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Original article

Soil CO_2 efflux in a beech forest: dependence on soil temperature and soil water content

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Abstract – Our objective was to quantify the annual soil carbon efflux in a young beech forest in north-eastern France (Hesse Forest, Euroflux site FR02) from measurements of soil CO_2 efflux. Soil CO_2 efflux exhibited pronounced seasonal variations which did not solely reflect seasonal changes in soil temperature. In particular, strong differences in soil CO_2 efflux were observed between summer 1996 and summer 1997 while the patterns of soil temperature were similar. This difference is at least partly explained by an inhibition of soil CO_2 efflux at low soil water content. Since changes in soil temperature (T) and soil volumetric water content at –10 cm (θ_v) affect soil CO_2 efflux, an empirical model is proposed ($y = A\ q_v\ e^{BT}$) which account for 86 % of the variation in soil CO_2 efflux. The difference between two estimates of annual soil carbon efflux (575 $g_C\ m^{-2}\ year^{-1}$ from June 1996 to May 1997 and 663 $g_C\ m^{-2}\ year^{-1}$ from December 1996 to November 1997) clearly highlights the dependence of soil carbon efflux on soil water content during summer. (© Inra/Elsevier, Paris.)

carbon cycle / *Fagus sylvatica* / soil water content / soil temperature / soil respiration

Résumé – Flux de CO_2 provenant du sol dans une hêtraie – relation avec la température du sol et le contenu en eau du sol. Notre objectif était de quantifier le flux annuel de carbone provenant du sol d'une jeune hêtraie du nord-est de la France (Forêt de Hesse, site Euroflux FR02) à partir de mesures de flux de CO_2 provenant du sol. Le flux de CO_2 provenant du sol montre de fortes variations saisonnières qui ne s'expliquent pas uniquement par des variations saisonnières de température du sol. En particulier, de fortes différences de flux de CO_2 provenant du sol ont été observées entre l'été 1996 et l'été 1997 alors que la température du sol était similaire. Cette différence s'explique au moins en partie par une inhibition du flux de CO_2 provenant du sol lorsque la teneur en eau du sol décroît. Comme les changements de température du sol (T) et d'humidité volumique à –10 cm (θ_v) affectent le flux de CO_2 provenant du sol, un modèle empirique ($y = A\ \theta_v\ e^{BT}$) expliquant 86 % de la variation du flux de CO_2 provenant du sol est proposé. La différence entre deux estimations du flux de carbone provenant du sol (575 $g_C\ m^{-2}\ an^{-1}$ de juin 96 à mai 97 et 663 $g_C\ m^{-2}\ an^{-1}$ de déc. 96 à nov. 97) montre clairement les effets de l'humidité du sol pendant l'été sur le flux de carbone provenant du sol. (© Inra/Elsevier, Paris.)

cycle du carbone / *Fagus sylvatica* / humidité du sol / respiration du sol / température du sol

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1. INTRODUCTION

The ability of forest soils to sequester carbon through both aboveground and belowground litter inputs is of particular interest since forest ecosystems potentially represent an increasing sink for carbon as atmospheric CO_2 is increased and photosynthesis stimulated [16]. Conversely, anticipated temperature increases resulting from increasing greenhouse gases in the atmosphere may counteract this increase in carbon accumulation in soils by stimulating the mineralization rate of organic carbon pools in soils by heterotrophic micro-organisms [10]. Therefore, changes in soil carbon storage abilities may in turn affect atmospheric CO_2 concentration during the next decades in different ways depending on local climate and site characteristics [12].

Soil CO_2 efflux has been measured in many forests all over the world [16]. However, only a few of these data concern European forests. In addition, most of these measurements were performed with static chambers using chemical traps for CO_2 and it was recently demonstrated that these methods often underestimated the actual soil CO_2 efflux [11, 15]. Since soil CO_2 efflux depends on species composition, site location (both climatic and edaphic conditions), stand ages and sylvicultural practices [1, 4, 6, 8, 14, 18], reliable estimates of soil CO_2 efflux are still required to provide a better estimate of the contribution of soil CO_2 efflux to the carbon budgets of European forests and to validate ecosystem models of carbon balance.

