



HAL
open science

Soil CO₂ efflux in a beech forest: the contribution of root respiration

Daniel Epron, Laetitia Farque, Eric Lucot, Pierre-Marie Badot

► **To cite this version:**

Daniel Epron, Laetitia Farque, Eric Lucot, Pierre-Marie Badot. Soil CO₂ efflux in a beech forest: the contribution of root respiration. *Annals of Forest Science*, 1999, 56 (4), pp.289-295. hal-00883273

HAL Id: hal-00883273

<https://hal.science/hal-00883273>

Submitted on 11 May 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Soil CO₂ efflux in a beech forest: the contribution of root respiration

Daniel Epron^{a*}, Laetitia Farque^a, Eric Lucot^b, Pierre-Marie Badot^{a,b}

^aÉquipe sciences végétales, laboratoire biologie et écophysiole, institut des sciences et des techniques de l'environnement, université de Franche-Comté, pôle universitaire, BP 71427, 25211 Montbéliard cedex, France

^bÉquipe 1975, sciences végétales, laboratoire biologie et écophysiole, institut des sciences et des techniques de l'environnement, université de Franche-Comté, place Leclerc, 25030 Besançon cedex, France

(Received 24 September 1998; accepted 17 December 1998)

Abstract – The contribution of root respiration to soil carbon efflux in a young beech stand was estimated by comparing soil CO₂ efflux from small trenched plots to efflux from undisturbed areas (main plot). Soil CO₂ efflux was measured every 2–4 weeks in 1997. An empirical model ($y = A q_v e^{BT}$) was fitted to the soil CO₂ efflux data and was used to calculate annual soil carbon efflux from soil temperature (T) and soil volumetric water content (q_v). The annual soil carbon efflux were 0.66 kg_C m⁻² year⁻¹ in the main plot and 0.42 kg_C m⁻² year⁻¹ in the trenched plots. The difference between these two estimations was corrected for the decomposition of roots that were killed following trenching. The heterotrophic component of soil carbon efflux accounts for 40 % of total soil carbon efflux (0.26 kg_C m⁻² year⁻¹) while root respiration accounts for 60 % of soil C release (0.40 kg_C m⁻² year⁻¹). (© Inra/Elsevier, Paris.)

carbon cycle / *Fagus sylvatica* L. / respiration / root / soil CO₂ efflux

Résumé – Flux de CO₂ provenant du sol dans une hêtraie : la contribution de la respiration des racines. La contribution de la respiration des racines au flux de carbone provenant du sol d'une jeune hêtraie a été estimée en comparant le flux de CO₂ provenant du sol sur des petites placettes isolées par une tranchée au flux de CO₂ provenant du sol mesuré sur la placette principale. Le flux de CO₂ provenant du sol a été mesuré toutes les 2 à 4 semaines en 1997. Un modèle empirique ($y = A \theta_v e^{BT}$) a été ajusté sur les données de flux de CO₂ provenant du sol, et utilisé pour calculer le flux annuel de carbone provenant du sol à partir de la température du sol (T) et de la teneur en eau volumique du sol (θ_v). Les flux annuels de carbone provenant du sol étaient de 0,66 kg_C m⁻² y⁻¹ pour la placette principale et de 0,42 kg_C m⁻² y⁻¹ pour les petites placettes isolées par une tranchée. La différence entre les deux estimations a été corrigée pour prendre en compte la décomposition des racines tuées lors de l'établissement de la tranchée. La composante hétérotrophe représente 40 % du flux total de carbone provenant du sol (0,26 kg_C m⁻² y⁻¹) alors que la respiration des racines représente 60 % du dégagement de carbone (0,40 kg_C m⁻² y⁻¹). (© Inra/Elsevier, Paris.)

cycle du carbone / *Fagus sylvatica* L. / respiration / racine / flux de CO₂ provenant du sol.

