



## Spatial and temporal variations of soil respiration in a *Eucalyptus* plantation in Congo

Daniel Epron<sup>a,f,\*</sup>, Yann Nouvellon<sup>b,c</sup>, Olivier Roupsard<sup>c</sup>, Welcome Mouvondy<sup>b</sup>,  
André Mabilia<sup>b</sup>, Laurent Saint-André<sup>c</sup>, Richard Joffre<sup>d</sup>, Christophe Jourdan<sup>c</sup>,  
Jean-Marc Bonnefond<sup>e</sup>, Paul Berbigier<sup>e</sup>, Olivier Hamel<sup>c</sup>

<sup>a</sup>Laboratoire de Biologie et Ecophysiologie, Université de Franche-Comté, Pôle Universitaire,  
BP427, 25211 Montbéliard cedex, France

<sup>b</sup>UR2PI, BP 1291, Pointe-Noire, Congo

<sup>c</sup>CIRAD, 2477 Avenue Agropolis, 34398 Montpellier cedex 5, France

<sup>d</sup>CEFE, CNRS, 1919 route de Mende, 34293 Montpellier cedex, France

<sup>e</sup>INRA Bioclimatologie BP 81, 33833 Villenave d'Ornon cedex, France

<sup>f</sup>UMR INRA UHP 'Ecologie et Ecophysiologie Forestières', Université Henri Poincaré,  
54506 Vandoeuvre cedex, France

Received 30 December 2002; received in revised form 5 May 2004; accepted 8 July 2004

### Abstract

Our objectives were to quantify soil respiration in a 3-year-old *Eucalyptus* plantation in coastal Congo and to investigate both temporal and spatial variations of this major component of ecosystem respiration. Soil respiration exhibited pronounced seasonal variations that clearly reflected those of soil water content, with minimum values below  $1.6 \mu\text{mol m}^{-2} \text{s}^{-1}$  at the end of the dry season in September and a maximum value of  $5.6 \mu\text{mol m}^{-2} \text{s}^{-1}$  after re-wetting in December. An empirical model describing the relationship between soil respiration and soil water content predicts the seasonal variations in soil respiration reasonably well ( $R^2 = 0.88$ ), even if the effects of soil temperature and soil water content may be confounded since both factors co-vary across seasons. Spatial heterogeneity of soil respiration was clearly affected by management practices with higher respiration rate in slash inter-rows which received higher amounts of detritus at the logging stage, and lower respiration rate in haulage inter-rows used for heavy vehicle traffic. Higher values of soil respiration were also recorded in the vicinity of trunks than in the middle of the inter-rows. While soil water content is the main determinant of seasonal variation of soil respiration, it poorly accounts for its spatial variability over the experimental stand, except for days with low soil water content. Soil respiration was related neither to root biomass nor to soil carbon content, but was positively correlated with both leaf and total aboveground litter (i.e. leaf, bark and woody debris). Plots exhibiting the highest soil respiration also contained the highest amounts of aboveground litter. Microbial respiration associated with litter decomposition is likely a major component of soil

\* Corresponding author. Present address: UMR INRA UHP 'Ecologie et Ecophysiologie Forestières', Université Henri Poincaré, 54506 Vandoeuvre cedex, France. Tel.: +33 3 83 68 42 49; fax: +33 3 83 68 42 40.

E-mail address: [daniel.epron@scbiol.uhp-nancy.fr](mailto:daniel.epron@scbiol.uhp-nancy.fr) (D. Epron).

respiration, and the spatial heterogeneity in litter fall probably accounts for most of its spatial variability in this *Eucalyptus* plantation.

© 2004 Elsevier B.V. All rights reserved.

*Keywords:* Carbon flux; Eucalyptus; Forest plantation; Soil respiration; Spatial variation; Temporal variation

---

## 1. Introduction

The evaluation of biospheric fluxes and stocks of carbon is of major importance in the context of increasing CO<sub>2</sub> concentration in the atmosphere and the related potential change in climate. Carbon sequestration in forested ecosystems often results from a small difference between photosynthetic carbon fixation (gross primary production) and ecosystem respiration (Granier et al., 2000; Valentini et al., 2000). Soil is the biggest carbon pool of the continental biosphere (Schimel, 1995) and requires a particular attention, especially for short rotation plantation because it is a major compartment for durable carbon sequestration, the aboveground biomass being frequently removed and transformed into wood products with short life-times. While conversion of forest to pasture (Fearnside and Barbosa, 1998) or forest to tree plantation (Smith et al., 2002) often led to a net loss of soil carbon, more variable results have been collected for afforestation depending on previous land used, climate, soil type and planted species (Paul et al., 2002). For example, growing an *Eucalyptus* plantation (*E. camaldulensis*) over tropical savanna on sandy Entisol in Brazil led to a 17% decrease in soil organic carbon after one cycle whereas there was a slight increase observed on loamy Oxisol (Zinn et al., 2002). The soil texture and the ability of clay minerals to protect organic matter from microbial mineralisation are thought to affect carbon dynamics in afforested areas (Paul et al., 2002).

Soil respiration is one of the main components of ecosystem respiration (Granier et al., 2000; Janssens et al., 2001), and small changes in soil respiration may strongly affect soil carbon sequestration (Raich and Schlesinger, 1992). Therefore, it is important to obtain good estimates of soil respiration and to understand environmental controls on the underlying processes. Soil respiration is the sum of an autotrophic component by roots and the associated rhizosphere and a

heterotrophic component by soil micro-organisms that decompose the organic materials from both aboveground and belowground litter (Bowden et al., 1993; Boone et al., 1998; Epron et al., 1999b, 2001). Several factors may affect these two processes. Soil respiration exhibits a high spatial and temporal variability. Spatial heterogeneity of soil respiration has been related to either root biomass, microbial biomass, litter amount, soil organic carbon, soil nitrogen, cation exchange capacity, soil bulk density, soil porosity, soil pH, or site topography (Hanson et al., 1993; Fang et al., 1998; La Scala et al., 2000; Xu and Qi, 2001). Seasonal variations of soil respiration have often been associated with either changes in soil temperature (Anderson, 1973; Edwards, 1975; Ewel et al., 1987a; Fang et al., 1998; Longdoz et al., 2000) or changes in both soil temperature and soil water content (Garret and Cox, 1973; Hanson et al., 1993; Davidson et al., 1998; Epron et al., 1999a; Qi and Xu, 2001; Xu and Qi, 2001).

Up to now, only few studies have dealt with soil respiration in tropical plantations (Ewel et al., 1987a,b; Lamade et al., 1996; Fang et al., 1998) despite their relevance to the “Clean Development Mechanism”. *Eucalyptus* plantations account for 25% of tropical plantations and cover about  $1.5 \times 10^5$  km<sup>2</sup>. In the past 25 years, 430 km<sup>2</sup> of clonal *Eucalyptus* plantations have been established in the littoral savannas of Congo and intensively managed for pulpwood production. The present study was done in the framework of an integrated program on carbon fluxes and sequestration in perennial tropical plantations (ATP CIRAD). Specifically, our objective was first to quantify the annual soil carbon efflux in a 3-year-old *Eucalyptus* plantation in coastal Congo. We investigated the effects of seasonal changes in soil temperature and soil water content on soil respiration. We further analysed the spatial variation of soil respiration within the stand and we attempted to relate these variations to the plantation structure and to local soil characteristics.

