterotrophic respiration components in the ecosystem) have been observed (Bonal et al. 2008; Hutyra et al. 2007). During dry periods, R_{eco} can decrease by as much as 30% (from 12.0 to 9.0 g_C m^{-2} day^{-1} in French Guiana; Bonal et al. 2008) in association with a large decrease in soil respiration (Bonal et al. 2008; Davidson et al. 2000). However, whether seasonal variations in E_s also contribute to seasonal variations in R_{eco} remains unknown. To date, contrasting seasonal patterns in E_s have been observed in Neotropical sites: a slight decrease in E_s was found during the dry season in Brazil (Nepstad et al. 2002); higher E_s values were observed during the dry and warm seasons at low altitudes in Tropical mountain forests in Ecuador (Zach et al. 2010b); no seasonal changes were observed in tropical lowland forests in Costa Rica (Cavaleri et al. 2006).

In temperate forests, the main abiotic factor contributing to seasonal variations in E_s is air temperature, and an exponential relationship is usually observed (Ceschia et al. 2002; Damesin et al. 2002). However, in Neotropical regions, seasonal variations in daily mean air temperature are slight (24.5–27.0°C; Bonal et al. 2008) and therefore are unlikely to explain seasonal variations in E_s. Zach et al. (2008, 2010b) confirmed that the influence of seasonal variations in temperature on E_s was negligible in a Tropical mountain forest in Ecuador. However, considerable seasonal variations in rainfall, air humidity, and to a lesser extent solar radiation do occur in Neotropical regions (e.g., Bonal et al. 2008). These variations lead to large seasonal variations in soil water content (Bonal et al. 2000a, b, 2008; Guehl 1984), which influences soil respiration or R_{eco} (Bonal et al. 2008; Davidson et al. 2000; Sotta et al. 2006) and emissions of methane, nitrous oxide, and nitric oxide from soils (Davidson et al. 2008). Under controlled conditions, simulated soil drought conditions were shown to contribute to a decrease in E_s on young temperate trees (Saveyn et al. 2007). Yet, no clear evaluation of the influence of seasonal variations in environmental factors on E_s has been conducted in Neotropical forests. The objective of this study was to characterize which environmental determinants help explain seasonal variations in E_s in a Neotropical rainforest in French Guiana. We conducted a comprehensive sampling of tree stem CO_2 efflux over 18 months encompassing large seasonal variations in climatic conditions.

Neotropical rainforests are also characterized by substantial spatial heterogeneity in soil conditions and topography, which results in large habitat gradients (Baraloto et al. 2007; Epron et al. 2006; Ferry et al. 2010). These gradients induce specialization of the tree species, particularly with regards to soil drought or flooded conditions (Baraloto et al. 2007). The influence of soil drought or flooded conditions on leaf gas exchange (e.g., Baraloto et al. 2007; Fernandez et al. 1999), tree transpiration (Bonal et al. 2000b), or tree growth (e.g., Baker et al. 2003) in tropical rainforests has been widely studied. A decrease in CO_2 and H_2O fluxes or in overall tree growth was generally observed. However, no studies have yet investigated whether Neotropical tree species living in habitats with contrasted soil water conditions display contrasted E_s and encounter distinct seasonal variations in E_s.

In this study, we hypothesized that seasonal variations in climatic conditions in the Neotropical rainforest in French Guiana would influence stem CO_2 efflux (E_s). We expected maximum values in E_s during periods with non-limiting soil water content and a decrease in E_s during periods of soil drought. We also hypothesized that contrasted seasonal patterns in E_s would be observed in *Terra Firme* forests (TFF) and in seasonally flooded forest (SFF); we expected no major difference in E_s between the two habitats under non-limiting soil water conditions, but large differences when these habitats encounter soil drought or flooded conditions. Furthermore, we expected no major influence of atmospheric conditions (air temperature, air humidity, solar radiation) on E_s.

2 Materials and methods

2.1 Study site

This study was conducted at Paracou, French Guiana, South America (5°16′54″N, 52°54′44″W), where the tropical wet climate is highly seasonal due to the north/south movement of the Inter-Tropical Convergence Zone (Fig. 1). This zone brings heavy rains when it is above French Guiana (December to February and April to July).

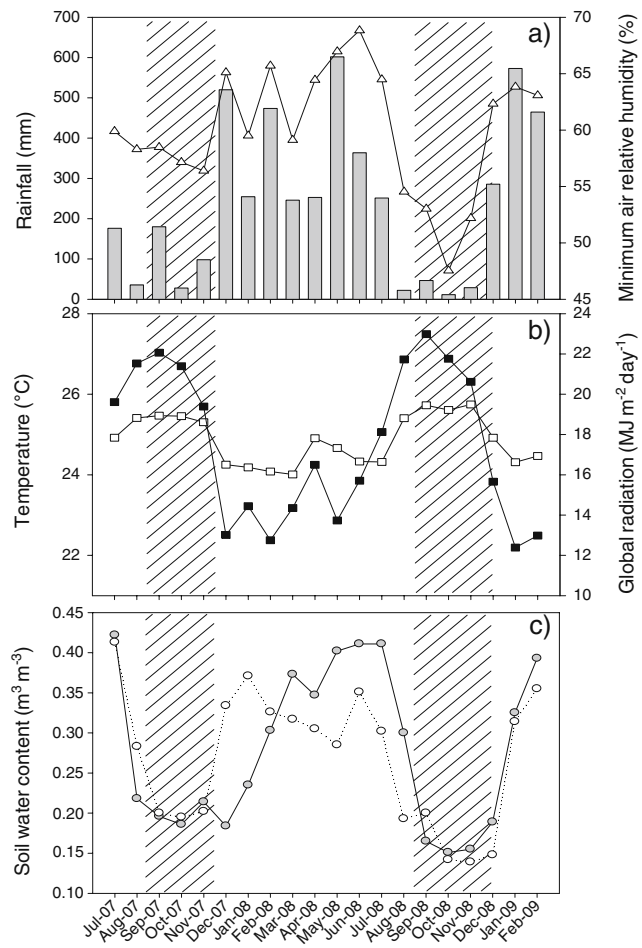

Fig. 1 Seasonal variations in climatic variables over the study period. **a** Monthly sum of rainfall (*bars*) and mean of daily minimum air relative humidity (*open triangle*), **b** monthly sum of global radiation (*closed squares*) and mean of air temperature (*open squares*), and **c** surface soil water content (SWC) in *Terra Firme* forest (TFF, *open circles*) and seasonal flooded forest (SFF, *gray circles*) at 20 cm. The *hatched areas* correspond to the long dry seasons in 2007 and 2008

When the Zone moves south of French Guiana, a short dry period (March) results and when it moves north, a long dry period (August to November) results (a dry month is defined as having less than 100 mm of rain).

Over the past decade, the average annual rainfall at our study site was 3,041 mm and the average air temperature was 25.7°C (Gourlet-Fleury et al. 2004). The site is located in the northernmost part of a region on the Guiana Plateau characterized by a succession of small, elliptical hills rising to 5–40 m a.s.l., sometimes associated with plateaus of similar altitude. The soils are mostly nutrient-poor acrisol (FAO-ISRIC-ISSS 1998) with pockets of sandy ultisols developed over a Precambrian metamorphic formation called the "Bonidoro series" and composed of schist and sandstone, sporadically traversed by veins of pegmatite, aplite, and quartz.

