Tree Physiology 21, 145–152

Seasonal dynamics of soil carbon dioxide efflux and simulated rhizosphere respiration in a beech forest

DANIEL EPRON,[1] VALERIE LE DANTEC,[2] ERIC DUFRENE[2] and ANDRE GRANIER[3]

[1] *Laboratoire de Biologie et Ecophysiologie, Institut des Sciences et des Techniques de l'Environnement, Université de Franche-Comté, BP 71427, 25211 Montbéliard cedex, France*

[2] *Laboratoire d'Ecophysiologie Végétale, Bâtiment 362, CNRS-UA 8079, Université de Paris XI, 91405 Orsay cedex, France*

[3] *Laboratoire d'Ecophysiologie Forestière, INRA Nancy, 54280 Champenoux, France*

Received November 6, 1999

Summary Respiration of the rhizosphere in a beech (*Fagus sylvatica* L.) forest was calculated by subtracting microbial respiration associated with organic matter decomposition from daily mean soil CO_2 efflux. We used a semi-mechanistic soil organic matter model to simulate microbial respiration, which was validated against "no roots" data from trenched subplots. Rhizosphere respiration exhibited pronounced seasonal variation from 0.2 g C m^{-2} day^{-1} in January to 2.3 g C m^{-2} day^{-1} in July. Rhizosphere respiration accounted for 30 to 60% of total soil CO_2 efflux, with an annual mean of 52%. The high Q_{10} (3.9) for *in situ* rhizosphere respiration was ascribed to the confounding effects of temperature and changes in root biomass and root and shoot activities. When data were normalized to the same soil temperature based on a physiologically relevant Q_{10} value of 2.2, the lowest values of temperature-normalized rhizosphere respiration were observed from January to March, whereas the highest value was observed in early July when fine root growth is thought to be maximal.

Keywords: Fagus sylvatica, root respiration, soil CO_2 efflux, temperature.

Introduction

Respiration is an important component of the carbon balance in temperate forests and is thought to consume a large proportion of the carbon assimilated by leaves (Raich and Nadelhoffer 1989, Vogt 1991, Raich and Schlesinger 1992). Together with photosynthesis, respiration of plant organs is, therefore, an important determinant of forest productivity and must be taken into consideration when determining the ability of forest ecosystems to sequester carbon (Ryan et al. 1996).

In contrast to other plant organs, direct measurements of respiration in roots are difficult to make reliably because excavation is thought to have a large influence on root respiration as a result of wounding effects and changes in root microenvironment. Indirect methods have been proposed to estimate root respiration from total soil CO_2 efflux. However, soil CO_2 efflux includes CO_2 released during decomposition of leaf and root litter, as well as CO_2 from root respiration. Estimates of the contribution of root respiration to total soil CO_2 efflux vary widely from 22% (Tate et al. 1993) to 90% (Thierron and Laudelout 1996). In part, this variability can be explained by differences in soil, vegetation or climate and their effects on soil CO_2 efflux and its root and microbial components (Sowell and Spomer 1986, Hanson et al. 1993, Burton et al. 1996, Zogg et al. 1996, Burton et al. 1998, Janssens and Ceulemans 1998). However, most of the variability is probably a result of limitations in the various methods that have been employed.

Root respiration can be estimated by comparing *in situ* soil CO_2 efflux and respiration of soil samples from which roots have been removed (Lamade et al. 1996, Thierron and Laudelout 1996). These methods often give high estimates of the contribution of root respiration to total soil CO_2 efflux, but the data are questionable because of high soil disturbance during soil sampling and processing. Kucera and Kirkham (1971) calculated root respiration in tall grass prairies from the regression of soil CO_2 efflux against root biomass. Root respiration can be estimated by comparing soil respiration before and after clear-felling (Nakane et al. 1983, 1996) or by subtracting the annual soil CO_2 efflux recorded on small trenched plots from that recorded on the main study plot (Ewel et al. 1987, Bowden et al. 1993, Epron et al. 1999*b*). These methods are thought to give reasonable estimates of annual root respiration, ranging from 50–60% of soil CO_2 efflux (Epron et al. 1999*b*). Root respiration can also be estimated by subtracting litter, root and soil organic matter decomposition rates from soil CO_2 efflux (Ewel et al. 1987). More recently, Lin et al. (1999) analyzed the stable isotope ratios of carbon and oxygen in CO_2 efflux in order to estimate the relative contributions of different components (rhizosphere respiration, microbial decomposition of surface litter and microbial decomposition of soil organic matter) to the overall soil CO_2 efflux in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) terracosms.