## 2. Materials and methods

### 2.1. Site description

The study site is located in the *Eucalyptus* plantation zone, which covers about 430 km<sup>2</sup> along the Atlantic coast in the Pointe Noire region (Congo, 4° S, 12° E, 100 m elevation). The mean annual air humidity and air temperature are high (85% and 25 °C) with low seasonal variations (about 2% and 5 °C, respectively). Mean annual precipitation is 1200 mm with a dry season between May and September. The soil is an arenosol according to the F.A.O. classification. The pH of the topsoil (0–20 cm) is about 4.8. These deep sandy soils have poor water retention and low ionic content.

The experimental stand (42.8 ha) is in its third rotation, first planted in April 1983 on a savanna burned 18 years ago, then coppiced after clear-cutting about 10 years ago, and planted again after clear-cutting in 1998 with the clone 1–41 at 3.0 m × 4.7 m spacing. This clone is one of the most productive of the hybrid PF1 (see Bouillet et al., 2002 for details on this clone). The stand density is about 700 trees per ha. The stand was 3 years old with a mean height of 12 m in January and a leaf area index ranging between 0.95 and 1.55 in 2001.

Three types of inter-rows (IR) are identified. Log IR were used to store de-barked wood, slash IR received branches, twigs and bark, and haulage IR were used for the passage of heavy vehicles. There were two log IR for one slash and one haulage IR. Herbaceous understorey vegetation was kept sparse by chemical weeding with glyphosate during the first year after plantation and mechanical weeding afterwards, when necessary.

### 2.2. Experimental design and procedure

Six plots were chosen within the experimental stand. Each potentially contained 25 trees (5 × 5) and covered four inter-rows (two log IR, one slash and one haulage IR). For each inter-row within each plot, three measurements were done. One was positioned close to a tree (about 0.5 m), one far from it (in the middle of the inter-row, i.e. 2.5 m from the tree), and a third in an intermediate location between the first two measurements (1.5 m from the tree). For each day of

measurement, 12 records of soil respiration, temperature and water content were done in each plot, leading to a total of 72 measurement over the experimental stand and over the course of the day. Such a stratified sampling procedure has been recommended for crops where the spatial variation in soil respiration is thought to be partly due to the plantation scheme (Rochette et al., 1991).

Measurements were initiated in January 2001 (day 17) and were continued at 2–4-week intervals until February 2002 (day 400). They extended from early morning to late afternoon.

### 2.3. Measurements of soil respiration, temperature and water content

Soil respiration ( $R_s$ ) was measured using the Li 6000-09 soil respiration chamber (LiCor Inc, Lincoln, NE, USA) in which the increase of the CO<sub>2</sub> concentration was recorded with the Li 6250 infrared gas analyser (LiCor Inc) as already described (Epron et al., 1999a). The chamber edge is inserted in the soil to a depth of 1.5 cm. The litter overlying the soil is thus included in the chamber during the measurement. The CO<sub>2</sub> concentration within the soil respiration chamber was dropped 15 μmol mol<sup>-1</sup> below ambient, and the increase in the CO<sub>2</sub> concentration was recorded until it increased by 30 μmol mol<sup>-1</sup>.

Soil temperature was monitored simultaneously with soil CO<sub>2</sub> efflux using a copper/constantan thermocouple penetration probe (Li6000-09 TC, LiCor Inc) inserted in the soil to a depth of 10 cm in the vicinity of the soil respiration chamber. Soil temperature data are lacking for 3 days because of sensor dysfunction. The volumetric soil water content in the topsoil layer (0–6 cm) was monitored with a theta probe (ML2, Delta-T Device Ltd, Cambridge, UK) just after respiration measurement at the chamber location.

### 2.4. Roots, litters and soil characteristics

On one occasion (January 2001), aboveground litter was collected in a 0.3 m × 0.3 m area covering the location of respiration measurements immediately after respiration measurements, sorted into bark, woody debris, decomposed leaves and non-decomposed leaves, oven-dried at 60 °C till constant weight

and weighed. Soil cores (6-cm-diameter, 80-cm-depth) were extracted from the location of respiration measurements and divided into four 20-cm-long samples. Soil samples were sieved and root fragments were washed, eye-distinguished between live and dead fractions, and categorised by diameter (<1 mm, 1–5 mm, 5–10 mm), oven-dried at 60 °C till constant weight and weighted. Coarse roots (>10 mm) were discarded as they were only scarcely found. A total of 286 soil samples were oven-dried at 60 °C till constant weight. They were next scanned with a near-infrared reflectance spectrophotometer (NIRSystems 6500) to predict their C and N contents (Fystro, 2002). The concentrations of nitrogen and carbon were determined on 90 samples with a Perkin Elmer elemental analyser (PE 2400 CHN). Calibration equations between spectral and chemical data were conducted using ISI software system (Shenk and Westerhaus, 1991) and according to the methods described by Joffre et al. (1992). The predicted values were obtained with standard errors of prediction of 0.042% for C and 0.0026% for N. Contents ( $\text{mg g}^{-1}$ ) were converted into carbon (Cs) and nitrogen (Ns) amounts per unit area using a soil bulk density of 1.5 for the 0–20 cm samples and 1.55 for the other samples (unpublished data).

### 2.5. Data analysis

Daily averages ( $n = 72$ ) and confidence intervals at  $P = 0.05$  were calculated. Analyses of variance followed by a posteriori tests (least significant difference,  $P = 0.05$ ) were conducted to assess the difference in soil respiration, in leaf and aboveground litter, in root biomass and necromass and in soil carbon and nitrogen between sampling locations. Plot, inter-rows and tree distance effects were considered separately.

Daily means of soil respiration, soil water content and soil temperature were used for examining seasonal trends. Both univariate (soil water content) and bivariate models (soil water content and soil temperature) were fitted against soil respiration data using non-linear regression analysis. Criteria for a valid model were a maximum coefficient of determination ( $R^2$ ), a minimum root mean square error (rmse) and no bias in the distribution of the residuals.

When the number of parameters was different between two models, we used the following test

$F[p_1 - p_2, n - p_1]$  to perform the comparison:

$$F_{\text{obs}} = \frac{(\text{SCE}_{\text{T2}} - \text{SCE}_{\text{T1}})/(\text{SCE}_{\text{T2}} - \text{SCE}_{\text{T1}})}{\text{SCE}_{\text{T1}}/(n - p_1)} \quad (1)$$

with  $p_1$  the number of parameters for the model 1,  $p_2$  the number of parameters for the model 2 ( $p_1 > p_2$ ),  $\text{SCE}_{\text{T1}}$  was the sum of square errors for the model 1,  $\text{SCE}_{\text{T2}}$  was the sum of square errors for the model 2, and  $n$  was the number of observations.  $F_{\text{obs}}$  was compared to the theoretical value given in the Fischer's table  $F[p_1 - p_2, n - p_1]$ . If  $F_{\text{obs}} > F[p_1 - p_2, n - p_1]$  then model 1 described the variation of respiration better than model 2 (Brown and Rothery, 1994).