The studied ecosystem is considered to be pristine, tropical wet forest. Tree density averages 620 trees ha^{-1} (diameter at breast height>0.1 m) and tree species richness is about 140 species ha^{-1} (Bonal et al. 2008). Mean tree height is 35 m, with emergent trees exceeding 40 m. Measurements were conducted in two of the ten inventory plots that were set up in 2003 in the footprint of the Guyaflux eddyflux tower (Bonal et al. 2008). In order to study the influence of habitat conditions on E_s, one plot (0.98 ha) was located on *Terra Firme* forest (TFF) and the other (0.49 ha) on seasonally flooded forest (SFF). The two plots are 200 m apart. Vegetation and soil characteristics in the two plots are given in Table 1. The mean altitude in the TFF plot is 40 m a.s.l. while it is 5 m in the SFF plot. The TFF plot experiences no flooding conditions during the rainy season and trees have no access to the riparian water table during the dry season (Ferry et al. 2010). The SFF plot experiences seasonal inundation during the rainy season and the permanent water table is never below 1.2 m depth during the dry season (Fig. 2). The floristic composition in the two plots is highly different: 33 species (only 17% of the total number of tree species in the two plots combined) were common to both plots, and only four of those species were represented by at least three individuals in each plot (*Carapa procera*, *Eperua falcata*, *Eschweilera coriacea*, *Symphonia* sp.). Except for floristic composition and soil properties, the other stand characteristics were relatively similar in both plots (Table 1).

Table 1 Vegetation and soil characteristics in the two plots in French Guiana representing *Terra Firme* forest (TFF) or seasonally flooded forest (SFF)

	TFF	SFF
Vegetation		
Basal area (m^2 ha^{-1})	34.83	31.81
Stand density (tree ha^{-1})	700	596
Number of species	114	73
Leaf area index (m^2 m^{-2})	5.9±0.3	6.4±0.3
Litterfall (t_C ha^{-1} $year^{-1}$)	6.1±1.2	7.8±1.7
Soil		
Clay content (%)	24.4±3.1	12.8±2.1
P content (mg kg^{-1})	4.4±0.4	8.0±0.7
C/N	16.2±0.4	15.8±0.5
pH	4.6±0.0	4.7±0.1

Soil characteristics are from Ferry et al. (2010) obtained in nearby plots at Paracou. Only trees with a DBH >0.1 m are included

2.2 Environmental conditions

In order to test whether or not climatic conditions contributed to seasonal variations in E_s, we used data from a complete automatic weather station atop the Guyaflux tower to calculate the daily sum of solar radiation and rainfall, and data from a temperature and humidity sensor located 2-m high in the forest understory near the tower to calculate daily mean air temperature and daily minimum air humidity (see Bonal et al. 2008 for more details on sensors). Daily minimum air humidity was preferred over daily mean humidity because the former variable enables a better characterization of seasonal variations in daily atmospheric water deficit. In order to characterize seasonal variations in daily mean volumetric soil water content (SWC, m^3 m^{-3}) in the upper soil layer, we used data from soil water content sensors set up by Bonal et al. (2008) in 2003 in these plots. They inserted 3-m-long polycarbonate tubes (Tecanat™ tubes; SDEC France, Reignac, France) with an external diameter of 42 mm into holes bored using a 40-mm auger. The tubes were sealed at the base and could be opened at the top to insert a probe. In the SFF plot, the tubes could not be inserted deeper than 1.3 m because of the presence of the permanent water table. Soil water content measurements were taken every 0.2 m in each tube using a time domain reflectometry probe (TRIME FM3; Imko, Ettlingen, Germany).

This study began in September 2007 and lasted 18 months, encompassing substantial seasonal variations in climate (Fig. 1, Table 2). In 2007, the long dry season, with low soil water content (LDS07), lasted from September to the end of November (Fig. 1). A wetter season, with monthly rainfall sums higher than 200 mm, lasted from December 2007 to mid-July 2008. A period of lower rainfall punctuated this wetter season and was used to separate the dry-to-wet transition period (DW-T08; from December to February) from the long wet season (LWS08; from March to mid-July). We defined the period between mid-July and the end of August as the wet-to-dry transition period (WD-T08). During this period, heavy rainfall events

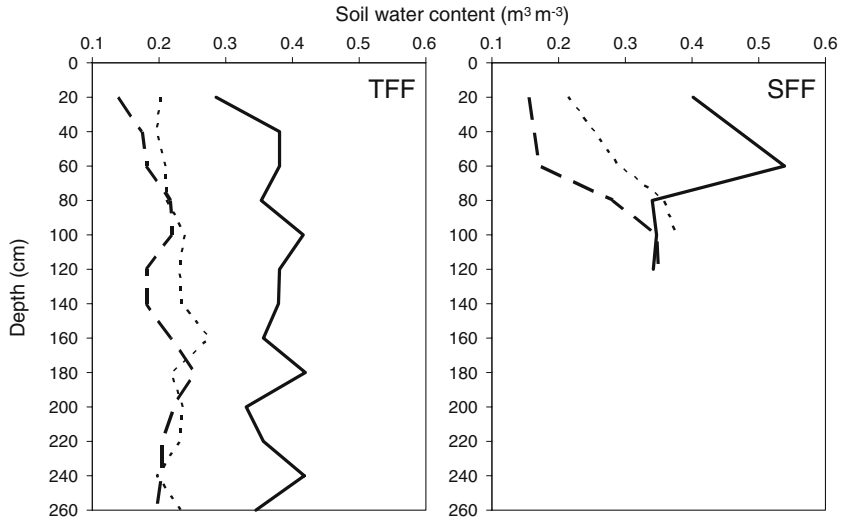

Fig. 2 Vertical profiles of soil water content (SWC) in *Terra Firme* forest (TFF) and seasonal flooded forest (SFF). Data presented are raw data measured at the end of three different seasons: end of the 2007 long dry season (*dotted line*), end of the 2008 long wet season (*solid line*), and end of the 2008 long dry season (*thick dashed line*)

were infrequent and soil water content in the upper layer decreased quickly (Fig. 1). In 2008, the long dry season (LDS08) went from the beginning of September and lasted until the 14th of December when heavy rainfall occurred. The 2009 dry-to-wet transition season (DW-T09) began in mid-December 2008 and continued until the end of February 2009. The 2007 long dry season was slightly wetter than the 10-year average and was considered to be a "La Niña" event (Fig. 1; NOAA 2009), whereas the 2008 long dry season was among the most severe in the past decade (Stahl et al. 2010).