In the present study, we attempted to separate the respiration of the rhizosphere from the microbial respiration associated with organic matter decomposition. Rhizosphere respiration included respiratory CO_2 released by roots,

mycorrhizae and root-associated microorganisms that consume root-derived materials like exudates and sloughed root cap cells (Vogt et al. 1991). Respiration of the rhizosphere was calculated by subtracting simulated microbial respiration associated with organic matter decomposition from daily mean soil CO_2 efflux. The heterotrophic contribution to soil CO_2 efflux was simulated by a semi-mechanistic soil organic matter model validated against "no roots" trenched plot data. Our objectives were to study the seasonal evolution of rhizosphere respiration in relation to changes in soil temperature, and to quantify its contribution to total soil CO_2 efflux.

Materials and methods

Study site

The experimental site is located in the state forest of Hesse (Moselle, France, 48°40′ N, 7°05′ E, elevation 305 m, area 5 km^2 (Epron et al. 1999*a*, Granier et al. 2000, Lebaude et al. 2000)). The main experimental plot covers 6×10^{-3} km^2 and consists mainly of 30-year-old beech (*Fagus sylvatica* L.) trees. The understory vegetation is sparse. Soil is a gleyic luvisol according to the FAO classification and is covered with a mull type humus. Soil carbon content is 2.8% in the 0–5 cm horizon and 1.0% in the 5–40 cm horizon. Two "no roots" subplots (2 × 1.5 m) were established in June 1996 by digging a trench (1 m deep) around each, lining the trench with polyethylene film, and replacing the soil. Roots initially present within the plot were killed by trenching and root regrowth into the subplots was prevented by the polyethylene film. Soil temperature was measured at depths of 5, 10 and 40 cm with six copper–constantan thermocouples. Data were acquired at 10-s intervals with a CR7 data logger (Campbell Scientific Inc., Logan, UT), which stored 30-min means. Volumetric water content of the soil was measured at 10- and 40-cm depths with a neutron probe (NEA, Denmark) in eight aluminum access tubes at 1- to 3-week intervals. Two distinct calibration curves were used for near-surface and deeper measurements. Additionally, a polyethylene reflector was used for near-surface measurements.

Soil carbon dioxide efflux

Soil CO_2 efflux was measured with a soil respiration chamber (LI-6000-09, Li-Cor, Inc., Lincoln, NE) coupled with an infrared gas analyzer (LI-625009, Li-Cor, Inc.) as described previously (Epron et al. 1999*a*). Soil CO_2 efflux was measured during an 8-h period from 0800 to 1600 h on 15 occasions between January 29, 1997 (Julian day 29) and November 19, 1997 (Julian day 323). Daily means (n = 72 for the main plot and n = 24 for the "no roots" subplots) and confidence intervals at P = 0.05 were calculated. Soil temperature was monitored simultaneously with soil CO_2 efflux, using a copper–constantan thermocouple penetration probe inserted in the soil to a depth of 10 cm in the vicinity of the soil respiration chamber.

Modeling soil organic matter decomposition and microbial respiration

The soil organic matter (SOM) model, based on the SOM sub-model of CENTURY (Parton et al. 1987), simulates the dynamics of carbon in the soil system at the daily time step. Soil organic carbon is divided into three major components that include active, slow and passive soil carbon (Figure 1). Active carbon includes live soil microbes plus microbial products. The slow pool includes resistant plant material (lignin-derived material) and soil-stabilized plant and microbial material. Passive material, which is highly resistant to decomposition includes physically and chemically stabilized soil organic matter. The model also includes a surface microbial pool (i.e., active carbon pool) that is associated with decomposing surface litter. Flows of carbon between these pools are controlled by decomposition rates and microbial respiration loss parameters, both of which may be a function of soil texture. The potential decomposition rate is reduced by multiplicative functions of soil water content (A_w) and soil temperature (A_t).

Carbon inputs to the soil from plant residues (leaves and roots) are partitioned into structural and metabolic plant components as a function of the lignin (L) to nitrogen (N) ratio of the dead plant material. High L:N ratios indicate more structural material. Metabolic material has a much higher decom-