1. Introduction

Soil carbon efflux is an important component of the carbon cycle in temperate forests and is thought to represent 60–80 % of ecosystem respiration [12, 23, 27]. Soil

carbon efflux includes both CO₂ released during decomposition of leaf and root litters and CO₂ from root respiration. Respiration rates of plant organs and leaf and fine root turnover are as important as photosynthesis in determining the ability of forest ecosystem to sequester car-

* Correspondence and reprints
depron@pu-pm.univ-fcomte.fr

bon through an increase in productivity [22]. Direct measurements of fine root respiration have highlighted the high specific respiration rates of fine roots of forest trees [6, 8, 9, 24, 28]. Therefore, root respiration is thought to be an important component of the carbon balance of trees in forest ecosystems. But available estimations of the contribution of root respiration to soil CO₂ efflux are still rather scarce, and the most reliable ones vary considerably from 30 to 60 % [4, 11, 17, 18]. Since both root and heterotrophic respiration are thought to depend on site characteristics (species, climate, stand age, management practices, etc. [23]), estimations of the contribution of root respiration to soil CO₂ efflux are still required to provide a better knowledge of carbon budgets of forest ecosystems.

However, direct measurements of root respiration are rather difficult in situ and digging to access the roots is thought to have a large influence on root respiration because of wounding effects. In addition, instantaneous measurements of root respiration are difficult to scale to the stand-level because CO₂ concentration within the soil pores changes greatly with time and depth [24]. A reduction in root respiration at high CO₂ has been reported but its importance is still controversial [3, 7, 9, 21]. Indirect methods have been proposed to quantify both heterotrophic and autotrophic contributions to total soil CO₂ efflux. Data obtained by comparing in situ soil CO₂ efflux and respiration of soil samples from which roots were removed are questionable because of high soil disturbance during soil sampling and processing. Root respiration can be estimated by subtracting litter, root and soil organic matter decomposition rates from soil CO₂ efflux [11] or by comparing soil respiration before and after clear-felling [17, 18]. Root respiration can be estimated in a similar fashion by comparing soil CO₂ efflux recorded on small trenched plots to the one recorded on the main plot [4, 11].

In this study, we adapted this latter approach to estimate the contribution of root respiration to soil CO₂ efflux in a young beech stand in north-eastern France, a site that belongs to a network of 15 representative forests extending over a large climatic range in Europe.

2. Materials and methods

2.1. Study site

The study site is located in the Hesse forest (north-eastern France, 48°40 N, 7°05 E, elevation 305 m, 7 km²) and is one of the Euroflux sites (European project ENV4-CT95-0078). The experimental plot covers 6 10⁻³ km² and is mainly composed of 30-year-old

beeches (*Fagus sylvatica*). Herbaceous understory vegetation is rather sparse. Leaf area index was 5.7 in 1996 and 5.6 in 1997, which corresponds to a leaf litter fall of 0.14 kg_C m⁻² year⁻¹ (Granier, pers. comm.). 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 ratio of 12.2 and an apparent density of 0.85 kg dm⁻³, and is covered with a mull type humus (see [10]).

Six sub-plots of about 100 m² each were randomly chosen within the experimental plot for soil CO₂ efflux measurements. Two 3-m² sub-plots (2 × 1.5 m) with no trees were established in June 1996 by digging a trench (1 m deep) around each, lining the trench with a polyethylene film and filling it back. The nearest trees were 1 m away from the trenches.

Soil temperature was measured at –10 cm by copper/constantan thermocouples. Data acquisition was made with a CR7 datalogger (Campbell Scientific Inc., USA) at 10-s. time interval. Thirty-minute averages were stored. In addition, soil temperature was also monitored simultaneously with soil CO₂ 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. Volumetric water content of the soil (θ_v) was measured every 10 cm in depth on the main plot with a neutron probe (NEA, Denmark) in eight aluminium access tubes (160 cm or 240 cm deep) at 1-week to 3-week intervals. Two distinct calibration curves were used for sub-surface (–10 and –20 cm) and deeper measurements. In addition, a polyethylene reflector was used for sub-surface measurements. Between two measurements, the volumetric water content of the soil was assumed to change linearly with time. This assumption can be wrong if rainfalls occurs during that period. Simulations of daily soil carbon efflux would be overestimated before the rainfall event and underestimated after it. However, it would not strongly affect our annual estimation of soil carbon efflux as overestimations would counterbalance underestimations on an annual basis. A TDR device (Trase system, Soil Moisture Equipment Corp., Santa Barbara, USA) was used for additional measurements of soil water content using 40-cm-long, vertically installed, stainless steel wave guides. Measurements were made on the six sub-plots of the main plots and on the two trenched plots (two measurements on each sub-plot) on several occasions between June and October 1997. A comparison between TDR and neutron probe data on the main plot from June to October 1997 allowed us to estimate seasonal variations of θ_v on the trenched plots during that period.