Correlation analysis was used to examine putative influences of soil factors (temperature, water content, carbon and nitrogen content, litter amounts and root biomass) on local values of soil respiration.

## 3. Results

### 3.1. Temporal trend in soil respiration

Soil respiration exhibited pronounced seasonal variations with minimum values below  $1.6 \mu\text{mol m}^{-2} \text{s}^{-1}$  at end of the dry season in September and a maximum value of  $5.6 \mu\text{mol m}^{-2} \text{s}^{-1}$  after re-wetting in December (Fig. 1). This pattern clearly reflected those of soil water content, which decreased from 10.8% in January to 3.1% in September. Soil temperature decreased from March (30 °C around day 70) to September (25 °C around day 260). There was a rather poor correlation between soil respiration and soil temperature even though soil respiration displayed a typical relationship with soil temperature (Fig. 2). Fitting exponential function ( $Q_{10}$ ), power function or Arrhenus equation on soil respiration against soil temperature data gave  $R^2$  values of 0.50, 0.51 and 0.52, respectively (data not shown). In contrast, there was a better correlation between soil respiration and soil water content (Fig. 2). Four empirical models that predicted an asymptotic or a maximum soil respiration at high soil water content ( $R_{\text{sm}}$ ) and a minimal soil water content ( $W_{\text{so}}$ ) were selected and fitted against soil respiration and soil water content data (Table 1). The  $R^2$  for these models

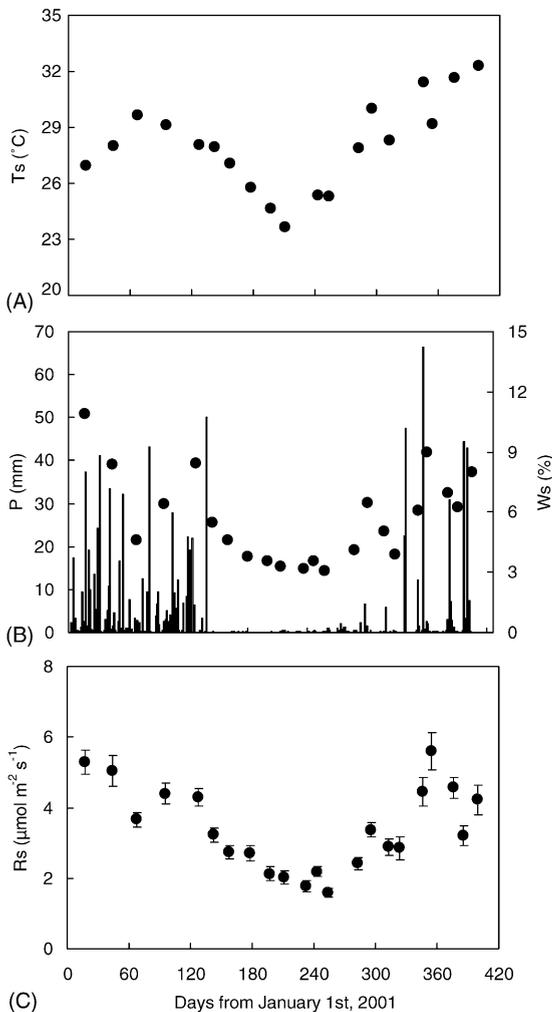


Fig. 1. Seasonal courses of (A) mean soil temperature ( $T_s$ ) at 10 cm depth, (B) precipitation (P) and mean soil volumetric water content ( $W_s$ ) in the top 6 cm and (C) mean soil respiration ( $R_s$ ). Vertical bars, when larger than the symbol, indicate the confidence interval of the mean.

were very similar (0.88). Predicted soil respiration using Eq. (T.3) agreed reasonably well with measured soil respiration (Fig. 3). Residuals were evenly distributed when plotted against time, soil temperature or soil water content (Fig. 4). Eq. (T.3) predicted accurate and unbiased values of soil respiration.

Bivariate models including soil temperature and soil water content functions did not explain seasonal variation of soil respiration better than univariate models with soil water content. For example,

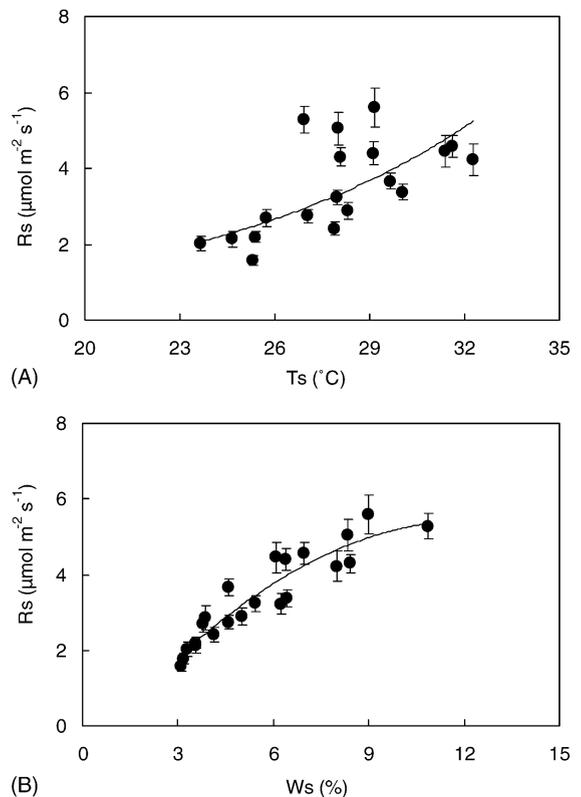


Fig. 2. Relationship between mean soil respiration ( $R_s$ ) and (A) mean soil temperature ( $T_s$ ) at a depth of 10 cm and (B) mean soil volumetric water content ( $W_s$ ) in the top 6 cm. Data are from Fig. 1. Lines are drawn for clarity.

combining Eq. (T.3) with an exponential function of soil temperature (Eq. (T.4), Table 1) only marginally improved the  $R^2$  and the rmse values. Eq. (T.4), which included soil temperature as a second variable, would therefore be unnecessarily complicated ( $F_{\text{obs}} = 0.94$ ;  $F_{[1,18]} = 4.41$ ;  $P = 0.05$ ). In addition, there were no substantial effects of rainfall events that would not be explained by an increase in soil water content. For example, the substantial rainfall during the nights preceding the measurements of day 17 (37 mm) and day 346 (12 mm) did not lead to higher (or lower) residuals than other day.