Our objective was to quantify annual soil carbon effluxes in a young beech forest in north-eastern France using a portable chamber connected to an infra-red gas analyser. We investigated the effects of seasonal changes in soil temperature and soil water content on the rate of soil CO_2 efflux. We propose an empirical relationship between soil CO_2 efflux and both soil temperature and soil water content at a depth of 10 cm. This relationship was used to estimate the annual soil carbon efflux of this beech forest.

2. MATERIALS AND METHODS

2.1. Site characteristics

The study site is located in the State forest of Hesse (eastern France, 48°40 N, 7°05 E, elevation 305 m, 7 km^2) and is one of the Euroflux sites (FR02). It is dominated by beech (*Fagus sylvatica*). Other tree species are *Carpinus betulus*, *Betula alba*, *Fraxinus excelsior*, *Prunus avium*, *Quercus petraea*, *Larix decidua*. The experimental plot covers 0.6 ha and is mainly composed of 30-year-old beeches. Herbaceous understory vegetation is rather sparse. Average annual precipitation and air temperature are 820 mm and 9.2 °C, respectively. Soil is a gleyic luvisol according to the F.A.O. classification. The pH of the top soil (0–30 cm) is 4.9 with a C/N of 12.2 and an apparent density of 0.85 kg dm^{-3}, and is covered with a mull-type humus. Leaf area index was 5.7 in 1996 and 5.6 in 1997 (Granier, pers. comm.) and fine root biomass was about 0.7 kg_{DM} m^{-2} in 1997 (unpublished data).

2.2. Soil CO_2 efflux

Measurements of soil CO_2 efflux were carried out with a portable infrared gas analyser (Li 6250, Li-Cor, USA) connected to a 0.854 dm^3 soil respiration chamber covering 0.72 dm^2 of soil (Li 6000-9). The chamber edge is inserted in the soil to a depth of 1.5 cm. After measuring the CO_2 concentration over the soil surface, the CO_2 concentration within the soil respiration chamber was decreased by 15 µmol mol^{-1}, and the increase in the CO_2 concentration was recorded for 60 s.

Six sub-plots of about 100 m^2 each were randomly chosen for soil respiration measurements. Twelve measurements were conducted at random locations in each sub-plot during an 8-h period from 8 a.m. to 4 p.m. On one occasion in July 1997, measurements were made during a 24-h period. The difference between the average value obtained over the 8-h period did not differ significantly from the one obtained over the other 16-h period (3.6 ± 0.4 and 3.3 ± 0.3 µmol m^{-2} s^{-1}, respectively). The lack of significant diurnal changes in soil CO_2 efflux under a closed canopy has already been reported [9]. Therefore, we assumed that our diurnal means were reliable estimates of daily means. Measurements were initiated in June 1996 and were continued at 2- to 4-week intervals until November 1997. Daily averages (n = 72) and confidence intervals at P = 0.05 were calculated. This high number of samples allowed the confidence intervals to be within 10 % of the mean despite a large spatial variability. Non-linear regressions (Marquardt-Levenberg method) with soil temperature and soil water content as input variables were fitted through soil respiration data (SigmaPlot software, Jandel Corp., USA).

2.3. Soil temperature and soil water content

Soil temperature was measured at –10 cm by six copper/constantan thermocouples. Data acquisition was made with a Campbell (UK) CR7 datalogger at 10-s time interval. Thirty-minute averages were stored. In addition, soil temperature was also monitored simultaneously with soil CO_2 efflux with a copper/constantan thermocouple penetration probe inserted in the soil to a depth of 10 cm in the vicinity of the soil respiration chamber. The average soil temperature recorded during the measuring period was very close to the daily averages because diurnal variation in soil temperature was very damped at –10 cm. Volumetric water content of the soil was measured every 10 cm with a neutron probe (NEA, Denmark) in eight aluminium access tubes (160 or 240 cm deep) at 1- to 3-week intervals. Between two measurements, the volumetric water content of the soil was assumed to change linearly with time.