2.2. Soil CO₂ efflux

Soil CO₂ efflux was measured using the Li 6000–09 (LiCor Inc., USA) soil respiration chamber in which the increase of the CO₂ concentration was recorded with the Li 6250 infrared gas analyser (LiCor Inc., USA) as already described [10]. Every 2 to 4 weeks, 12 measurements were recorded on each sub-plots during an 8-h period from 8 am to 4 pm. Daily averages ($n = 72$ for the main plot and $n = 24$ for the trenched plots) and confidence intervals at $P = 0.05$ were calculated. An empirical model was fitted to the soil CO₂ 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 fitted parameters. The correlation between soil water content and soil CO₂ efflux was less significant for deeper soil layer [10]. The model was then used to calculate annual soil carbon efflux from 1 December 1996 to 30 November 1997.

2.3. Root biomass, root growth and root decay

Root biomass was determined from vertical profiles of root densities of 11 representative trees. Trenches were dug at a distance 150, 100, 50 and 25 cm from the trunks. Roots were counted by diameter classes from the soil surface to a depth of 100 cm using a 10 × 10-cm grid affixed to the smoothed wall of the trench [5, 14]. The number of roots in each diameter class was converted into root volume knowing the average root length of roots. Average root lengths were calculated from ramification patterns of roots of each diameter class, which were deduced from excavated root systems. Root volume was converted into root biomass using a root mass per unit volume of 0.8 kg_{DM} dm⁻³ (unpublished data). The relationships observed between root biomass per tree and trunk circumference were then used to estimate the mean root biomass knowing the distribution of trunk circumference. Fine root biomass (diameter < 2 mm) was also estimated from eight soil cores (8 cm in diameter, 12 cm high) collected monthly from March to July 1997. Cores were stored in plastic bags at 4 °C until fine roots were washed free of soil, sorted into live and dead fractions and dried at 60 °C for 48 h. Fine root biomass calculated from soil cores (0.31 kg_{DM} m⁻²) accounts for 45 % of the total fine root biomass in this site (0.69 kg_{DM} m⁻²) according to the vertical profiles of root impacts.

Fine root growth into 14 root-free cores was used to estimate annual fine root production from the number of roots grown into the cores over 1 year [19, 20]. Soil

cores (8 cm in diameter, 12 cm high) were taken in March 1997, all roots were carefully removed, and the sifted soil was replaced within the hole. In April 1998, these ingrowth cores were retrieved and processed as above. This estimation of annual fine root production was corrected for the spatial and vertical variations of fine root biomass, assuming that fine root biomass in soil cores represents 45 % of the total fine root biomass.

Fine root decomposition was estimated by coring and sorting remaining dead roots in the trenched plots 2 years after trenching. The remaining fine root necromass was then compared to initial fine root biomass and necromass in soil cores. Coarse roots (2–10 mm in diameter) excavated during the installation of the trenched plots were washed free of soil, cut into pieces of 4–6 cm long and placed into 10 × 15-cm litter bags (1 mm mesh size). Bags were then placed at a soil depth of 10–15 cm. On five occasions during a 20-month period, 14 litter bags were collected. Roots were carefully washed free of soil and dried at 60 °C for 5 days. Simple exponential decay functions ($M_t = M_0 e^{-kt}$) were fitted to the data, M_t and M_0 being the remaining and the initial root dry mass, respectively, t being time and k the decay constant. Carbon loss as CO₂ during root decomposition was calculated as $(1 - a) c M_0 (1 - e^{-kt})$. c , the initial carbon concentration in root was set at 44 %; a is the fraction of carbon which is incorporated into soil organic matter while $1 - a$ is the fraction lost as CO₂ by microbial respiration during initial belowground litter decay; a was set to 0.22 [13].