### 3.2. Correlation analysis

A correlation analysis was done between local values of soil respiration recorded on January 2001 (day 17) and root biomass, root necromass, above-

Table 1

Estimated parameters ( $a$ ,  $b$ ,  $c$ ), maximum soil respiration at high soil water content ( $R_{sm}$ ), minimal soil water content ( $W_{s0}$ ),  $Q_{10}$  values, coefficients of determination ( $R^2$ ) and root mean square error (rmse) for three univariate and one bivariate empirical models describing the relationship between soil respiration ( $R_s$ ) and soil water content in the top 6 cm ( $W_s$ , Eqs. (T.1)–(T.3)) and soil temperature at 10 cm depth ( $T_s$ , Eq. (T.4))

Fitted function	Equation no.	Fitted and derived parameters							
		$a$	$b$	$c$	$R_{sm}$	$W_{s0}$	$Q_{10}$	$R^2$	rmse
$R_s = aW_s^2 + bW_s + c$	(T.1)	-0.04	1.04	-0.95	5.81	0.95	-	0.88	0.41
$R_s = aR_{sm}(W_s - W_{s0})/[a(W_s - W_{s0}) + R_{sm}]$	(T.2)	1.49	-	-	8.92	1.59	-	0.88	0.40
$R_s = R_{sm}[1 - \exp(-a(W_s - W_{s0}))]$	(T.3)	0.19	-	-	6.49	1.33	-	0.88	0.40
$R_s = R_{sm}[1 - \exp(-a(W_s - W_{s0}))] \exp[b(T_s - 27)]$	(T.4)	0.15	0.015	-	6.86	1.05	1.16	0.89	0.39

ground litter, and soil carbon (Table 2). Among sampling locations, soil respiration was weakly but significantly and positively correlated with leaf litter ( $r = 0.33$ ), aboveground litter (0.30) while soil respiration was not correlated with either root biomass, root necromass or soil carbon, and only slightly correlated with the soil carbon over nitrogen ratio. There was no significant correlation between soil variables (i.e. litter amount, soil carbon or nitrogen and root biomass or necromass). Local variation of soil water content did not account for spatial variation in soil respiration during the wet season, but positive correlations between local values of soil respiration and local values of soil water content were sometimes observed during the dry season (Fig. 5). Surprisingly, there was sometimes a negative correlation between local values of soil respiration and local values of soil temperature (Fig. 5). A mulch effect due to litter accumulation may account for this unexpected negative correlation between soil respiration and soil temperature.

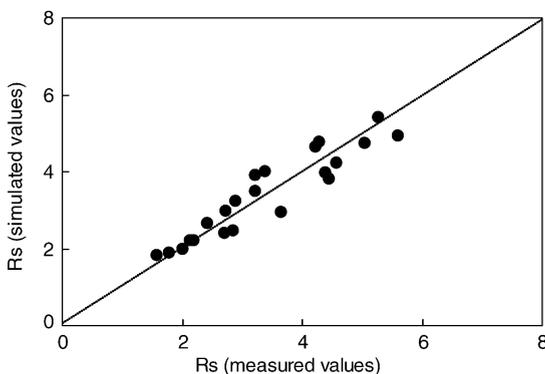


Fig. 3. Relationship between measured and predicted values of soil using Eq. (T.3) (see Table 1,  $R^2 = 0.88$ ; rmse = 0.40).

### 3.3. Spatial trends in soil respiration

The high number of samples (72) allowed the confidence intervals of the mean of soil respiration to be within 10% of the daily mean despite a large spatial variability. The coefficient of variation of soil respiration ranged between 25 and 50%.

Mean values for fine and coarse root biomass and necromass, leaf and aboveground litter, and soil carbon are given in Table 3. There were significant differences in soil respiration between sampling locations as shown in Fig. 6 and Table 4. Plots 3 and 6 exhibited the highest soil respiration, while the lowest rates were observed in plot 2. Interestingly, the latter had low aboveground litter amount ( $0.27 \text{ kg m}^{-2}$ ) while the other two plots had high aboveground litter amounts ( $0.51$  and  $0.63 \text{ kg m}^{-2}$ , respectively, Fig. 7). Differences in root biomass or soil carbon between plots did not account for differences in soil respiration.

Haulage inter-rows, which exhibited lower rates of respiration than log and slash inter-rows (Fig. 6, Table 4), also exhibited low amounts of aboveground litter (Table 3), and particularly low amounts of woody debris ( $0.05$  compared to  $0.14$  and  $0.16 \text{ kg m}^{-2}$  in normal and slash inter-rows). Decreasing soil respiration with increasing distance to tree (Fig. 6, Table 4) was also clearly related to a decrease in leaf litter amount ( $0.35$ ,  $0.26$  and  $0.21 \text{ kg m}^{-2}$ , respectively, Table 3).

## 4. Discussion

Seasonal variation in soil respiration is thought to be largely explained by either soil temperature alone

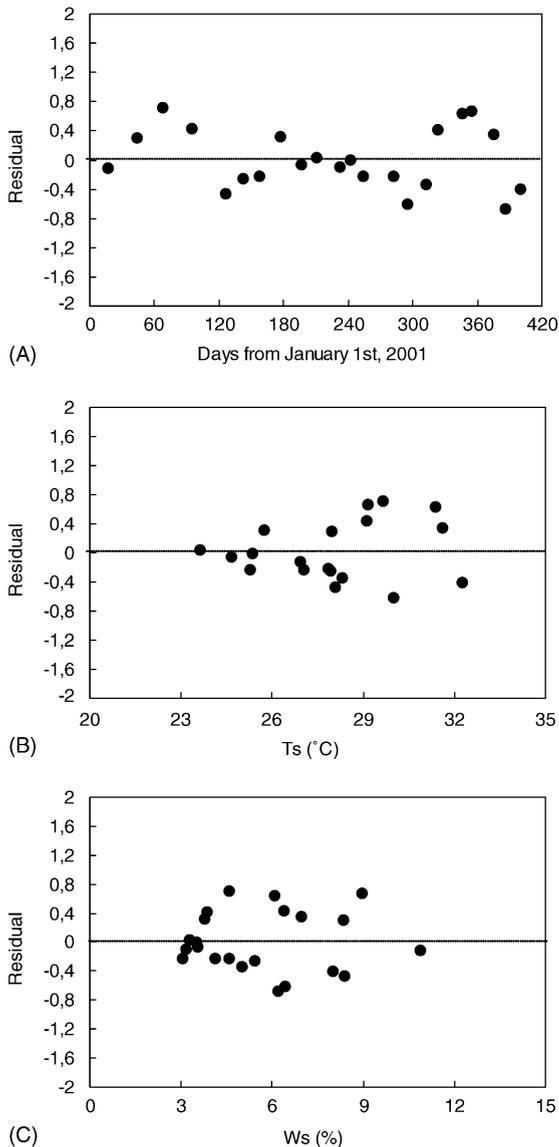


Fig. 4. Residual error term of predicted soil respiration as a function of (A) time, (B) mean soil temperature ( $T_s$ ) at a depth of 10 cm and (C) mean soil volumetric water content ( $W_s$ ) in the top 6 cm. Soil respiration was predicted using Eq. (T.3) (see Table 1).