3. RESULTS

Soil CO_2 efflux exhibited pronounced seasonal variations (*figure 1A*) which clearly reflected seasonal changes in soil temperature (*figure 1B*). Daily average values of soil CO_2 efflux ranged from 0.4 μmol m^{-2} s^{-1} in winter (soil temperature at –10 cm, 2.1 °C) to 4.1 μmol m^{-2} s^{-1} in August 1997 (soil temperature at –10 cm, 17.8 °C). However, strong differences in soil CO_2 efflux were observed between summer 1996 and summer 1997 while the patterns of soil temperature were similar. Therefore, there was a poor correlation between soil CO_2 efflux and soil temperature for soil temperature ranging between 12 and 16 °C even if soil CO_2 efflux displayed a typical exponential relationship with soil temperature (*figure 2*, $r^2 = 0.69$).

During summer, when soil temperature ranged between 12 and 16 °C, a strong reduction in soil CO_2 efflux was associated with a decline in soil water content at –10 cm (*figure 3*, $r^2 = 0.73$). The correlation was less significant for deeper soil layer. Determination coefficients (r^2) were 0.65 using soil water content at –20 cm and 0.61 at –30 and –40 cm. There was no significant correlation with soil water content recorded below –40 cm. The soil volumetric water content at –10 cm (see *figure 1C*) was maximal (0.4) in June and early July 1997, but was below 0.2 in August 1996 and in September 1997. The increase in soil CO_2 efflux between September 1997 (1.13 μmol m^{-2} s^{-1}) and October 1997 (1.64 μmol m^{-2} s^{-1}) while the soil temperature decreased (12.9 and 8.4 °C, respectively) was clearly ascribed to the recovery of a maximal soil volumetric water content after mid-September rainfall (0.18 and 0.27 in September and October 1997, respectively).

Since changes in soil temperature and soil water content affect soil CO_2 efflux, an empirical model was fitted to the soil CO_2 efflux data:

$$y = A\,\theta_v\,e^{BT}$$

with θ_v the soil volumetric water content at –10 cm, T the soil temperature at –10 cm, and A and B two fitting parameters. Combining the data of both years the model accounts for 86 % of the variation in soil CO_2 efflux, with A and B values of 1.13 and 0.136. There was a close agreement between predicted and observed soil CO_2 efflux as shown in *figure 4*.