3. Results

On the main plot, soil CO₂ efflux varied greatly during the year, from less than 0.5 μmol m⁻² s⁻¹ in winter to more than 4 μmol m⁻² s⁻¹ in summer (*figure 1C*). Changes in soil CO₂ efflux were mainly related to changes in soil temperature, but a decrease in soil water content strongly affected late summer values. Therefore, soil CO₂ efflux was best described with an empirical model including θ_v the soil volumetric water content at –10 cm and T the soil temperature at –10 cm ($y = A \theta_v e^{BT}$, *figure 2*). Soil CO₂ efflux was lower on the trenched plots than on the main plot from May to October, except in September when soil CO₂ efflux on the main plot was inhibited by a pronounced decline in soil water content. Elimination of tree transpiration by trenching clearly influenced soil water content (*figure 1A*) while soil temperatures were almost the same on the main plot and on the trenched plots (*figure 1B*).

The A and B values in *table 1* were used to simulated soil CO₂ efflux on a daily basis from soil temperature

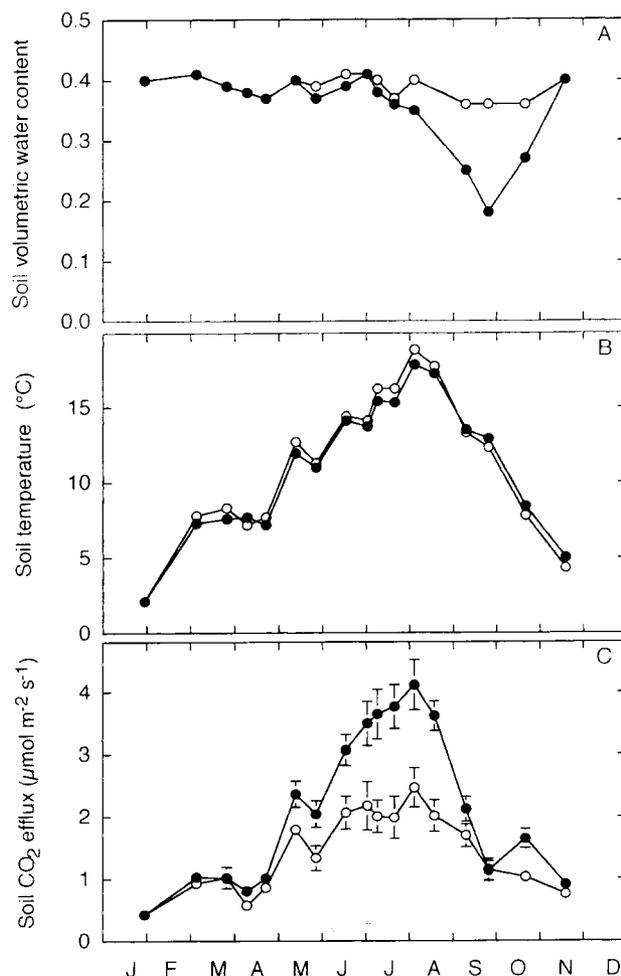


Figure 1. Seasonal courses of soil water content at 10 cm deep (A), soil temperature at 10 cm deep (B) and soil CO₂ efflux (C) on the main (closed circles) and on the trenched plots (open circles) in the Hesse Forest in 1997. Vertical bars, when larger than the symbol, indicate the confidence interval of the daily mean soil CO₂ efflux ($P = 0.05$). θ_v was measured with a neutron probe on the main plot, while variations of θ_v on the trenched plots from June to October 1997 were deduced from a cross calibration between neutron probe and TDR data (see section 2.1).

and soil volumetric water content at -10 cm recorded on the main plot. These predictions were then used to calculate annual soil carbon efflux from 1 December 1996 to 30 November 1997 (table I). The annual soil carbon efflux were $0.66 \text{ kg}_C \text{ m}^{-2} \text{ year}^{-1}$ on the main plot and $0.42 \text{ kg}_C \text{ m}^{-2} \text{ year}^{-1}$ on the trenched plots. The difference between the two estimations has to be corrected for the decomposition of roots that were killed by trenching to