(Anderson, 1973; Edwards, 1975; Longdoz et al., 2000) or soil temperature and water content in sites exhibiting a dry season as in some temperate areas or under Mediterranean climate (Garret and Cox, 1973; Hanson et al., 1993; Keith et al., 1997; Davidson et al., 1998; Epron et al., 1999a; Qi and Xu, 2001; Rey et al., 2002). Soil temperature exerted a strong influence on

soil respiration in tropical pine plantations in Florida (Ewel et al., 1987a; Fang et al., 1998) and in oil palm in Benin (Lamade et al., 1996) while it did not in a cattle pasture or in a forested areas in eastern Amazonia (Davidson et al., 2000). In this study, and despite a large change in soil temperature at 10-cm-depth over the entire season (9 °C), seasonal variations in soil respiration were better explained by parallel changes in soil water content. A positive covariation between soil temperature and soil water content is commonly observed in tropical regions where the dry season is often cooler than the wet season. Therefore, it may be very difficult to distinguish between the effect of declining temperature and declining soil water content as both occur together from May to September, and both reverse from November to April. A similar overlapping effect of soil water content on the effect of soil temperature on soil respiration has been reported for tropical rain forests (Kiese and Butterbach-Bahl, 2002). The empirical relationships between soil respiration and soil water content may, in fact, confound the effects of both temperature and soil water content since both factors co-vary across seasons. Indeed, the  $Q_{10}$  value (2.9) estimated by fitting an exponential function to the relationship between soil respiration and soil temperature was within the range of published values for soil respiration (Davidson et al., 1998; Epron et al., 1999a) but dropped to 1.1 when a bivariate model including the effect of soil water content was used.

Linear relationships have often been used to describe the relationship between soil respiration and soil water content (Holt et al., 1990; Epron et al., 1999a; Rey et al., 2002). In this study, the relation was clearly non-linear and was best predicted with functions exhibiting a positive  $x$ -intercept and a maximum soil respiration at high soil water content. A positive  $x$ -intercept assumes that a minimal soil water content is required for biological processes, i.e. free water in the soil pores. Decreased soil respiration at high soil water content due to reduced oxygen diffusion has sometimes been reported in clay-rich soil (Davidson et al., 1998; Xu and Qi, 2001) but it is unlikely in a well-drained sandy soil.

Using Eq. (T.3) to simulate daily soil respiration for estimating annual soil carbon efflux would ideally require daily values of soil water content that could be automatically recorded or alternatively simulated

Table 2

Bravais-Pearson correlation coefficients among soil respiration ( $R_s$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) as recorded on January 17, 2001, and leaf litter amount (LL), aboveground litter amount (AL), root biomass (RB), root necromass (RN), soil carbon amounts (Cs), soil nitrogen amounts (Ns) and their ratio (Cs/Ns) in the top 20 or 80 cm of the soil

	LL	AL	RB (0–20)	RB (0–80)	RN (0–20)	RN (0–80)	Cs (0–20)	Cs (0–80)	Ns (0–20)	Ns (0–80)	Cs/Ns (0–20)	Cs/Ns (0–80)
$R_s$	0.33**	0.30**	0.03	0.14	0.13	0.06	0.23	0.15	-0.16	0.12	0.26*	0.24*
LL		0.79***	0.06	-0.01	0.13	-0.03	-0.02	-0.01	-0.00	0.04	0.00	-0.05
AL			0.27*	0.06	0.11	-0.15	0.07	0.03	-0.02	0.00	0.08	0.03
LRB 0–20				0.63***	0.13	-0.08	0.10	0.10	0.18	0.12	-0.03	-0.02
LRB 0–80					0.10	-0.13	0.23	0.22	0.13	0.05	0.11	0.14
DRN 0–20						0.41***	0.19	0.16	0.04	0.02	0.15	0.13
DRN 0–80							0.12	0.12	-0.01	0.03	0.13	0.09
Cs 0–20								0.91***	-0.02	0.01	0.84***	0.83***
Cs 0–80									0.12	0.36**	0.70***	0.61***
Ns 0–20										0.67***	-0.53***	-0.44***
Ns 0–80											-0.34**	-0.51***
Cs/Ns 0–20												0.92***

Samples were collected after soil respiration measurements ( $n = 72$ ). Values followed by \*, \*\* and \*\*\* are significant at 0.05, 0.01 and 0.001, respectively.

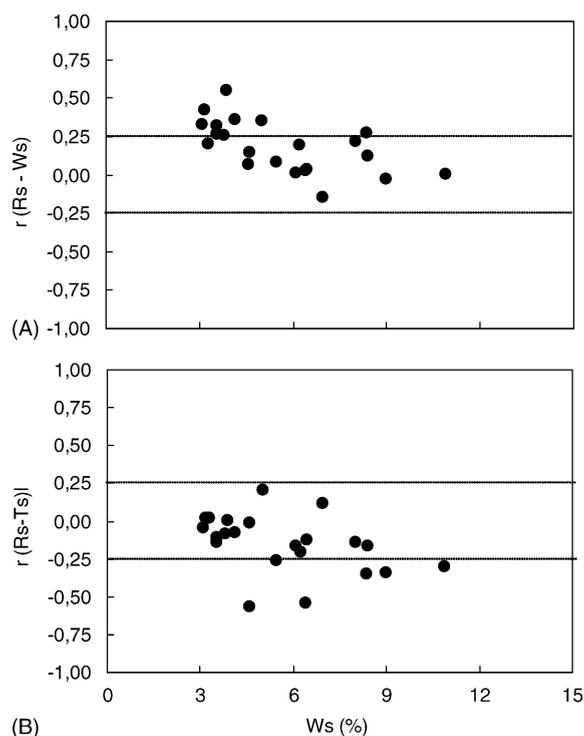


Fig. 5. Relationship between mean soil volumetric water content ( $W_s$ ) in the top 6 cm and the Bravais-Pearson correlation coefficient between local soil respiration and (A) local soil water content ( $r(R_s - W_s)$ ) and (B) local soil temperature ( $r(R_s - T_s)$ ) for each day of measurements. The horizontal lines indicate the threshold values of  $r$  at  $P = 0.05$  for  $n = 72$ .

using a water balance model with rainfall and evapotranspiration as input variables. Here, the daily values of soil respiration were simply interpolated between two successive measurements, leading to an annual soil carbon efflux of around  $1.25\text{--}1.30 \text{ kg}_C \text{ m}^{-2}$ . This value is within the range of published values for tropical and subtropical forests ( $0.90\text{--}1.50 \text{ kg}_C \text{ m}^{-2}$ , Raich and Schlesinger, 1992) and close to those reported for an oil palm plantation in Benin ( $1.6 \text{ kg}_C \text{ m}^{-2}$ , Lamade et al., 1996). As reported by Keith et al. (1997), annual soil efflux in *Eucalyptus* forests ranged from  $0.4$  to  $1.2 \text{ kg}_C \text{ m}^{-2}$ ) depending on climatic conditions and site locations. However, such comparisons are complicated by the discrepancies which frequently arise when soil respiration measuring systems are cross-compared (Nay et al., 1994; Pongracic et al., 1997; Le Dantec et al., 1999; Janssens et al., 2000).