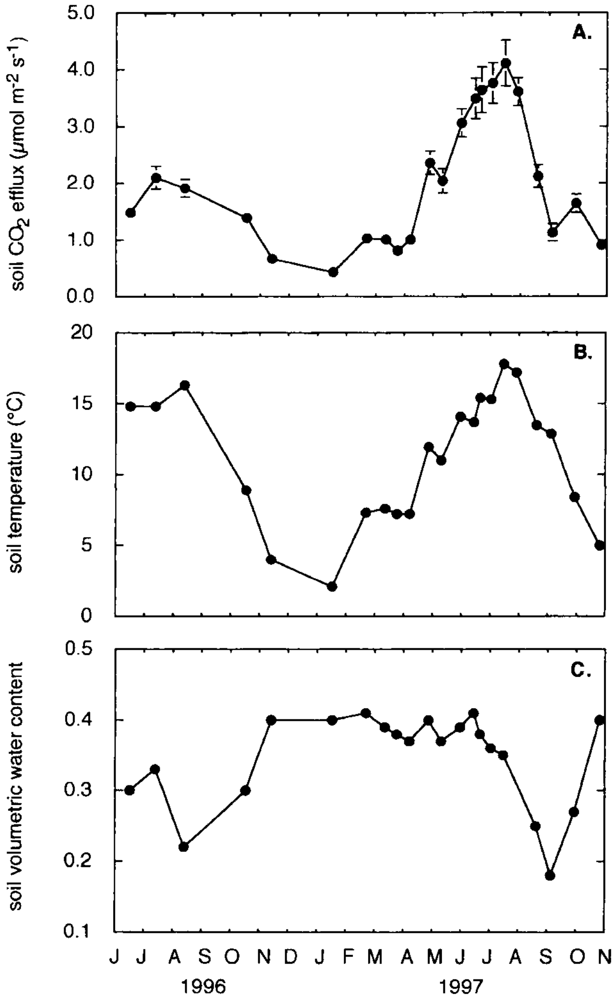

Figure 1. Seasonal courses of soil CO_2 efflux (A), soil temperature at a depth of 10 cm (B) and soil volumetric water content at a depth of 10 cm (C) in the Hesse Forest. Soil CO_2 efflux and soil temperature were simultaneously monitored. Soil volumetric water contents at the time of soil CO_2 efflux measurement were estimated from measured values assuming that soil volumetric water content changes linearly with time between two measurements. Vertical bars, when larger than the symbol, indicate the confidence interval of the mean of 72 measurements of soil CO_2 efflux from 8 a.m. to 4 p.m.

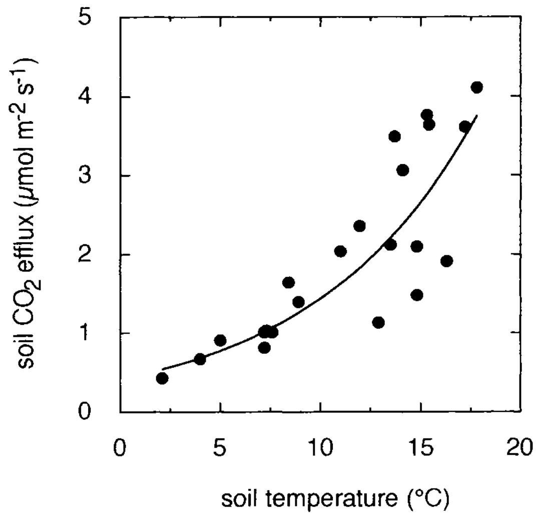

Figure 2. Relationship between soil CO_2 efflux and soil temperature at a depth of 10 cm. An exponential function is fitted through the data (r^2 = 0.69). See the caption of *figure 1* for details.

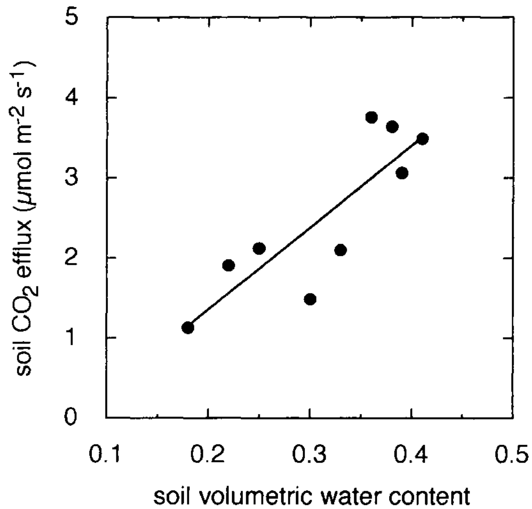

Figure 3. Relationship between soil CO_2 efflux and soil volumetric water content at a depth of 10 cm. The soil temperature range was restricted from 12 to 16 °C. A linear regression is fitted through the data (r^2 = 0.73). See the caption of *figure 1* for details.