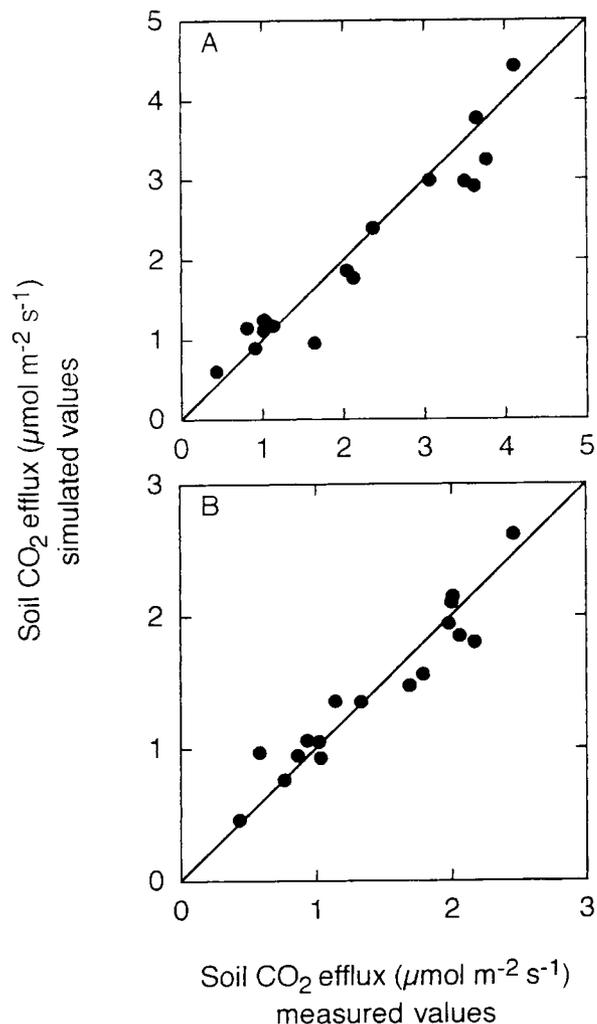


Figure 2. Relationship between measured and predicted values of soil CO₂ efflux with an exponential function ($y = A \theta_v e^{BT}$) for the main plot (A) and for the trenched plots (B) with θ_v and T the volumetric water content and the temperature of the soil at a depth of 10 cm. A and B are given in table I.

account for the heterotrophic component of soil carbon efflux.

The comparison of remaining fine root necromass 2 years after trenching to initial fine root biomass and necromass indicated that 53 % of killed fine roots disappeared within 2 years ($k = 0.38$, table II). The decay constant obtained by fitting exponential decay model over the time course of mass loss in litter bags was 0.22 for

Table I. Predicted parameter values and determination coefficients (r^2) for the empirical model ($y = A \theta_x e^{BT}$) fitted over seasonal courses of soil CO_2 efflux on the main and on the trenched plots, and estimated annual soil carbon efflux from 1 December 1996 to 30 November 1997.

		Main plot	Trenched plots
Fitted parameters ^a	A	1.13	1.33
	B	0.136	0.085
	r^2	0.86	0.89
Soil carbon efflux ($\text{kg}_C \text{ m}^{-2} \text{ year}^{-1}$) ^b		0.66	0.42

^a Five additional data obtained in 1996 on the main plot were used to determine A and B. Without these additional data A and B were 1.14 and 0.139, respectively, for the main plot.

^b Annual soil carbon efflux on the trenched plots was calculated from soil temperature and soil volumetric water content recorded on the main plot. Otherwise, it was $0.50 \text{ kg}_C \text{ m}^{-2} \text{ year}^{-1}$.

Table II. Root biomass in the trenched plots at the time of trenching, decay constant of freshly killed fine and coarse roots, and carbon efflux due to CO_2 released during the decomposition of these roots.

	Root diameter	
	$\leq 2 \text{ mm}$	$> 2 \text{ mm}$
Biomass ($\text{kg}_{\text{DM}} \text{ m}^{-2}$)	1.10	1.03
decay constant	0.38	0.22 ^a
Carbon efflux ($\text{kg}_C \text{ m}^{-2} \text{ year}^{-1}$) ^b	0.10	0.06

Roots were killed by trenching in June 1996 and the carbon efflux was estimated from 1 December 1996 to 30 November 1997.

^a This value of decay constant was obtained for roots of 2–10 mm diameter ($r^2 = 0.90$) and we assumed that it is valuable for bigger roots.

^b Carbon loss as CO_2 during root decomposition was calculated assuming that the initial carbon concentration in root was 44 % and the fraction of carbon lost as CO_2 by microbial respiration during initial belowground litter decay was 0.78 [13].

coarse roots ($r^2 = 0.90$, *table II*). Fine and coarse root biomasses deduced from root profiles and root cores were 0.69 and $2.06 \text{ kg}_{\text{DW}} \text{ m}^{-2}$, respectively, for the main plot. However, since trenched plots were established at least 1 m away from trees, fine and coarse root biomasses in trenched plots at the time of trenching were 1.10 and $1.03 \text{ kg}_{\text{DW}} \text{ m}^{-2}$, respectively.