A sharp increase in soil respiration after rainfall events have been observed in many studies (Holt et al., 1990; Rochette et al., 1991; Davidson et al., 2000; Liu et al., 2002), and this could account for the interannual variability of soil carbon efflux (Rey et al., 2002). In this study, no effect of rainfall on soil respiration has been detected that was not predicted by the increase in soil water content. However, only 2 days of measurement were preceded by substantial rainfall, and they were during the wet season. Additional measurements following heavy rainfall either during

Table 3

Mean values and confidence intervals at  $P = 0.05$  ( $n = 72$ ) for leaf litter amount (LL), aboveground litter amount (AL), root biomass (RB), root necromass (RN), soil carbon amounts (Cs), soil nitrogen amounts (Ns) and their ratio (Cs/Ns) in the top 20 or 80 cm of the soil, and analyses of variance for these variables as affected by sampling locations, i.e. either plots, types of inter-row or distance to tree

	LL	AL	RB (0–20)	RB (0–80)	RN (0–20)	RN (0–80)	Cs (0–20)	Cs (0–80)	Ns (0–20)	Ns (0–80)	Cs/Ns (0–20)	Cs/Ns (0–80)
Mean values	0.27	0.41	0.13	0.30	0.06	0.21	2.7	5.5	0.10	0.25	28	22
with CI	(0.03)	(0.04)	(0.03)	(0.05)	(0.02)	(0.04)	(0.2)	(0.2)	(0.01)	(0.01)		
Plot ( $F$ , $df = 5$ )	3.27*	5.27***	2.17	2.58*	1.11	1.04	2.97*	2.72*	6.12***	11.1***	3.84*	8.80***
Inter-row ( $F$ , $df = 2$ )	1.19	3.27*	0.53	0.00	0.93	0.44	1.90	1.09	0.94	0.89	4.71*	4.07*
Tree distance ( $F$ , $df = 2$ )	6.10**	4.38*	0.39	1.27	0.03	0.83	0.40	0.31	1.30	0.22	0.12	0.10

$F$  ratio followed by \*, \*\* and \*\*\* are significant at 0.05, 0.01 and 0.001, respectively ( $df$ : degree of freedom). Amounts are in  $\text{kg m}^{-2}$ .

the dry season or during the re-wetting phase at the beginning of the wet season would be required to investigate the putative effects of rainfall frequency on the annual soil carbon efflux.

While we found that soil water content are the main determinant of seasonal variation of soil respiration, it does not account for spatial variability over the experimental plot. Spatial variation of soil respiration has often been related to change in root biomass, litter amount, soil organic matter, microbial biomass, soil chemistry or soil physical properties, alone or in combination (Fang et al., 1998; La Scala et al., 2000; Stoyan et al., 2000; Tufekcioglu et al., 2001; Xu and Qi, 2001). Rhizosphere respiration that included respiratory  $\text{CO}_2$  released by roots, mycorrhizae and root-associated micro-organisms consuming root-derived materials, is thought to be a major component of soil respiration in forest ecosystems (Ewel et al., 1987b; Bowden et al., 1993; Nakane et al., 1996; Boone et al., 1998; Epron et al., 1999b, 2001), and close correlation between root biomass and soil respiration have been frequently reported (Fang et al., 1998; Stoyan et al., 2000). Surprisingly, soil respiration was not related to root biomass in this study. Belowground biomass accounts for less than 20% of the total biomass of *Eucalyptus* in this plantation throughout the rotation, and the stump represented 50% of belowground biomass (Laclau et al., 2000). One may therefore expect a low contribution of root respiration in this young *Eucalyptus* plantation and that would explain the lack of correlation between root biomass and soil respiration. However, this hypothesis should be confirmed by designing a trenched-plot experiment.

In this study, soil respiration was only significantly correlated with either leaf or total aboveground litter (leaves, bark and woody debris), but neither of these explained more than 10% of the spatial variation in soil respiration recorded just before sampling. Adding other measured variables in a multiple regression analysis failed to increase the explained variance. Our results contrasted with those obtained on a slash pine plantation where soil respiration was correlated with root biomass, litter amount and soil organic matter, and where soil respiration was best predicted using a linear model including the three variables (Fang et al., 1998).

Spatial heterogeneity of soil respiration was clearly affected by the management practice with higher respiration rate in slash inter-rows which received higher amount of detritus at the logging stage, and lower respiration rate in haulage inter-rows used for heavy vehicle traffic which received lower amount of detritus (Bouillet et al., 1997). Although haulage inter-rows contained lower amounts of woody litter than slash or log inter-rows, they did not exhibit significant differences in soil carbon or root biomass. Lower soil respiration was also reported for inter-rows compacted by tractor wheels when compared to the non-compacted inter-rows in maize fields (Rochette et al., 1991). A putative increase in soil strength due to engine traffic would probably not affect root biomass because soil strength up to 6000 kPa did not prevent root development in these *Eucalyptus* plantations (Laclau et al., 2001). The plantation under study was logged and replanted 3 years ago, suggesting that management practices yield long-lasting effects that would deserve specific studies in the framework of

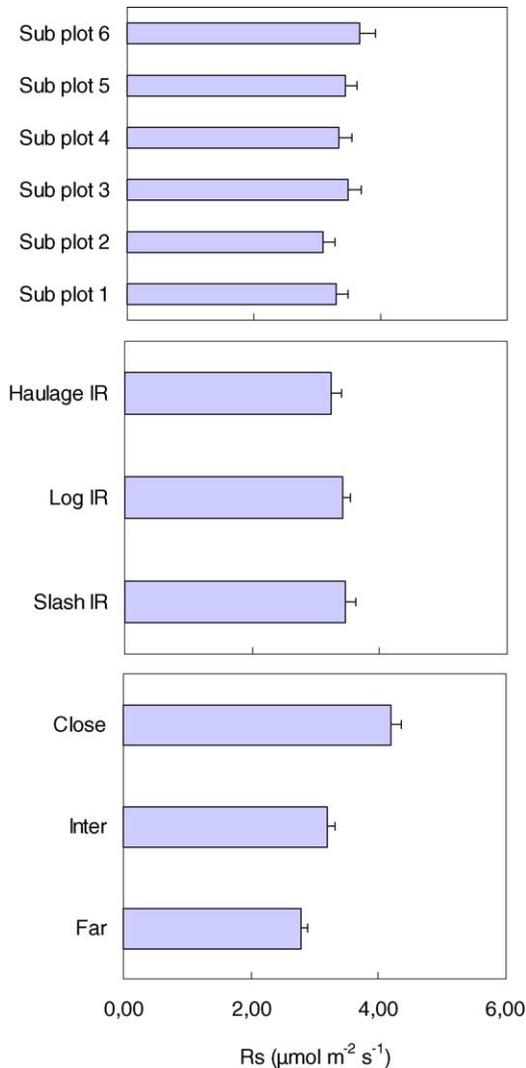


Fig. 6. Average values of soil respiration ( $R_s$ ) from 22 days of measurements between January 2001 and February 2002 recorded on (A) six different plots within the experimental stand, (B) three kind of inter-row (IR) used for storing de-barked wood (log IR), for receiving branches, twigs and bark (slash IR), and for the passage of heavy vehicles (haulage IR), and (C) three positions within the inter-row, i.e. 0.5 (close), 1.5 (intermediate) and 2.5 m (far) from the trunk. Bars indicate the confidence interval of the mean (see Table 4 for the analyses of variance).

the sustainability of soil organic matter for the long term.