2.3 Tree selection

We selected only dominant canopy trees whose crowns received at least some direct side light, i.e., Dawkins crown classification of 4 or 5 (Dawkins 1958). Measurements were taken on 95 trees the first year. The resulting dataset was augmented with 39 trees the second year in order to increase the number of individuals per species in TFF. Overall, we sampled 102 trees in TFF and 32 trees in SFF, for a total of 35 species (with one to 11 individuals per species). Growth and dynamic characteristics of the species

Table 2 Details of environmental parameters for each season over the study period: long dry season 2007 (LDS07), transition between the dry and the wet period 2008 (DW-T08), long wet season 2008 (LWS08), transition between the wet and the dry period 2008 (WD-T08), long dry season 2008 (LDS08), and transition between the dry and the wet period 2009 (DW-T09)

	Seasons					
	LDS07	DW-T08	LWS08	WD-T08	LDS08	DW-T09
Date	01/09/07–15/11/07	16/11/07–29/02/08	01/03/08–15/07/08	16/07/08–31/08/08	01/09/08–13/12/08	14/12/08–28/02/09
Duration (days)	76	106	137	47	104	77
Global radiation (MJ m^{-2} day^{-1})	21.6	14.0	15.4	20.9	21.3	13.2
Atmospheric pressure (mbar)	1,006.4	1,006.0	1,006.5	1,006.7	1,005.8	1,004.3
Air temperature (°C)	25.4	24.3	24.5	25.1	25.6	24.4
Minimum relative humidity (%)	64.9	76.6	76.7	70.2	63.3	80.9
Vapor pressure deficit (kPa)	10.4	7.0	7.1	9.3	11.0	6.2
Maximum vapor pressure deficit (kPa)	15.5	10.3	10.8	15.4	16.7	10.2
Rainfall (mm)	218.3	1,336.2	1,549.4	188.0	112.0	1,200.2
Wind direction (°)	123.1	92.2	109.3	139.7	127.2	132.2
Wind speed (m s^{-1})	2.8	3.1	2.7	2.6	2.7	2.2
Soil water content (m^3 m^{-3}) TFF	0.19	0.33	0.35	0.19	0.14	0.35
Soil water content (m^3 m^{-3}) SFF	0.14	0.30	0.41	0.30	0.15	0.37
Soil temperature (°C) (TFF)	25.5	24.9	24.8	25.2	25.6	25.0

Daily means of each parameter are represented, except for rainfall (sum). Minimum relative humidity and temperature were recorded at 2-m high. Soil water content and temperature were recorded at a depth of 0.2 m

TFF Terra Firme forest, *SFF* seasonally flooded forest

sampled were quite different (Ollivier et al. 2007). Diameter at breast height (1.3 m from the ground; DBH) of the selected trees in the two habitats ranged from 14.1 to 83.7 cm.

2.4 Gas exchange measurements

The CO_2 efflux of the stem (E_s, μmol CO_2 m^{-2} s^{-1}) was measured using home-made transparent Plexiglas chambers applied temporarily to the stem surface and operated in a closed system. Transparent chambers could be used because the high leaf area index in these forests (≈6.0 m^2 m^{-2}, Table 1) allows very limited solar radiation to reach the ground (less than 10% at 2-m high, Baraloto et al. 2005), thus virtually eliminating any potential stem photosynthesis. Chambers were connected to a CO_2 infrared gas analyzer (IRGA, EGM1, or EGM4; PPSystems, Hitchin, UK). One week before each dry season measurement, the stems were gently brushed in order to remove algae, lichens, and skinned bark. A mark larger than the chamber size was painted on each stem in order to ensure that all further measurements were taken at the same position. The chambers were sealed to the bark using a malleable rubber sealant (Terostat-7; Teroson, Ludwisburg, Germany). In order to ensure air-tight closure of the chamber, straps were tied around the stem and the chamber. Two types of chambers were used: one with a volume of 1,403.2 cm^3 which covered 145.8 cm² of bark for large trees, and one with a volume of 286.8 cm^3 which covered 44.8 cm² for smaller trees. The measurements were carried out at DBH or 0.50 m above buttresses (up to a height of 3 m). The IRGA pump maintained a constant air flow (10^{-4} $m^3 min^{-1}$) in the system and a fan located inside the chamber mixed the air. Readings were taken every 5 s. CO_2 concentrations were recorded only when the initial concentration was close to the ambient level (380–450 ppm). To reduce the effect on the CO_2 efflux caused by the initial disturbance of pressing the chamber onto the trunk, data were recorded only between 100 and 205 s (i.e., over more than 1 min after installation). Measurements were recorded between 9 am and 4 pm. Quality checks were performed on these data and measurements were retained only when the coefficient of determination of the linear relationship between time and CO_2 concentration was higher than 97.0%. The CO_2 efflux (E_s), expressed on the basis of stem area, was then calculated based on the chamber volume (V_{ch}, l) and surface area (S_{ch}, m²) using the following equation:

$$E_s = \frac{\Delta[CO_2]}{\Delta t} * \frac{V_{ch}}{S_{ch}} * vol.mol * \frac{273}{273 + T°\text{air}},$$

where $\Delta[CO_2]/\Delta t$ is the CO_2 concentration increase during the 100–205-s period (ppm s^{-1}), vol.mol is the volume of a mole of CO_2 (0.044642 mol l^{-1}), and T°air (°C) is the temperature of the air recorded at 2-m high. The mean air temperature at 2 m for all measurements was 27.7±1.9°C (min=22.1°C and max=31.4°C, n=1,311).

Some studies have suggested that E_s accounts for only one part of total stem respiration because a substantial amount of locally respired CO_2 can be transported away from the place of measurement by the sap stream (e.g., Teskey et al. 2008). However, other studies have demonstrated the lack of correlation between E_s and sap flow density (e.g., Edwards and Wullschleger 2000) or have shown that E_s is mainly derived from the metabolism of external tissues (phloem and cambium) (Maier and Clinton 2006). We therefore carried out a preliminary test on a subsample (n=13) of sampled trees over 24 h to determine whether (1) there were daily variations in E_s, and (2) there was any relationship between E_s and sap flow density measured using thermal dissipation (Granier's type; Granier 1985) with 30-mm-long sensors (TDP-30; Dynamax Inc., Houston, TX, USA).

In order to study the seasonal variations in E_s, 11 campaigns were conducted over the 18-month period. The timing of the campaigns was based on observation of the variations in rainfall and surface soil water content (SWC) at the Guyaflux site. The percentage of variation in E_s within a given period (ΔE_s) was calculated as the difference between the E_s at the beginning and at the end of the given period divided by the E_s at the beginning of the given period.

2.5 Tree water status

In order to identify any potential influence of tree water status on E_s during periods of soil water deficit, we used a Scholander-type pressure chamber (model 1000; PMS Instruments, Corvalis, OR, USA) to determine predawn leaf water potential (Ψ_{pd}) on one leaf per tree in each dry season on similarly clear days. In 2007, such measurements were conducted on 52 trees in TFF and 24 trees in SFF; in 2008, the measurements were conducted on 57 trees in TFF and 19 trees in SFF. Forty TFF trees and 19 SFF trees were common to the two dry-season leaf water campaigns.

2.6 Statistical analyses

2.6.1 Preliminary test

We used linear regression models (R 2.11.1, R-project software, http://www.r-project.org) to analyze (1) the relationship between daily variation in E_s and sap flow density in TFF, and (2) the relationship between predawn leaf water potential at the end of the 2008 long dry period and the variation of E_s (ΔE_s) during the wet-to-dry transition period (WD-T08) in each habitat.

2.6.2 Habitat effect

The influence of habitat on E_s for the four species that were abundant on both plots was tested for each species using a repeated measure ANOVA, with the different campaigns as repeated measures (proc MIXED, SAS 6.2, SAS Institute, Cary, NC, USA).