The CO_2 released during the decomposition of killed roots from 1 December 1996 to 30 November 1997 was estimated as $0.10 \text{ kg}_C \text{ m}^{-2} \text{ year}^{-1}$ and $0.06 \text{ kg}_C \text{ m}^{-2} \text{ year}^{-1}$ for fine and coarse roots, respectively. The heterotrophic component of soil carbon efflux was therefore $0.42 - (0.10 + 0.06)$, i.e. $0.26 \text{ kg}_C \text{ m}^{-2} \text{ year}^{-1}$ and accounted for 40 % of total soil carbon efflux while root respiration was thought to represent 60 % of soil C release (i.e. $0.40 \text{ kg}_C \text{ m}^{-2} \text{ year}^{-1}$).

Fine root biomass in ingrowth core after 1 year ranged from 0.06 to 0.63 g with an average value of 0.29 g ($n = 14$). Fine root biomass in soil cores (8 cm in diameter, 12 cm high) is thought to represent 45 % of the total fine root biomass, taking into account both the spatial and vertical distribution of fine roots deduced from root profiles. We therefore calculated that fine root production was $0.13 \text{ kg}_{\text{DM}} \text{ m}^{-2} \text{ year}^{-1}$, which correspond to $0.06 \text{ kg}_C \text{ m}^{-2} \text{ year}^{-1}$ assuming a carbon concentration in root of 44 %.

4. Discussion

Our estimation of the contribution of root respiration to soil carbon efflux in a 30-year-old beech stand in north-eastern France (60 %) is similar to the one reported by Ewel et al. [11] for a 29-year-old slash pine plantation in Florida and slightly higher than those reported by Nakane et al. [17, 18] who estimated that root respiration contributes about half of soil carbon efflux in a 80-year-old Japanese red pine stand and in a 102-year-old oak forest (*table III*). In contrast, Bowden et al. [4] calculated that root respiration accounted for 33 % of soil carbon efflux in a temperate mixed hardwood forest in Massachusetts. However, they neglected in their calculation the release of carbon from decomposition of roots killed by trenching because they postulated that decomposition of freshly killed root was negligible at the time of their measurements. If their assumption was untrue, they estimated that root respiration would account for about one half of soil carbon efflux.

Our estimation of the partitioning between root and heterotrophic contributions to soil carbon efflux is sensitive to the assumption we have made to account for the decomposition of freshly killed root. The decay constants we used are within the range of published values for both fine and coarse roots of woody species [1, 15, 25]. McLaugherty et al. [15] argued that fine roots were still connected to larger roots and therefore that carbohydrates and nutrients stored in coarse roots may delay the decomposition of fine roots in trenched plots. They also showed that fine root decomposition followed a two-phased pattern, and that dry matter loss was more rapid during the first stage than during the second. Our k value for fine roots, which was simply obtained by comparing the remaining fine root mass 2 years after trenching to fine root mass in soil cores, should therefore be considered as a rough estimation. Nevertheless, we calculated that a 20 % variation in the values of the decay constants would change our estimation of the contribution of root respiration to soil carbon efflux by less than 5 %.

Table III. Annual estimations of root respiration and of its contribution to soil carbon efflux in various forest ecosystems.

Forest type	Age	Location	Root respiration		Ref.
			kg _C m ⁻² year ⁻¹	%	
<i>Pinus densiflora</i>	80	Japan	0.66	51	18
<i>Pinus elliottii</i>	29	Florida, USA	0.81	62	11
Mixed deciduous	??	Massachusetts, USA	0.18 ^a	49	4
<i>Quercus serrata</i>	80	Japan	0.48	51	17
<i>Fagus sylvatica</i>	30	France (this study)	0.40	60	

^a Assuming that root decomposition occurred at the time of the measurements (refer to [4] for the discussion of this hypothesis).

In other reports using trenched plots to partition root and heterotrophic contributions to soil carbon efflux [4, 11], differences in soil water content between normal and trenched plots have been neglected. In our study, trenching strongly influences soil water content by eliminating tree transpiration. In late summer and early autumn 1997, the soil water content was twice as high in the trenched plots than in the main plot. In a previous paper [10], we showed that a decrease in soil water content strongly influenced soil CO₂ efflux in summer. If we had neglected the differences in seasonal courses of soil water content between the main and the trenched plots, the contribution of root respiration to soil carbon efflux would have been underestimated (52 % instead of 60 %).