Another cause of spatial heterogeneity of soil respiration is clearly the tree distance, with higher values in the vicinity of trunks and lower values in the

Table 4

Analyses of variance for soil respiration as affected by date of measurements and sampling locations, i.e. either plots, types of inter-row or distance to tree

Source of variation	Soil respiration		
	df	F	P > F
Plot	5	7.47	***
Date	21	70.17	***
Plot x date	105	1.13	NS
Inter-row	2	4.22	*
Date	21	60.41	***
Inter-row x date	42	1.50	NS
Tree distance	2	267.3	***
Date	21	97.48	***
Tree distance x date	42	1.45	NS

F ratio followed by either NS, \*, \*\* or \*\*\* are non-significant or significant at 0.05, 0.01 and 0.001, respectively (df: degree of freedom).

middle of the inter-row. This is a classical pattern for maize (Rochette et al., 1991) or oil palm plantations (Lamade et al., 1996). However, in contrast to what is observed in the oil palm plantations, this was not due to higher root biomass in the vicinity of the tree. No gradient of fine root biomass was already reported from the edge of the planting row to the middle of the inter-row in similar *Eucalyptus* plantations (Bouillet et al., 2002). Soil respiration was also concentrated around the trunk of poplars in a 9-year-old plantation, and it was ascribed to a higher soil water content as a result of stem flow (Stoyan et al., 2000). However,

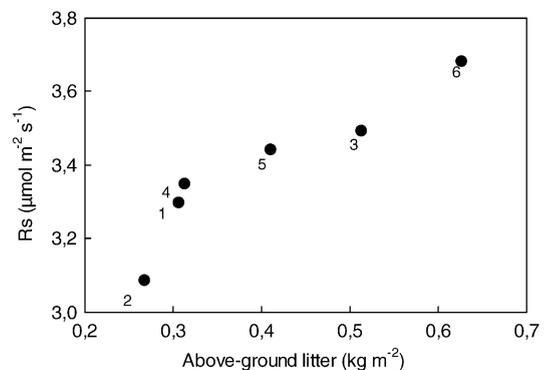


Fig. 7. Relationship between the average values of soil respiration ( $R_s$ ) from 22 days of measurements between January 2001 and February 2002 recorded on six different plots within the experimental stand and mean aboveground litter amount. Data from the six plots are numbered.

higher soil water content close to the stem was not observed in this study. It may be associated with higher amounts of leaf litter close to the trunk. Large inter-rows (4.7 m) and the typical form of *Eucalyptus* trees may account for this heterogeneity of litter deposition within an inter-row. Higher litter fall in the stem area than in the interstem area has also been reported in a beech plantation and was thought to influence microbiological processes such as NO and N<sub>2</sub>O production (Butterbach-Bahl et al., 2002; Gasche and Papen, 2002).

Average aboveground litter amount in a given plot seems to be a good predictor of the soil respiration of the plot. Microbial respiration in the surface layer associated with a high decomposition rate of litter components is likely a major component of soil respiration in this young *Eucalyptus* plantation. Accordingly, it would be more appropriate to monitor the physical properties of the litter compartment, i.e. temperature and moisture. At a larger scale, the opportunity of using litter amount, litter fall or even leaf area index to predict spatial variation of soil respiration has to be considered in further developments of predictive models of net carbon exchange of *Eucalyptus* plantations.

## Acknowledgements

This research activity was carried out in the framework of the CIRAD funded 'ATP Carbon' project. UR2PI and ECO-SA (Eucalyptus Du Congo, SA) have provided additional funding and research facilities.

## References

- Anderson, J.M., 1973. Carbon dioxide evolution from two temperate, deciduous woodland soils. *J. Appl. Ecol.* 10, 361–378.
- Boone, R.D., Nadelhoffer, K.J., Canary, J.D., Kaye, J.P., 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature* 396, 570–572.
- Bouillet, J.P., Nizinski, G., Nzila, J.D., Ranger, J., 1997. The sustainability of Eucalyptus commercial plantations: the congolese approach. In: Proceedings of the IUFRO Conference on Improvement and culture of Eucalyptus, vol. 4. Salvador, Brazil, pp. 232–237.
- Bouillet, J.P., Laclau, J.P., Arnaud, M., Thongo M'Bou, A., Saint-André, L., Jourdan, C., 2002. Changes with age in the spatial distribution of roots of Eucalyptus clone in Congo. Impact of water and nutrient uptake. *For. Ecol. Manage.* 171, 43–57.
- Bowden, R.D., Nadelhoffer, K.J., Boone, R.D., Melillo, J.M., Garrison, J.B., 1993. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. *Can. J. For. Res.* 23, 1402–1407.
- Brown, D., Rothery, P., 1994. *Models in Biology: Mathematics, Statistics and Computing*, Wiley, Chichester, England.
- Butterbach-Bahl, K., Rothe, A., Papen, H., 2002. Effect of tree distance on N<sub>2</sub>O and CH<sub>4</sub>-fluxes from soils in temperate forest ecosystems. *Plant Soil* 240, 91–103.
- Davidson, E.A., Beck, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biol.* 4, 217–227.
- Davidson, E.A., Verchot, L.V., Cattânio, J.H., Ackerman, I.L., Carvalho, J.E.M., 2000. Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. *Biogeochemistry* 48, 53–69.
- Edwards, N.T., 1975. Effects of temperature and moisture on carbon dioxide evolution in a mixed deciduous forest floor. *Soil Sci. Soc. Am. J.* 39, 361–365.
- Epron, D., Farque, L., Lucot, E., Badot, P.M., 1999a. Soil CO<sub>2</sub> efflux in a beech forest: dependence on soil temperature and soil water content. *Ann. For. Sci.* 56, 221–226.
- Epron, D., Farque, L., Lucot, E., Badot, P.M., 1999b. Soil CO<sub>2</sub> efflux in a beech forest: the contribution of root respiration. *Ann. For. Sci.* 56, 289–295.
- Epron, D., Le Dantec, V., Dufrêne, E., Granier, A., 2001. Seasonal dynamics of soil carbon dioxide efflux and simulated rhizosphere respiration in a beech forest. *Tree Physiol.* 21, 145–152.
- Ewel, K.C., Cropper, W.P., Gholz, H.L., 1987a. Soil CO<sub>2</sub> evolution in Florida slash pine plantations. I. Changes through time. *Can. J. For. Res.* 17, 325–329.
- Ewel, K.C., Cropper, W.P., Gholz, H.L., 1987b. Soil CO<sub>2</sub> evolution in Florida slash pine plantations. II. Importance of root respiration. *Can. J. For. Res.* 17, 330–333.
- Fang, C., Moncrieff, J.B., Gholz, H.L., Clark, K.L., 1998. Soil CO<sub>2</sub> efflux and its spatial variation in a Florida slash pine plantation. *Plant Soil* 205, 135–146.
- Fearnside, P.M., Barbosa, R.I., 1998. Soil carbon changes from conversion of forest to pasture in Brazilian Amazonia. *For. Ecol. Manage.* 108, 147–166.
- Fystro, G., 2002. The prediction of C and N content and their potential mineralisation in heterogeneous soil sample using Vis-NIR spectroscopy and comparative methods. *Plant Soil* 246, 139–149.
- Garret, H.E., Cox, G.S., 1973. Carbon dioxide evolution from the floor of an oak-hickory forest. *Soil Sci. Soc. Am. Proc.* 37, 641–644.
- Gasche, R., Papen, H., 2002. Spatial variability of NO and NO<sub>2</sub> flux rates from soil of spruce and beech forest ecosystems. *Plant Soil* 240, 67–76.