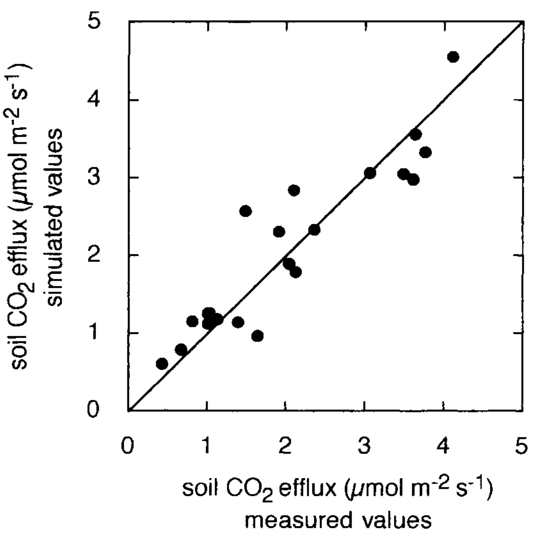

Figure 4. Relationship between measured and predicted values of soil CO_2 efflux with an exponential function ($y = 1.13\ \theta_v\ e^{0.136T}$, $r^2 = 0.86$) with q_v and T the volumetric water content and the temperature of the soil at a depth of 10 cm.

The model was then used to simulate soil CO_2 efflux on a daily basis from daily mean soil temperature and interpolated soil volumetric water content (see Material and methods). These predictions were then used to calculate the annual soil carbon flux from 1 June 1996 to 31 May 1997 and from 1 December 1996 to 30 November 1997 (*table I*). These two 1-year-long periods include two distinct summers. During the first period, which includes the 1996 dry summer (171 mm from 1 June to 14 September), the calculated annual carbon flux was 575 $g_C\ m^{-2}\ year^{-1}$. During the second period, which includes the 1997 wet summer (307 mm from 1 June to 14 September), the calculated annual carbon flux was higher that during the previous period (663 $g_C\ m^{-2}\ year^{-1}$). During summer (from June 1 to September 14), calculated soil carbon efflux was 272 $g_C\ m^{-2}\ year^{-1}$ in 1996 and 352 $g_C\ m^{-2}\ year^{-1}$ in 1997. During the remainder of the year, the difference in soil carbon efflux between both periods was negligible (302 $g_C\ m^{-2}\ year^{-1}$ for period 1 and 311 $g_C\ m^{-2}\ year^{-1}$).

4. DISCUSSION

The dependence of soil CO_2 efflux on soil temperature has been frequently described [13]. We used an empirical exponential function rather than the well-known Q_{10} function. Both were successfully used for biochemical reactions or physiological processes even if both are inherently wrong [13]. However, soil respiration involves various microbial and macrofaune populations

Table I. Annual soil carbon efflux calculated by cumulating simulated soil CO_2 efflux from 1 June 1996 to 31 May 1997 (period 1) and from 1 December 1996 to 30 November 1997 (period 2). Cumulative annual and summer precipitations, and average annual and summer soil temperatures at a depth of 10 cm are given for these two periods. Summer values were calculated from 1 June to 14 September.

	Period 1	Period 2
Annual soil carbon efflux (g_C m^{-2} $year^{-1}$)	575	663
Cumulative annual precipitation (mm)	819	837
Average annual soil temperature (°C)	9.2	9.6
Summer soil carbon efflux (g_C m^{-2} $year^{-1}$)	273	352
Cumulative summer precipitation (mm)	171	307
Average summer soil temperature (°C)	14.8	15.7

that are thought to change during a seasonal cycle and to have different temperature sensitivities. Soil CO_2 efflux also includes root respiration, which is thought to increase in spring and early summer because of active root growth from April to the first week of July (unpublished data). Soil CO_2 efflux may be altered by seasonal changes in soil properties (gas diffusion for instance) and by seasonal changes in organic matter inputs. Then, the use of a Q_{10} function to examine temperature sensitivities of a complex combination of biochemical and physical processes may add confusion. We therefore preferred a simple exponential function to examine temperature effects on soil CO_2 efflux (Ae^{BT}), with B being related to the Q_{10} parameter ($Q_{10} = e^{10B}$). The B value reported here corresponds to a Q_{10} value of 3.9, which is a rather high value in comparison to values ranging between 1.7 and 2.3 frequently reported for physiological processes such as root or microbial respiration [5, 19]. However, Q_{10} values are thought to increase with decreasing temperature. For example, the Q_{10} of organic matter decomposition is about 2.5 at 20 °C and 4.5 at 10 °C [12]. Since soil temperature ranged from 1 to 18 °C in this study, with an annual mean of 9 °C, a rather high Q_{10} value is not unexpected.