Fine root production in our stand (0.13 kg_{DM} m⁻² year⁻¹) is lower than those reported for older beech forests (0.44 in a 120-year-old stand [26] and 0.39 in a 145-year-old stand [2]), but falls within the range of values compiled by Nadelhoffer and Raich [16] and Persson [20] for forest ecosystems. In many studies, fine root production were not corrected for the spatial variations of fine root biomass. In our case, it would have led to an overestimation of fine root production (0.21 instead of 0.13 kg_{DM} m⁻² year⁻¹) since there is less fine root in the vicinity of trunks than at 1 m away. Our estimation of fine root production may be underestimated since disturbances associated with soil coring may have restricted root ingrowth in early spring [19]. Whatever the case, the difference between the maximum and the minimum fine root biomass in soil cores collected monthly from March to July 1997 gave a similar estimation of fine root production (i.e. 0.12 kg_{DM} m⁻² year⁻¹).

In order to test the accuracy of our estimation of the contribution of root respiration to soil carbon efflux, we used soil carbon budget to calculate the carbon allocation to root respiration and turnover. This calculation assumed that changes in soil carbon content and changes in fine root biomass are negligible in comparison with carbon fluxes, i.e. that soil organic matter and fine root biomass are in steady state. Another assumption is that soil CO₂ efflux is the only output pathway of soil carbon.

Therefore, leaching of dissolved carbon is neglected. Carbon allocation to root respiration and turnover as estimated by the difference between soil respiration and litterfall (i.e. 0.52 kg_C m⁻² year⁻¹) is within the range of published values for temperate broad-leaves forests [22], but is higher than the sum of fine root production (0.06 kg_C m⁻² year⁻¹) and root respiration (0.40 kg_C m⁻² year⁻¹). However, the former calculation of carbon allocation to root respiration and turnover is thought to be overestimated as it ignored the decomposition of coarse woody detritus [22]. In our site, the input of carbon in the soil from dead branches that were left in the stand after a recent thinning may at least partly account for the difference between our two estimations of carbon allocation to root respiration and turnover [22]. In addition, an underestimation of fine root production cannot be excluded, as mentioned earlier.

This study highlights the important contribution of root respiration to total soil CO₂ efflux in a 30-year-old beech stand. Further works are needed to characterise the influence of species composition, site location (both climatic and edaphic conditions), stand ages and management practices on the partitioning of root and heterotrophic contributions to soil carbon efflux.

Acknowledgements: Soil temperature and water content data were provided by André Granier (Inra Nancy, unité d'écophysiologie forestière). This work was supported by the European programme Euroflux (ENV4-CT95-0078) and by Office national des forêts (ONF). The District urbain du Pays de Montbéliard (DUPM) is also acknowledged for financial supports.

References

- [1] Aber J.D., Melillo J.M., McLaugherty C.A., Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems, *Can. J. Bot.* 68 (1990) 2201–2208.