- Granier, A., Ceschia, E., Damesin, C., Dufrière, E., Epron, D., Gross, P., Lebaube, S., Le Dantec, V., Le Goff, N., Lemoine, D., Lucot, E., Ottorini, J.M., Pontaville, J.Y., Saugier, B., 2000. The carbon balance of a young beech forest. *Functional Ecol.* 14, 312–325.
- Hanson, P.J., Wullschlegel, S.D., Bohlman, S.A., Todd, D.E., 1993. Seasonal and topographic patterns of forest floor CO<sub>2</sub> efflux from an upland oak forest. *Tree Physiol.* 13, 1–15.
- Holt, J.A., Hodgen, M.J., Lamb, D., 1990. Soil respiration in the seasonally dry tropics near Townville, North Queensland. *Aust. J. Soil Res.* 28, 737–745.
- Janssens, I.A., Kowalski, A.S., Longdoz, B., Ceulemans, R., 2000. Assessing forest soil CO<sub>2</sub> efflux: an in situ comparison of four techniques. *Tree Physiol.* 20, 23–32.
- Janssens, I.A., Lankreijer, H., Matteucci, G., Kowalski, A.S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E.J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R., Gudmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N.O., Vesala, T., Granier, A., Schulze, E.-D., Lindroth, A., Dolman, A.J., Jarvis, P.G., Ceulemans, R., Valentini, R., 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biol.* 7, 269–278.
- Joffre, R., Gillon, D., Dardenne, P., Agneessens, R., Biston, R., 1992. The use of near-infrared reflectance spectroscopy in litter decomposition studies. *Ann. For. Sci.* 49, 481–488.
- Keith, H., Jacobsen, K.L., Raison, R.J., 1997. Effects of soil phosphorus availability, temperature and moisture on soil respiration in *Eucalyptus pauciflora* forest. *Plant Soil* 190, 127–141.
- Kiese, R., Butterbach-Bahl, K., 2002. N<sub>2</sub>O and CO<sub>2</sub> emissions from three different tropical sites in the wet tropics of Queensland. *Aus. Soil Biol. Biochem.* 34, 975–987.
- La Scala Jr., N., Marques Jr., J., Pereira, G.T., Cora, J.E., 2000. Carbon dioxide emission related to chemical properties of a tropical bare soil. *Soil Biol. Biochem.* 32, 1469–1473.
- Laclau, J.-P., Bouillet, J.-P., Ranger, J., 2000. Dynamics of biomass and nutrient accumulation in a clonal plantation of *Eucalyptus* in Congo. *Forest Ecol. Manage.* 128, 181–196.
- Laclau, J.-P., Arnaud, M., Bouillet, J.P., Ranger, J., 2001. Spatial distribution of *Eucalyptus* roots in a deep sandy soil in the Congo: relationships with the ability of the stand to take up water and nutrients. *Tree Physiol.* 21, 129–136.
- Lamade, E., Djegui, N., Leterme, P., 1996. Estimation of carbon allocation to the roots from soil respiration measurements of oil palm. *Plant Soil* 181, 329–339.
- Le Dantec, V., Epron, D., Dufrière, E., 1999. Soil CO<sub>2</sub> efflux in a beech forest: comparison of two closed dynamic systems. *Plant Soil* 214, 125–132.
- Liu, X., Wan, S., Su, B., Hui, D., Luo, Y., 2002. Response of soil CO<sub>2</sub> efflux to water manipulation in a tallgrass prairie ecosystem. *Plant Soil* 240, 213–223.
- Longdoz, B., Yernaux, M., Aubinet, M., 2000. Soil CO<sub>2</sub> efflux measurements in a mixed forest: impact of chamber disturbances, spatial variability and seasonal evolution. *Global Change Biol.* 6, 907–917.
- Nakane, K., Kohno, T., Horikoshi, T., 1996. Root respiration rate before and just after clear-felling in a mature, deciduous, broad-leaved forest. *Ecol. Res.* 11, 111–119.
- Nay, S.M., Mattson, K.G., Bormann, B.T., 1994. Biases of chamber methods for measuring soil CO<sub>2</sub> efflux demonstrated with a laboratory apparatus. *Ecology* 75, 2460–2463.
- Paul, K.I., Polglase, P.J., Nyakuengama, J.G., Khanna, P.K., 2002. Change in soil carbon following afforestation. *Forest Ecol. Manage.* 166, 251–257.
- Pongracic, S., Kirschbaum, M.U.F., Raison, R.J., 1997. Comparison of soda lime and infrared gas analysis techniques for in situ measurements of forest soil respiration. *Can. J. For. Res.* 27, 1890–1895.
- Qi, Y., Xu, M., 2001. Separating the effects of moisture and temperature on soil CO<sub>2</sub> efflux in a coniferous forest in the Sierra Nevada mountains. *Plant Soil* 237, 15–23.
- Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B, 81–99.
- Rey, A., Pegoraro, E., Tedeschi, V., De Parri, I., Jarvis, P., Valentini, R., 2002. Annual variation in soil respiration and its components in a coppice oak forest in central Italy. *Global Change Biol.* 8, 851–866.
- Rochette, P., Desjardins, R.L., Pattey, E., 1991. Spatial and temporal variability of soil respiration in agricultural fields. *Can. J. Soil Sci.* 71, 189–196.
- Schimel, D.S., 1995. Terrestrial ecosystems and the carbon cycle. *Global Change Biol.* 1, 77–91.
- Shenk, J.S., Westerhaus, M.O., 1991. Population definition, sample selection, and calibration procedure for near infrared reflectance spectroscopy. *Crop Sci.* 31, 1548–1555.
- Smith, C.K., De Assis Oliveira, F., Gholz, H.L., Baima, A., 2002. Soil carbon stocks after forest conversion to tree plantations in lowland Amazonia, Brazil. *Forest Ecol. Manage.* 166, 257–263.
- Stoyan, H., De-Polli, H., Böhm, S., Robertson, G.P., Paul, E.A., 2000. Spatial heterogeneity of soil respiration and related properties at the plant scale. *Plant Soil* 222, 203–214.
- Tufekcioglu, A., Raich, J.W., Isenhardt, T.M., Schultz, R.C., 2001. Soil respiration within riparian buffers and adjacent crop fields. *Plant Soil* 229, 117–124.
- Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, Ü., Berbigier, P., Lousteau, D., Gudmundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000. Respiration as the main determinant of European forests carbon balance. *Nature* 404, 861–865.
- Xu, M., Qi, Y., 2001. Soil-surface CO<sub>2</sub> efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. *Global Change Biol.* 7, 667–677.
- Zinn, Y.L., Resck, D.V.S., Da Silva, J.E., 2002. Soil organic carbon as affected by afforestation with *Eucalyptus* and *Pinus* in the *Cerrado* region of Brazil. *Forest Ecol. Manage.* 166, 285–294.