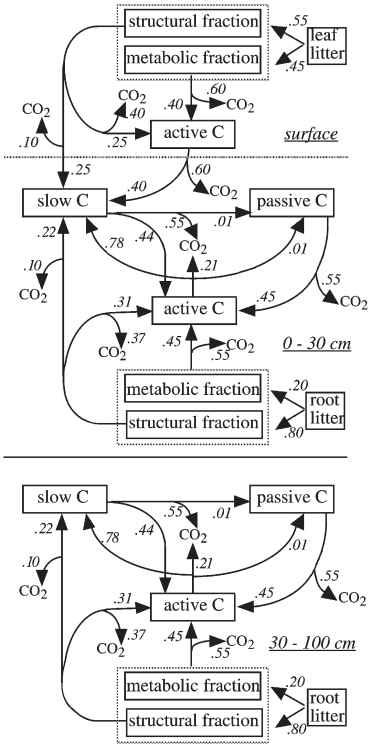

Figure 1. Schematic diagram of carbon flows in the soil organic matter model. Partitioning coefficients of carbon flow between sinks are given close to the arrows. The soil is divided into three layers: a surface layer, a superficial soil layer (0–30 cm) and the deep soil layer (30–100 cm).

position rate than structural material, and structural material is assumed to contain all of the lignin. The decomposition rate of the structural material is a function of the lignin fraction in the structural material. The metabolic material and the non-lignin fraction of the structural pool material is transferred to the active carbon pool. The lignin fraction of the plant material is assumed to go directly to the slow carbon pool as the structural plant material decomposes. The surface microbial pool turnover rate is independent of soil texture, and material flows directly into the slow carbon pool. Soil texture influences the turnover rate of the active carbon pool (higher rates for sandy soils) and the efficiency with which active carbon pool material is stabilized by conversion into slow carbon pool material (higher stabilization rates for clay soils). Formation of passive carbon is a function of the clay content only (higher for clay soils). It is primarily controlled by stabilization of active carbon into stable clay-associated micro-aggregates. Some passive carbon is also created by decomposition of the slow carbon pool. The model assumes that all carbon pool decomposition flows are associated with microbial activity and that microbial respiration (i.e., CO_2 efflux) occurs for each of these flows.

In this soil model, structural and metabolic fractions are located in the soil profile, which is divided into three layers (Figure 1). The first is the surface litter layer, which contains both metabolic and structural fractions calculated from leaf litter biomass and the associated microbial pool. The superficial (0–30 cm) and the deep (30–100 cm) layers of the soil contain all types of C pools (i.e., both metabolic and structural fractions of root litter and the active, slow and passive soil organic carbon pools). No migration of carbon is simulated between the soil layers, with the exception that the slow pool of the superficial soil layer is supplied with organic carbon from the structural fraction and the active carbon pools of the surface layer.

The relative amounts of carbon that flow from one pool to another when the first pool decomposes and the carbon is lost as CO_2 from microbial respiration are shown next to the arrows in Figure 1. Values were calculated according to Parton et al. (1987) based on silt and clay concentrations of the soil and lignin and nitrogen concentrations of plant residues.

The decomposition of each carbon pool was calculated as follows:

$$\frac{dC}{dt} = KL_c A_w A_t C \tag{1}$$

for the structural fraction,

$$\frac{dC}{dt} = KT_m A_w A_t C \tag{2}$$

for the soil active carbon pool, and

$$\frac{dC}{dt} = KA_w A_t C \tag{3}$$

for the slow carbon pool, the passive carbon pool, the surface active carbon pool and the metabolic fraction. Parameter K is the maximum decomposition rate, C is the carbon mass of the state variable (Table 1), T_m is the effect of soil texture on active SOM turnover, and L_c, A_w and A_t are the impact factors on decomposition of the lignin content of structural material, the soil water content and the soil temperature, respectively.

$$T_m = (1 - 0.75(T_s + T_c)), \tag{4}$$

where T_s and T_c are the proportions of silt and clay, respectively. Values of T_s and T_c were 68 and 26%, respectively, in the superficial layer, and 62 and 32%, respectively, in the deepest layer.

The decomposition rate of the structural material is a function of the lignin content of the structural material:

$$L_c = e^{(-3L_s)}, \tag{5}$$

where L_c is the impact of lignin content of structural material (L_s) on structural decomposition. Values of L_s were 0.35 (unpublished data) and 0.38 (Curie and Aber 1997) for leaf and root litters, respectively. Nitrogen and lignin concentrations were 1.25 and 20.6%, respectively, for leaf litter (unpublished data), and 0.7 (Khanna and Ulrich 1991) and 25.4%, respectively, (Curie and Aber 1997) for root litter.

The impact of soil water content on decomposition rates was calculated as:

$$A_w = 1/(1 + 30\exp(-8.5(W_t/W_{max})), \tag{6}$$

where W_t is soil water content at time t, and W_{max} is maximum soil water content.