- [2] Bauhus J., Bartsch N., Fine-root growth in beech (*Fagus sylvatica*) forest gaps, *Can. J. For. Res.* 26 (1996) 2153–2159.
- [3] Bouma T., Nielsen K.L., Eissenstat D.M., Lynch J.P., Estimating respiration of roots in soil: Interactions with soil CO₂, soil temperature and soil water content, *Plant Soil* 195 (1997) 221–232.
- [4] Bowden R.D., Nadelhoffer K.J., Boone R.D., Melillo J.M., Garrison J.B. Contributions of aboveground litter, below-ground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest, *Can. J. For. Res.* 23 (1993) 1402–1407.
- [5] Bréda N., Granier A., Barataud F., Moyne C., Soil water dynamics in an oak stand. Part I. Soil moisture, water potentials and water uptake by roots, *Plant Soil* 172 (1995) 17–27.
- [6] Burton A.J., Pregitzer K.S., Zogg G.P., Zak D.R., Latitudinal variation in sugar maple fine root respiration, *Can. J. For. Res.* 26 (1996) 1761–1768.
- [7] Burton A.J., Zogg G.P., Pregitzer K.S., Zak D.R., Effect of measurement CO₂ concentration on sugar maple root respiration, *Tree Physiol.* 17 (1997) 421–427.
- [8] Cropper W.P. Jr, Gholz G.L., In situ needle and fine root respiration in mature slash pine (*Pinus elliottii*) trees, *Can. J. For. Res.* 21 (1991) 1589–1595.
- [9] Epron D., Badot P.M., Fine root respiration in forest trees, in Puech J.C., Latché A., Bouzayen M. (Eds.), *Plant Sciences 1997*, SFPV, Paris, 1997, pp. 199–200.
- [10] Epron D., Farque L., Lucot E., Badot P.M., Soil CO₂ efflux in a beech forest: dependence on soil temperature and soil water content, *Ann. Sci. For.* 56 (1999) 221–226.
- [11] Ewel K.C., Cropper W.P., Gholz H.L., Soil CO₂ evolution in Florida slash pine plantations. II. Importance of root respiration, *Can. J. For. Res.* 17 (1987) 330–333.
- [12] Goulden M.L., Munger J.W., Fan S.M., Daube B.C., Wofsy S.C., Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy, *Global Change Biol.* 2 (1996) 162–182.
- [13] Jenkinson D.S., The turnover of organic carbon and nitrogen in soil, *Phil. Trans. R. Soc. Lond. B* 329 (1990) 361–368.
- [14] Lucot E., Badot P.M., Bruckert S., Influence de l'humidité du sol et de la distribution des racines sur le potentiel hydrique du xylème dans des peuplements de chêne (*Quercus* sp.) de basse altitude, *Ann. Sci. For.* 52 (1995) 173–182.
- [15] McLaugherty C.A., Aber J.D., Melillo J.M., Decomposition dynamics of fine roots in forested ecosystems, *Oikos* 42 (1984) 378–386.
- [16] Nadelhoffer K.J., Raich J.W., Fine root production estimates and belowground carbon allocation in forest ecosystems, *Ecology* 73 (1992) 1139–1147.
- [17] Nakane K., Kohno T., Horikoshi T., Root respiration rate before and just after clear-felling in a mature, deciduous, broad-leaved forest, *Ecol. Res.* 11 (1996) 111–119.
- [18] Nakane K., Yamamoto M., Tsubota H., Estimation of root respiration rate in a mature forest ecosystem, *Jpn. J. Ecol.* 33 (1983) 397–408.
- [19] Neill C., Comparison of soil coring and ingrowth methods for measuring belowground production, *Ecology* 73 (1992) 1918–1921.
- [20] Persson H.A., The distribution and productivity of fine roots in boreal forests, *Plant Soil* 71 (1983) 87–101.
- [21] Qi J., Marshall J.D., Mattson K.G., High soil carbon dioxide concentrations inhibit root respiration of Douglas fir, *New Phytol.* 128 (1994) 435–442.
- [22] Raich J.W., Nadelhoffer K.J., Belowground carbon allocation in forest ecosystems: global trends, *Ecology* 70 (1989) 1346–1354.
- [23] Raich J.W., Schlesinger W.H., The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate, *Tellus* 44B (1992) 81–99.
- [24] Ryan M.G., Hubbard R.M., Pongracic S., Raison R.J., McMurtrie R.E., Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status, *Tree Physiol.* 16 (1996) 333–343.
- [25] Scheu S., Schauermaun J., Decomposition of roots and twigs: Effects of wood type (beech and ash), diameter, site of exposure and macrofauna exclusion, *Plant Soil* 163 (1994) 13–24.
- [26] Van Praag H.J., Sougnez-Remy S., Weissen F., Carletti G. Root turnover in a beech and a spruce stand of the Belgian Ardennes, *Plant Soil* 105 (1988) 87–103.
- [27] Wofsy S.C., Goulden M.L., Munger J.W., Fan S.M., Bakwin P.S., Daube B.C., Bassow S.L., Bazzaz F.A., Net exchange of CO₂ in a mid-latitude forest, *Science* 260 (1993) 1314–1317.
- [28] Zogg G.P., Zak D.R., Burton A.J., Pregitzer K.S., Fine root respiration in northern hardwood forests in relation to temperature and nitrogen availability, *Tree Physiol.* 16 (1996) 719–725.