In contrast, the effects of soil water content on soil CO_2 efflux are still unclear. Some studies reported only weak relationships between soil CO_2 efflux and soil water content [1, 3, 6]. However, inhibition of soil CO_2 efflux by low soil water content as observed in this study has already been reported [2, 7, 8]. Moreover, we found a similar effect on the microbial respiration of sieved soil placed in 3-L pots at various soil volumetric water content (unpublished data). Strong drought is thought to alter micro-organism and root metabolism. But at moderate soil drought, microbial respiration is probably limited by the diffusion of soluble organic substrates. Skopp et al. [17] proposed a diffusion-based model of the form $y = a\,\theta_v^{\,f}$ to account for this limitation. We used a simplified form of this model (i.e. f set to 1) since we obtained an f value of 1.03 in first runs.

Inhibition of soil CO_2 efflux by high soil water content was also reported [2, 3] and was ascribed to the limitation of oxygen diffusion in soil pore spaces filled with water. Despite a rather high water table in autumn, winter and spring, it was not possible to include a statistically significant parameter to account for a limitation of soil CO_2 efflux by high soil water content in our study. In fact, it may be very difficult to distinguish between the effect of declining temperature and increasing soil water content as both occur together in autumn and winter, and both reverse together in spring and summer. Davidson et al. [2] suggested that the empirical Q_{10} parameter confounds the effects of both temperature and excess soil water content since both factors co-vary across seasons. Such a confounding effect of soil temperature and excess soil water content may account for the rather high Q_{10} value we obtained (3.9). Both low soil temperature and excessive soil water content may account for low soil CO_2 efflux in autumn, winter and spring, while the positive effect of high temperature in summer may be enhanced by better soil water conditions. In agreement with this hypothesis, Davidson et al. [2] reported Q_{10} values of 3.5 in well-drained sites and 4.5 in a very poorly drained site in the Harvard forest ecosystem. In addition, root growth respiration may also contribute to high soil CO_2 efflux in early summer [8].

Averaging our two estimates of annual soil carbon efflux gives an average value of 620 g_C m^{-2} $year^{-1}$. There are very few published data obtained with gas exchange chambers connected to infrared gas analysers. Up to now, none of them were from temperate European deciduous forests. Slightly higher values than ours were reported for the Harvard forest ecosystem dominated by red oak and red maple (720 g_C m^{-2} $year^{-1}$, Massachusetts, 42.3°N, 72.1°W, 340 m elev. [2]) or for the Walker Branch Watershed dominated by chestnut oaks, white oaks and yellow-poplars (830 g_C m^{-2} $year^{-1}$, Tennessee, 35.8°N, 84.2°W [8]). However, these two forests were submitted to higher annual rainfall and higher average annual temperatures than ours. Comparisons with past studies are difficult since most of them were made with static chambers using chemical traps for CO_2, a method which is thought to underestimate the actual soil CO_2 efflux [11, 15]. Using potassium chloride as a chemical trap, Anderson [1] reported a slightly lower annual carbon efflux (575 g_C m^{-2} $year^{-1}$) for a beech forest in southern England which was older than ours (40–60 years old).

In our site, soil carbon efflux accounts for 70 % of the whole ecosystem respiration estimated by a micrometeorological method (Granier, pers. comm.). Therefore, it is an important component of the net ecosystem carbon exchange. However, soil carbon efflux is often simulated by empirical relationships with soil temperature as the single input variables [13, 16]. Edwards [3] concluded that temperature accounts for more of the variation in soil respiration in a deciduous forest in Tennessee with high precipitation. In contrast, the difference between our two estimates of annual soil carbon efflux (June 1996–May 1997 and December 1996–November 1997) clearly highlights the dependence of soil carbon efflux on soil water content during summer. Since summer drought may occur at irregular intervals in western Europe, and may become more frequent in future decades, we need to incorporate soil water content in further development of predictive models of net ecosystem carbon exchange.

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