2.6.3 Seasonal variations in E_s

A linear mixed-effects model (lme, R 2.11.1) was used to detect seasonal patterns in E_s, with habitat and sampling time as a fixed effect and tree included as a random effect. A repeated measure analysis was used to test the percentage of variation in E_s (ΔE_s) during each period and for each habitat (proc MIXED, SAS). Following this test, a least squares mean analysis was used to test whether ΔE_s in each habitat and for each period was significantly higher or lower than zero. We also tested whether seasonal variations in maximum daily sap flow density were correlated with variations in E_s.

2.6.4 Environmental effect on seasonal variations in E_s

Using a principal component analysis (PCA), we tested the degree to which environmental variables co-varied over the study period (daily values) and whether one or two simple factors (1 or 2 axis) could be extracted from these variables. A repeated measure analysis was then used to test the effect of these factors on E_s in TFF, with trees included as a random effect and the different campaigns as repeated measures (proc MIXED, SAS). Finally, an analysis of covariance (lm, R 2.11.1) was used to test whether the relationship between E_s and SWC varied between habitats. In SFF, this test was conducted with or without outlier data (long wet season 2008, LWS08).

3 Results

As expected, we observed low seasonal variations in atmospheric pressure, air temperature, or soil temperature (Fig. 1, Table 2). However, this study encompassed large seasonal variations in global radiation, vapor pressure deficit, and rainfall that resulted in large seasonal variations in soil water content (SWC) in the two habitats (Fig. 2, Table 2). In TFF, SWC decreased strongly along the whole profile from the end of the wet season to the end of the dry period. On average, SWC was around 0.37 $m^3\ m^{-3}$ at the end of the wet season and 0.22 and 0.20 $m^3\ m^{-3}$ at the end of the dry season in 2007 and 2008, respectively. SWC values from the soil surface to 1.7-m depth were lower in 2008 than in 2007. In SFF, SWC values also strongly decreased from the wet to the dry season in the upper layers, but did not differ at deeper layers (below 0.8 m in depth). The permanent water table in SFF was around 0.8–1.0-m deep all year long. In SFF, during the dry periods, SWC values were always lower in 2008 than in 2007.

3.1 Preliminary test

We did not observe any clear daily variations in E_s for any of the selected trees, so we conducted all further measurements stochastically between 9 am and 4 pm. We found no significant relationships between daily variations in E_s and daily variations in sap flow density (All $p>0.10$; data not shown).

In TFF, predawn leaf water potential varied between −1.40 and −0.20 MPa in LDS07 and between −1.70 and −0.15 MPa in LDS08. In SFF, predawn leaf water potential was less negative: we observed a minimum of −0.65 and −0.40 MPa in LDS07 and LDS08, respectively. There was no significant effect of Ψ_{pd} in the 2008 long dry period on the variation of E_s (ΔE_s) during the wet-to-dry transition period (WD-T08) in either habitat ($p>0.10$; data not shown).

In both habitats, large differences in E_s were found among species (Table 3). At the species level, in LWS08, E_s ranged from 0.91 to 4.04 μmol $CO_2 m^{-2}\ s^{-1}$ in TFF and 0.54 to 1.71 μmol $CO_2 m^{-2}\ s^{-1}$ in SFF. At the end of the long dry season in 2008, E_s ranged from 0.41 to 2.94 μmol $CO_2 m^{-2}\ s^{-1}$ in TFF and 0.39 to 2.01 μmol $CO_2 m^{-2}\ s^{-1}$ in SFF.

3.2 Habitat effect

Among the four species that were abundant in the two habitats, only *E. coriacea* presented a significant effect of habitat on E_s throughout the seasons ($p=0.04$) (Table 4). For the other species, there was no significant effect of habitat (All $p>0.10$).

3.3 Seasonal variations in E_s

We observed significant seasonal variations in E_s ($F=13.3$; $p<0.001$) and a significant interaction between habitat and sampling time ($F=2.4$; $p=0.008$), but no significant effect of habitat alone ($F=0.3$; $p=0.59$). In TFF, we observed maximum E_s values at the end of the long wet season followed by a sharp decrease from July 2008 to September 2008 (Fig. 3). The lowest values were found at the end of the dry seasons, followed by a sharp increase during the dry-to-wet transition period (Fig. 3). Values at the end of the dry season in 2007 and 2008 were not significantly different (Fig. 4). In SFF, we did not observe a clear peak in E_s at the end of the wet season as we did in TFF (Figs. 3 and 4).

The percentage of variation in E_s during a given period (ΔE_s) differed greatly among trees (Fig. 4), with positive

Table 3 Mean values of diameter at breast height (DBH), stem CO_2 efflux (E_s) in long wet season in 2008 (LWS08) and long dry season in 2008 (LDS08), and number of sampled trees per species (n) in the two plots in French Guiana representing *Terra Firme* forest (TFF) and seasonally flooded forest (SFF)

Species	Family	DBH (cm)	E_s (μmol CO_2 m^{-2} s^{-1})		n
			LWS08	LDS08	
TFF					
Aspidosperma album	Apocynaceae	29.3	1.91	2.31	1
Bocoa prouacensis	Papilionaceae	38.0±2.8	1.56±0.35	0.83±0.21	3
Carapa procera	**Meliaceae**	**34.8±4.2**	**1.00±0.15**	**0.67±0.12**	8
Chaetocarpus schomburgkianus	Euphorbiaceae	32.7±0.0	1.37±0.16	0.71±0.03	2
Chrysophyllum sanguinolentum	Sapotaceae	36.0±8.8	1.00±0.15	0.86±0.06	6
Dicorynia guianensis	Caesalpiniaceae	44.3±10.6	2.17±0.23	1.33±0.21	8
Eperua falcata	**Caesalpiniaceae**	**47.6±10.9**	**2.08±0.36**	**1.02±0.28**	**6**
Eschweilera coriacea	**Lecythidaceae**	**31.6±6.8**	**1.20±0.17**	**0.83±0.19**	**4**
Eschweilera sagotiana	Lecythidaceae	42.3±7.9	1.26±0.15	0.63±0.08	9
Goupia glabra	Celastraceae	75.5	1.70	1.45	1
Hirtella bicornis	Chrysobalanaceae	14.8	2.88	2.94	1
Iryanthera sagotiana	Myristicaceae	34.2	1.13	0.84	1
Lecythis poiteaui	Lecythidaceae	34.1	1.03	0.70	1
Lecythis zabucajo	Lecythidaceae	27.4	4.04	1.64	1
Licania alba	Chrysobalanaceae	34.8±3.7	1.40±0.25	1.06±0.02	3
Licania heteromorpha	Chrysobalanaceae	19.8±3.0	1.22±0.23	1.24±0.33	2
Licania membranacea	Chrysobalanaceae	34.8±4.0	1.25±0.22	1.45±0.24	3
Moronobea coccinea	Clusiaceae	52.9	2.01	0.77	1
Pradosia cochlearia	Sapotaceae	58.6±11.3	1.46±0.26	0.97±0.09	6
Recordoxylon speciosum	Caesalpiniaceae	44.7±3.6	1.59±0.18	1.17±0.29	7
Sloanea sp.	Elaeocarpaceae	47.7	0.94	0.76	1
Sterculia pruriens	Sterculiaceae	50.8	2.02	1.24	1
Swartzia polyphylla	Papilionaceae	48.3	1.15	0.41	1
***Symphonia* sp.**	**Clusiaceae**	**32.0±1.5**	**1.50±0.16**	**1.13±0.17**	**7**
Tapura capitulifera	Dichapetalaceae	42.6±5.6	1.07±0.29	0.75±0.01	2
Vantanea sp.	Humiriaceae	40.5	1.57	2.12	1
Virola michelii	Myristicaceae	34.6±4.4	1.49±0.23	0.89±0.11	5
Vouacapoua americana	Caesalpiniaceae	36.2±8.8	1.39±0.12	0.80±0.13	8
Xylopia nitida	Annonaceae	29.9	0.91	1.11	1
SFF					
Carapa procera	**Meliaceae**	**29.0±14.9**	**1.15±1.30**	**0.96±0.31**	**3**
Cecropia obtusa	Cecropiaceae	29.3	0.54	0.39	1
Eperua falcata	**Caesalpiniaceae**	**34.0±3.4**	**1.15±0.28**	**0.80±0.15**	**5**
Eschweilera coriacea	**Lecythidaceae**	**34.4±4.2**	**1.41±0.33**	**2.01±0.34**	**4**
Goupia glabra	Celastraceae	35.9	1.43	0.83	1
Moronobea coccinea	Clusiaceae	73.9	1.71	1.09	1
Recordoxylon speciosum	Caesalpiniaceae	38.7±5.1	1.60±1.03	1.11±0.31	2
Sloanea grandiflora	Elaeocarpaceae	27.1	0.95	0.93	1
Sterculia pruriens	Sterculiaceae	53.8±7.1	1.24±0.54	1.26±0.16	2
***Symphonia* sp.**	**Clusiaceae**	**65.2±17.5**	**1.13±0.11**	**1.08±0.16**	**4**
Tabebuia insignis	Bignoniaceae	34.6±8.3	0.85±0.10	0.51±0.10	5
Tapirira guianensis	Anacardiaceae	34.7	1.40	0.70	1
Virola surinamensis	Myristicaceae	64.2±12.3	1.36±0.35	1.41±0.13	2