According to Parton et al. (1987), the impact of temperature on decomposition rates within the soil was calculated as:

$$A_t = \left(\frac{45 - T}{10}\right)^{0.2} \exp\left(0.076\left(1 - \left(\frac{45 - T}{10}\right)^{2.63}\right)\right), \tag{7}$$

whereas the impact of temperature on decomposition rates in the surface layer was calculated as:

$$A_t = \left(\frac{45 - T}{20}\right)^{0.2} \exp\left(0.076\left(1 - \left(\frac{45 - T}{20}\right)^{4.9}\right)\right), \tag{8}$$

Carbon pools were established from the vertical distributions of carbon concentrations and residence times in soil (Elzein and Balesdent 1995), and from the vertical distribution of microbial biomass in soil (Wolters and Joergensen 1991, Ross et al. 1996). Leaf litter input was measured from 42 litter traps (Granier et al. 2000), which gave an annual input of 275 $g_{DW}\ m^{-2}$. Root litter inputs were calculated from root biomass (690 $g_{DW}\ m^{-2}$ and 2060 $g_{DW}\ m^{-2}$ for fine and coarse roots, respectively; Epron et al. 1999*b*), based on an annual root turnover rate of 60% for fine roots (Van Praag et al. 1988)

Table 1. Values of maximal decomposition rates (K, Parton et al. 1987) and equilibrium values for carbon content (C) obtained after a 20-year simulation period for the different pools of soil organic matter in the surface layer, the superficial soil layer (0–30 cm) and the deepest soil layer (30–100 cm). Values in brackets are for the "no roots" subplots and include additional carbon inputs from roots killed by trenching.

	K (day^{-1})		C (g C m^{-2})		
	Surface	Soil	Surface	0–30 cm	30–100 cm
Metabolic fraction	4.05×10^{-2}	5.07×10^{-2}	43	22 (86)	7 (31)
Structural fraction	1.07×10^{-2}	1.34×10^{-2}	335	320 (743)	113 (265)
Active pool	1.64×10^{-2}	2.00×10^{-2}	35	230	104
Slow pool	–	5.48×10^{-4}	–	2833	1442
Stable pool	–	1.23×10^{-5}	–	827	2400

and 10% for coarse roots. Leaf litter inputs occur mainly during October and were simulated based on a constant coefficient of leaf mortality during this period. Equilibrium values for carbon pools obtained after a 20-year simulation period are given in Table 1. Additional carbon inputs from roots killed by trenching were added when simulating respiratory carbon loss in the "no roots" subplots.

Results

Seasonal changes in soil CO_2 efflux

Measured soil CO_2 efflux ranged from 0.5 g C m^{-2} day^{-1} in winter (soil temperature at 10-cm depth = 2.1 °C) to 2.6 g C m^{-2} day^{-1} in August (17.8 °C) on the "no roots" subplots (Figure 2A) and 4.3 g C m^{-2} day^{-1} on the main plot (Figure 2B). Soil CO_2 efflux was significantly lower on the "no roots" subplots than on the main plot during most of the season. The 1997 summer was wet and soil water content probably did not inhibit soil CO_2 efflux except in September (Julian day 269) when soil CO_2 efflux on the main plot was low (1.2 g C m^{-2} day^{-1}) despite a soil temperature of 12.8 °C. This observation was excluded from the dataset because soil water content conditions on the "no roots" subplots deviated too widely from the study plot conditions to validate the SOM model at low soil water content.

Validation of the soil organic matter decomposition model

The SOM model was evaluated by simulating respiratory carbon loss from microbial activity in the "no roots" subplots (Figure 2A) and comparing results with measurements from the "no roots" subplots. There was close agreement between simulated and observed soil CO_2 efflux on the "no roots" subplots (Figure 3; slope = 0.97, $r^2 = 0.93$, $n = 15$). The model was run with soil temperatures at 5-, 10- and 40-cm depths for the surface layer, topsoil layer and deep layer, respectively. Use of air temperature rather than soil temperature at 5-cm depth for the surface layer gave a lower coefficient of determi-