Values are means±1 SE. Species in bold are those with three or more trees sampled for E_s measurements in the two plots

(increase) or negative (decrease) values in either season. Furthermore, there was a strong seasonal effect on ΔE_s (df= 490; F=14.7; p<0.001), with no significant effect of habitat (F=1.4; p=0.24), even though there was a significant interaction between habitat and seasons (F=3.1; p=0.009). In TFF, the mean pattern in ΔE_s was highly positive (i.e.,

Table 4 Effect of habitat type (*Terra Firme* forest, TFF, and seasonally flooded forest, SFF) on stem CO_2 efflux for the four species common to both habitats

Species	Number of trees		Habitat effect	
	TFF	SFF	*F*	*p* value
Carapa procera	8	3	1.30	0.28
Eperua falcate	6	5	1.73	0.23
Eschweilera coriacea	4	4	7.85	0.04
Symphonia sp.	7	4	0.01	0.94

The tests were conducted from the long wet season 2008 (LWS08) to the dry-to-wet transition period 2009 (DW-T09)

increase in E_s) during the two dry-to-wet transition seasons and during the long wet season ($p<0.001$); it was highly negative (i.e., decrease in E_s) during the wet-to-dry transition period ($p<0.001$), but it did not significantly differ from zero during the long dry seasons ($p=0.13$ and 0.63 in 2007 and 2008, respectively) (Fig. 4a). In SFF, the mean pattern in ΔE_s was highly positive (i.e., increase in E_s) during the two dry-to-wet transition seasons, whereas no significant effect was observed during the other seasons ($p>0.05$) (Fig. 4b). Among all the trees that displayed a decrease in E_s during LDS07, 54% in TFF also displayed a decrease or stable value during LDS08 as did 73% in SFF.

3.4 Environmental effect on seasonal variations in E_s

The first axis of the PCA analysis explained 75.0% of the variance (data not shown) and was strongly positively correlated with global radiation and air temperature and negatively correlated with rainfall and minimum relative humidity. We therefore conducted further analyses using the loadings of this "climatic factor" along this first axis. The second axis was strongly explained by surface soil water content and was characterized as a "soil water" axis. The multifactor model analyses showed that variations in E_s in

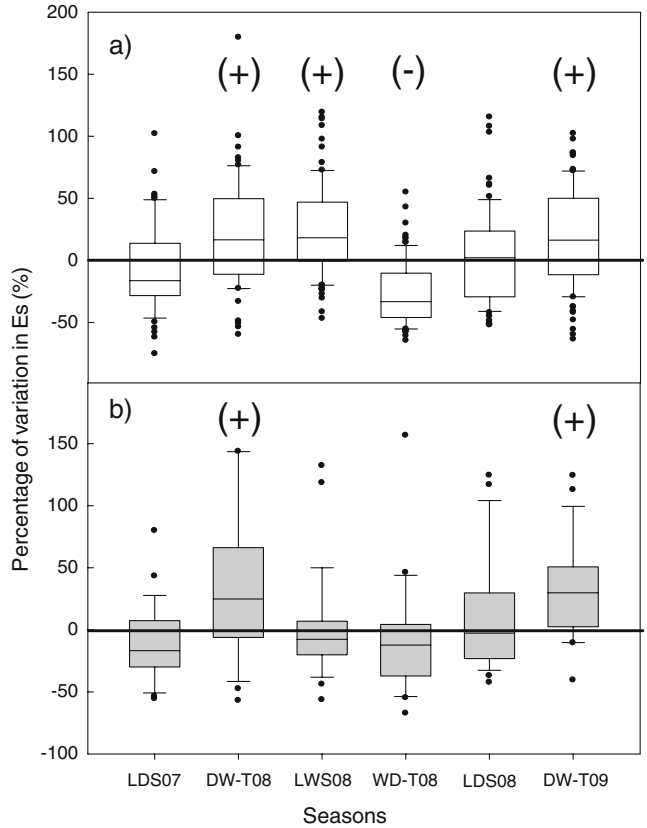

Fig. 4 Percentage of variation in E_s during a given period (ΔE_s) in (**a**) *Terra Firme* forest (TFF, *white box*) and (**b**) seasonally flooded forest (SFF, *gray box*): long dry season 2007 (LDS07), transition between the dry and the wet period 2008 (DW-T08), long wet season 2008 (LWS08), transition between the wet and the dry period 2008 (WD-T08), long dry season 2008 (LDS08), and transition between the dry and the wet period 2009 (DW-T09). The *symbols* denote the mean pattern in ΔE_s when it was significantly different from zero ($p<0.05$), i.e., increase (+) or decrease (−). Overall, there was a significant effect of seasons on ΔE_s ($df=490$; $F=14.7$; $p<0.001$) and a significant interaction between habitat and seasons ($F=3.1$; $p=0.009$), but no significant effect of habitat alone on ΔE_s ($F=1.4$; $p=0.24$)

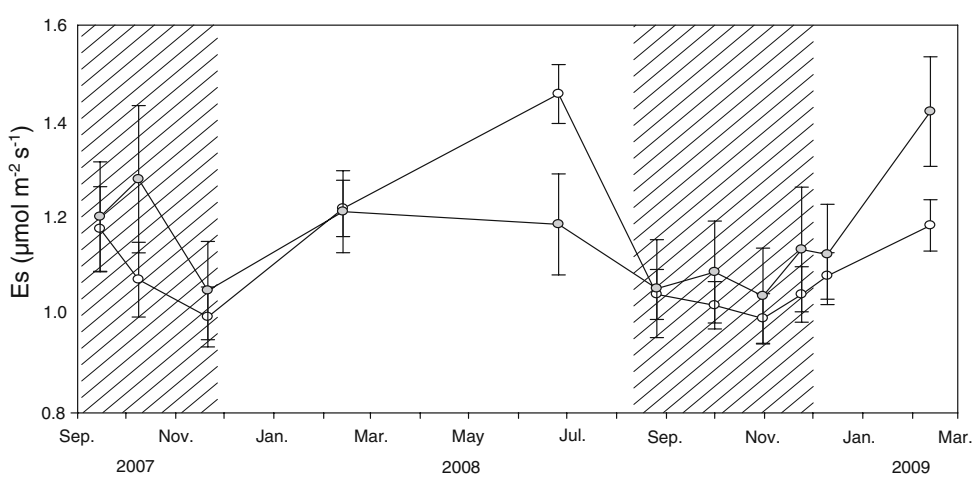

Fig. 3 Seasonal variations in stem CO_2 efflux (E_s) averaged over all trees in the *Terra Firme* forest (TFF, *open circles*) and the seasonally flooded forest (SFF, *gray circles*) (mean±SE). The *hatched areas* correspond to the long dry seasons in 2007 and 2008

TFF were significantly explained by the "soil water" axis (F=56.31, p<0.001) but not by the "climatic factor" axis (F=0.41, p=0.52).

We found a positive linear relationship between E_s and SWC in TFF (p=0.003, R^2=0.64) (Fig. 5). In SFF, this relationship was not significant when all the campaigns were included (p=0.09), but became significant when the long wet season (black square) was removed from the analysis (p=0.03, R^2=0.47). When this outlier point (the long wet season value) was removed, the slopes of the relationship between E_s and SWC in the two habitats were not significantly different (p=0.25).

4 Discussion

4.1 Between-tree variability

In the *Terra Firme* forest (TFF), under both non-limiting and limiting soil water conditions (wet season/dry season), a large variability in stem CO_2 efflux was observed among trees (Table 3); the range of E_s values was similar to previous observations made in tropical rainforest ecosystems (Cavaleri et al. 2006; Chambers et al. 2004; Meir and Grace 2002; Nepstad et al. 2002; Ryan et al. 1994; Zach et al. 2008, 2010b) and confirmed the large variability in functional characteristics observed to date for Neotropical rainforest species at the stem level (e.g., wood density—Patiño et al. 2008, bark thickness—Paine et al. 2010). In a study on functional explanations for variation in bark thickness in Neotropical trees, Paine et al. (2010) concluded there was no significant relationship between bark thickness and E_s. Whether other functional stem characteristics such as sapwood density and thickness account for part of the interspecific variability observed in E_s remains an open question.

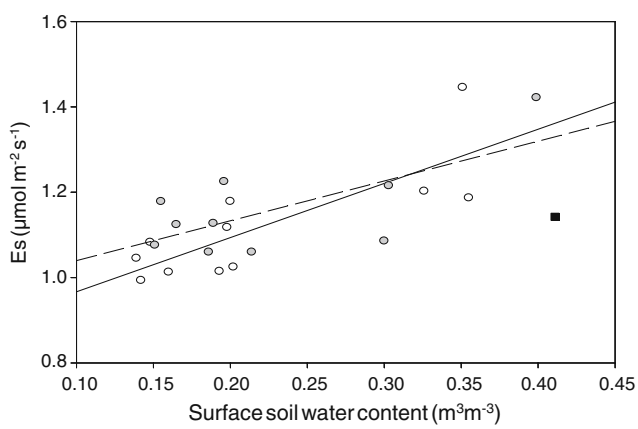

Fig. 5 Relationship between stem CO_2 efflux (E_s) and surface soil water content (SWC) in *Terra Firme* forest (TFF) (*open circles*) and seasonally flooded forest (SFF) (*gray circles*). Each *point* corresponds to the mean of each campaign. The *solid line* corresponds to the linear regression for all campaigns in TFF (p=0.003, R^2=0.64). There was no significant relationship between E_s and SWC for any campaigns in SFF (p=0.09). The *dashed line* corresponds to the linear regression for all campaigns in SFF when the value during the long wet season 2008 was excluded (*black square*) (p=0.03, R^2=0.47)

4.2 Habitat effect

For three of the four species abundant in both habitats, we observed no clear influence of habitat on E_s (Table 4). Our results thus suggest that these three species have generalist E_s characteristics with regards to soil water content. According to Baraloto et al. (2007), a large proportion of tropical rainforest species is found in a large range of habitats with different soil characteristics, and these species have a high plasticity in functional traits. For these three species here, our results suggest high plasticity in the physiological mechanisms associated with stem CO_2 efflux.

4.3 Seasonal variations

Large seasonal variations in E_s were found in both habitats (Figs. 3 and 4). Most trees displayed a strong decrease in E_s during the wet-to-dry transition period (85% and 59% of the trees in TFF and SFF, respectively), and either a slight decrease or rather constant values during the long dry seasons (Fig. 4). Furthermore, in both habitats, we observed a sharp increase in E_s for most trees (66% and 77% of the trees in TFF and SFF, respectively) at the onset of the dry-to-wet transition seasons (DW-T). Seasonal variations in E_s at our TFF site were within the same range of change as those observed in *Terra Firme* forests in Brazil (Nepstad et al. 2002). Nevertheless, our high sampling frequency allowed us to reveal that the fastest and most significant changes in E_s occurred during climatic transition periods, rather than during the dry or the wet seasons. These results underline the speed with which E_s processes respond to seasonal changes in rainfall regime. Interestingly, the timing of these changes was also consistent with seasonal changes in R_{eco} or soil respiration at the site (Bonal et al. 2008). This suggests that physiological mechanisms associated with autotrophic (stem, leaf, root) or heterotrophic (soil micro-organisms) CO_2 efflux in Neotropical forests may be subject to similar environmental constraints (see below). Nevertheless, it must be recalled that E_s accounts for only a small proportion of R_{eco} (≈9% in this study, and see Cavaleri et al. 2008) as compared to total soil respiration (≈40%, Bonal et al. 2008; Cavaleri et al. 2008) or leaf respiration (≈37%) (Cavaleri et al. 2008).

In SFF, seasonal patterns in E_s followed those in TFF, except during the long wet season when no major changes in E_s were observed in SFF (Fig. 4). We thus suspect that flooded conditions during the long wet season (Figs. 1 and 2) influenced tree stem CO_2 efflux (Table 4). When the

groundwater level is close to the surface (Fig. 2), soil hypoxic conditions might induce a decrease in metabolic processes associated with stem respiration, as previously observed for photosynthesis (Fernandez et al. 1999). The flooded conditions during the long wet season might thus have prevented any clear increase in E_s. To our knowledge, no study has yet directly tested the effect of hypoxic conditions on E_s. The main effect of flooded conditions on plant carbon metabolism is through the deprivation of oxygen to the root system, which usually leads to a decrease in carbon and energy metabolism at the whole plant level and can induce morphological or phenological adaptations (Parelle et al. 2006; Parolin 2001). Our results suggest that these same processes influence stem CO_2 efflux. Further studies to analyze the direct impact of hypoxic conditions on stem respiration processes are greatly needed.

4.4 Influence of biotic and abiotic factors

Seasonal variations in E_s could be explained by biotic or abiotic factors, or a combination of both. It has been shown that variations in biotic factors such as sap flow density (Teskey et al. 2008), bark photosynthesis (Damesin 2003), water status (Saveyn et al. 2007), or secondary growth (Damesin et al. 2002; Maseyk et al. 2008) could contribute to explaining seasonal variations in E_s in temperate or Mediterranean forests. In our study, daily variations in E_s were very small for all tested trees and did not correlate at all with the wide daily fluctuations in sap flow density. Thus, for these trees, even though a decrease in soil respiration during the dry season (Bonal et al. 2008) might have induced a decrease in CO_2 dissolved in the sap, our results confirm the absence of a direct impact of CO_2 dissolved in the sap on seasonal variations in E_s (Edwards and Wullschleger 2000). Nevertheless, our results do not preclude that part of the respired CO_2 could have been transported up the xylem stream with the sap flow (Teskey et al. 2008). Indeed, the diffusion of dissolved CO_2 outside the stem and the transport of CO_2 respired by the stem in the sap flow might balance out for these trees. We did not test whether bark photosynthesis could contribute to these changes because high leaf area index values and low solar radiation reaching the ground at the site (Baraloto et al. 2005) prevented any potential photosynthetic activity along the stem where E_s was measured. Seasonal variations in E_s could not be attributed to seasonal variations in tree water status either since the latter were relatively slight for the studied trees. These limited variations in tree water status are consistent with what was previously found at the site (Bonal et al. 2000b) or in other Neotropical rainforests (e.g., Fisher et al. 2006). Finally, we were not able to precisely evaluate the influence of seasonal variations in tree growth on E_s in this study. Stem circumference is strongly influenced by atmospheric air conditions and seasonal variations in daily minimum air humidity induce large seasonal variations in stem circumference (positive or negative effect on bark water content) (Stahl et al. 2010). Using seasonal variations in stem circumference (commonly measured using dendrometers) as a surrogate for seasonal variations in tree growth is thus not possible. Seasonal variations in cambial cell multiplication would have to be measured to test for any relationship between secondary growth and E_s, but this was beyond the scope of our study.

Among the abiotic factors tested, our study showed that atmospheric conditions did not explain seasonal variations in E_s. Particularly, in contrast with temperate forests (Ceschia et al. 2002; Damesin et al. 2002), air temperature was not a major cause of the seasonal variations in E_s in our Neotropical rainforest. One reason for this discrepancy lies in the limited seasonal range of daily mean temperatures observed in French Guiana (Fig. 1b, Table 2, Bonal et al. 2008). Furthermore, our results are consistent with Zach et al. (2010a) who suggested that daily variations in air temperature were poorly correlated with E_s in tropical forests. The other atmospheric conditions involved were closely correlated with air temperature and none contributed to seasonal variations in E_s.

In contrast, the amount of water available to the trees in the surface soil layer was strongly correlated with seasonal variations in E_s (Fig. 5). In both habitats, the decrease in soil water content during the dry season was the main cause of variations in E_s. Additionally, in SFF, hypoxic conditions prevented high E_s values during the long wet season. Our results therefore suggest that soil water content in the upper layer is the main abiotic determinant of seasonal variations in E_s in both habitats. The direct mechanisms explaining the correlation between soil water content and E_s have not yet been studied, but physiological processes associated with both maintenance and growth respiration could be affected by variations in SWC (Saveyn et al. 2007). We also suspect that the origin of the reverse seasonal patterns in E_s observed for some trees (i.e., an increase during dry seasons; Fig. 4) could be associated with deeper rooting systems (Nepstad et al. 1994; Bonal et al. 2000a) that allow them to avoid the detrimental effects of a decrease in surface SWC during long dry seasons.

In conclusion, our results show large seasonal variations in E_s for most trees in either habitat. The main variations occurred during climatic transition periods, which was consistent with the timing of seasonal variations in soil and total ecosystem respiration observed at the site. Seasonal variations in atmospheric conditions, including air temperature, did not explain seasonal variations in E_s. In contrast, seasonal variations in surface soil water content were clearly correlated to seasonal variations in E_s in each habitat. Both soil drought and flooded conditions induced a decrease in E_s.

Our results emphasize the need to integrate the influence of soil water content on E_s in global models designed to simulate the response of forest ecosystem fluxes to climate change.

Acknowledgments We thank J. Cazal, F. Bompy, J. Cigna, Z. Colin, C. Hequet, and J. Sermage for their help in the measurements of stem efflux and sap flow density, and P. Benavides for his help in making the respiration chambers. We thank J. Beauchêne and B. Thibaut for fruitful discussions. We also thank C.E.T. Paine and V. Moore who greatly improved this manuscript and two anonymous reviewers. C. Stahl received an assistantship from CNRS (50%) and INRA (50%). The ORE "Ecosystèmes Forestiers" managed by GIP–Ecofor contributed to the funding of these experiments.

References

Baker TR, Burslem DFRP, Swaine MD (2003) Associations between tree growth, soil fertility and water availability at local and regional scales in Ghanaian tropical rain forest. J Trop Ecol 19:109–125

Baraloto C, Goldberg DE, Bonal D (2005) Performance trade-offs among tropical tree seedlings in contrasting microhabitats. Ecology 86:2461–2472

Baraloto C, Morneau F, Bonal D, Blanc L, Ferry B (2007) Seasonal water stress tolerance and habitat associations within four Neotropical tree genera. Ecology 88:478–489

Bonal D, Atger C, Barigah TS, Ferhi A, Guehl J-M, Ferry B (2000a) Water acquisition patterns of two wet tropical canopy trees of French Guiana as inferred from $H_2{}^{18}O$ extraction profiles. Ann For Sci 57:717–724

Bonal D, Barigah TS, Granier A, Guehl J-M (2000b) Late stage canopy tree species with extremely low $\delta^{13}C$ and high stomatal sensitivity to seasonal soil drought in the tropical rainforest of French Guiana. Plant Cell Environ 23:445–459

Bonal D, Bosc A, Ponton S, Goret J-Y, Burban B, Gross P, Bonnefond J-M, Elbers J, Longdoz B, Epron D, Guehl J-M, Granier A (2008) Impact of severe dry season on net ecosystem exchange in the Neotropical rainforest of French Guiana. Glob Chang Biol 14:1917–1933

Cavaleri MA, Oberbauer SF, Ryan MG (2006) Wood CO_2 efflux in a primary tropical rain forest. Glob Chang Biol 12:2442–2458

Cavaleri MA, Oberbauer SF, Ryan MG (2008) Foliar and ecosystem respiration in an old-growth tropical rain forest. Plant Cell Environ 31:473–483

Ceschia E, Damesin C, Lebaube S, Pontailler J-Y, Dufrêne E (2002) Spatial and seasonal variations in stem respiration of beech trees (*Fagus sylvatica*). Ann For Sci 59:801–812

Chambers JQ, Tribuzy ES, Toledo LC, Crispim BF, Higuchi N, dos Santos J, Araujo AC, Kruijt B, Nobre AD, Trumbore SE (2004) Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. Ecol Appl 14:S72–S88

Damesin C (2003) Respiration and photosynthesis characteristics of current-year stems of *Fagus sylvatica*: from the seasonal pattern to an annual balance. New Phytol 158:465–475

Damesin C, Ceschia E, Le Goff N, Ottorini J-M, Dufrene E (2002) Stem and branch respiration of beech: from tree measurements to estimations at the stand level. New Phytol 153:159–172

Davidson EA, Verchot LV, Cattânio JH, Ackerman IL, Carvalho JEM (2000) Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. Biogeochemistry 48:53–69

Davidson EA, Nepstad DC, Ishida FY, Brando PM (2008) Effects of an experimental drought and recovery on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest. Glob Chang Biol 14:2582–2590

Dawkins HC (1958) The management of tropical high forest with special reference to Uganda. Imperial Forestry Institute Paper 34

Edwards NT, Wullschleger SD (2000) Carbon dioxide efflux rates from stems of mature *Quercus prinus* L. and *Acer rubrum* L. trees do not appear to be affected by sapflow rates. J Sustain For 10:125–131

Epron D, Bosc A, Bonal D, Freycon V (2006) Spatial variation of soil respiration across a topographic gradient in a tropical rain forest in French Guiana. J Trop Ecol 22:565–574

Fernandez MD, Pieters A, Donoso C, Herrera C, Tezara W, Rengifo E, Herrera A (1999) Seasonal changes in photosynthesis of trees in the flooded forest of the Mapire River. Tree Physiol 19:79–85

Ferry B, Morneau F, Bontemps J-D, Blanc L, Freycon V (2010) Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. J Ecol 98:106–116

Fisher RA, Williams M, Do Vale RL, Da Costa AL, Meir P (2006) Evidence from Amazonian forests is consistent with isohydric control of leaf water potential. Plant Cell Environ 29:151–165

Gourlet-Fleury S, Laroussinie O, Guehl J-M (2004) Ecology and management of a Neotropical rainforest. Lessons drawn from Paracou, a long-term experimental research site in French Guiana. Elsevier, Paris, p 311

Granier A (1985) Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. Ann For Sci 42:193–200

Guehl J-M (1984) Dynamique de l'eau dans le sol en forêt tropicale humide guyanaise. Influence de la couverture pédologique. Ann For Sci 41:195–236

Hutyra LR, Munger JW, Saleska SC, Gottlieb E, Daube BC, Dunn AL, Amaral DF, De Camargo PB, Wofsy S (2007) Seasonal controls on the exchange of carbon and water in an Amazonian rain forest. J Geophys Res 112:G03008. doi:03010.01029/02006JG000365

Janssens IA, Kowalski AS, Ceulemans R (2001) Forest floor CO_2 fluxes estimated by eddy covariance and chamber-based model. Agric For Meteorol 106:61–69

Maier CA, Clinton BD (2006) Relationship between stem CO_2 efflux, stem sap velocity and xylem CO_2 concentration in young loblolly pine trees. Plant Cell Environ 29:1471–1483

Maseyk K, Grünzweig JM, Rotenberg E, Yakir D (2008) Respiration acclimation contributes to high carbon-use efficiency in a seasonally dry pine forest. Glob Chang Biol 14:1553–1567

Meir P, Grace J (2002) Scaling relationships for woody tissue respiration in two tropical rain forests. Plant Cell Environ 25:963–973

Nepstad DC, De Carvalho CR, Davidson EA, Jipp PH, Lefebvre PA, Negreiros GH, Da Silva ED, Stone TA, Trumbore SE, Vieira S (1994) The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature 372:666–669

Nepstad DC, Moutinho P, Dias-Filho MB, Davidson E, Cardinot G, Markewitz D, Figueiredo RO, Vianna N, Chambers J, Ray D, Guerreiros JB, Lefebvre P, Sternberg L, Moreira M, Barros L, Ishida FY, Tohlver I, Belk E, Kalif K, Schwalbe K (2002) The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest. J Geophys Res 107(D20):8085. doi:8010.1029/2001JD000360

NOAA (2009) National Weather Service, Maryland, USA. Available at http://www.cpc.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml

Ollivier M, Baraloto C, Marcon E (2007) A trait database for Guianan rain forest trees permits intra- and inter-specific contrasts. Ann For Sci 64:781–786

Paine CET, Stahl C, Courtois EA, Patiño S, Sarmiento C, Baraloto C (2010) Functional explanations for variation in bark thickness in tropical rain forest trees. Funct Ecol 24:1202–1210

Parelle J, Brendel O, Bodénès C, Berveiller D, Dizengremel P, Jolivet Y, Dreyer E (2006) Differences in morphological and physiological responses to water-logging between two sympatric oak species (*Quercus petraea* [Matt.] Liebl., *Quercus robur* L.). Ann For Sci 63:849–859

Parolin P (2001) Morphological and physiological adjustments to waterlogging and drought in seedlings of Amazonian floodplain trees. Oecologia 128:326–335

Patiño S, Lloyd J, Paiva R, Quesada CA, Baker TR, Santos AJB, Mercado LM, Malhi Y, Phillips OL, Aguilar A, Alvarez E, Arroyo L, Bonal D, Costa ACL, Czimczik CI, Gallo J, Herrera R, Higuchi N, Horna V, Hoyos EJ, Jimenez EM, Killeen T, Leal E, Luizão F, Meir P, Monteagudo A, Neill D, Núñez-Vargas P, Palomino W, Peacock J, Peña-Cruz A, Peñuela MC, Pitman N, Priante Filho N, Prieto A, Panfil SN, Rudas A, Salomão R, Silva N, Silveira M, Soares de Almeida S, Torres-Lezama A, Turriago JD, Vásquez-Martínez R, Schwarz M, Sota A, Schmerler J, Vieira I, Villanueva B, Vitzthum P (2008) Branch xylem density variations across Amazonia. Biogeo Discuss 5:2003–2047

Ryan MG, Hubbard RM, Clark DA, Sanford RLJ (1994) Woody-tissue respiration for *Simarouba amara* and *Minquartia guianensis*, two tropical wet forest trees with different growth habits. Oecologia 100:213–220

Saveyn A, Steppe K, Lemeur R (2007) Drought and the diurnal patterns of stem CO_2 efflux and xylem CO_2 concentration in young oak (*Quercus robur*). Tree Physiol 27:365–374

Sotta ED, Veldkamp E, Guimaraes BR, Paixao RK, Ruivo MLP, Almeida SS (2006) Landscape and climatic controls on spatial and temporal variation in soil CO_2 efflux in an Eastern Amazonian Rainforest, Caxiuana, Brazil. For Ecol Manag 237:57–64

Stahl C, Burban B, Bompy F, Jolin ZB, Sermage J, Bonal D (2010) Seasonal variation in atmospheric relative humidity contributes to explaining seasonal variation in trunk circumference of tropical rain-forest trees in French Guiana. J Trop Ecol 26:393–405

Teskey RO, Saveyn A, Steppe K, McGuire MA (2008) Origin, fate and significance of CO_2 in tree stems. New Phytol 177:17–32

Zach A, Horna V, Leuschner C (2008) Elevational change in woody tissue CO_2 efflux in a tropical mountain rain forest in southern Ecuador. Tree Physiol 28:67–74

Zach A, Horna V, Leuschner C (2010a) Diverging temperature response of tree stem CO_2 release under dry and wet season conditions in a tropical montane moist forest. Trees 24:285–296

Zach A, Horna V, Leuschner C, Zimmermann R (2010b) Patterns of wood carbon dioxide efflux across a 2,000-m elevation transect in an Andean moist forest. Oecologia 162:127–137