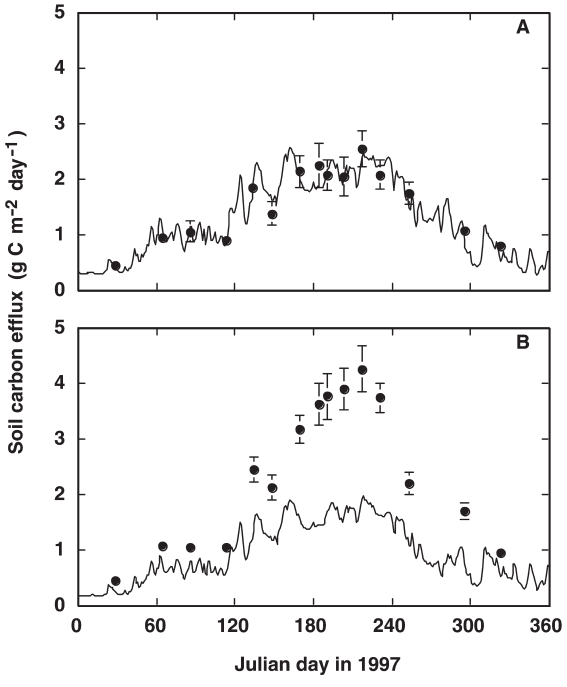

Figure 2. Seasonal courses of measured soil CO_2 efflux (●) and simulated microbial respiration associated with organic matter decomposition (solid lines) on (A) the "no roots" subplots and (B) the main plot. Vertical bars indicate the confidence interval of the daily mean soil CO_2 efflux ($P = 0.05$).

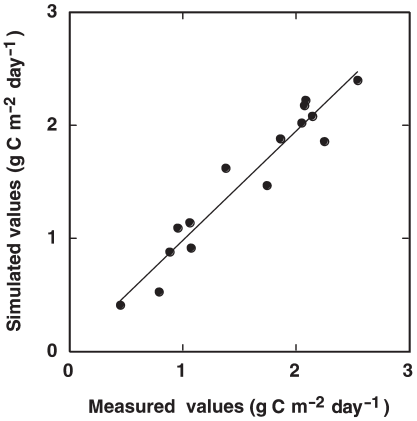

Figure 3. Comparison of measured soil CO_2 efflux and simulated microbial respiration associated with organic matter decomposition on the "no roots" subplots. The solid line is the regression line ($y = 0.97x$; $r^2 = 0.93$; $n = 15$).

nation (0.87).

Because of the contribution of root respiration, measured soil CO_2 efflux on the main plot was much higher than simulated microbial respiration (Figure 2B).

Seasonal changes in rhizosphere respiration

Rhizosphere respiration on the main plot was estimated as the difference between soil CO_2 efflux and simulated respiratory carbon loss from microbial activity. Rhizosphere respiration exhibited pronounced seasonal variations (Figure 4B) that reflected seasonal changes in soil temperature (Figure 4A). Estimated values of rhizosphere respiration ranged from 0.2 g C m^{-2} day^{-1} in January to 2.3 g C m^{-2} day^{-1} in summer. Data were normalized to the same soil temperature (10 °C at 10-cm depth) based on a Q_{10} of 2.2 (see Discussion). The temperature-normalized rhizosphere respiration increased from early spring (R_{10} = 0.4 g C m^{-2} day^{-1} in March) to early summer (R_{10} = 1.6 g C m^{-2} day^{-1} in July), and then decreased slowly until November (Figure 4B).

An exponential curve ($y = Ae^{BT}$) was fitted to the estimated values of rhizosphere respiration versus soil temperature, T, and two fitting parameters, A and B. Parameter B is closely related to Q_{10} ($Q_{10} = e^{10B}$). This empirical model accounted for 86% of the variation in rhizosphere respiration when soil temperature at 10-cm depth was used. At greater soil depths (40 cm) the relationship between T and soil respiration was not so close (R^2 = 0.77, data not shown). Based on the soil temperature at 10-cm depth, B was 0.137, which corresponds to a Q_{10} of 3.9 (Figure 5).

The contribution of rhizosphere respiration to soil CO_2 efflux decreased from October (55%) to March (30%), increased again in spring and summer up to 60% in July, and remained high until October (Figure 4C). Despite this seasonal trend, the contribution of rhizosphere respiration to soil CO_2 efflux was poorly related to soil temperature (r^2 = 0.46). On average, rhizosphere respiration was about 52% of soil CO_2 efflux.

Sensitivity analysis

A sensitivity analysis was performed on the SOM model to assess whether small changes (i.e., a 10% increase or decrease) in litter composition and litter input affect the Q_{10} for rhizosphere respiration and the contribution of rhizosphere respiration to soil CO_2 efflux. The contribution of rhizosphere respiration to soil CO_2 efflux was slightly sensitive to changes in leaf litter or root litter input. The Q_{10} was slightly sensitive to changes in leaf litter composition and input (Table 2). In this analysis, the contribution of rhizosphere respiration to soil CO_2 efflux (annual mean) ranged from 0.50 to 0.54 and the Q_{10} for rhizosphere respiration ranged from 3.8 to 4.0.

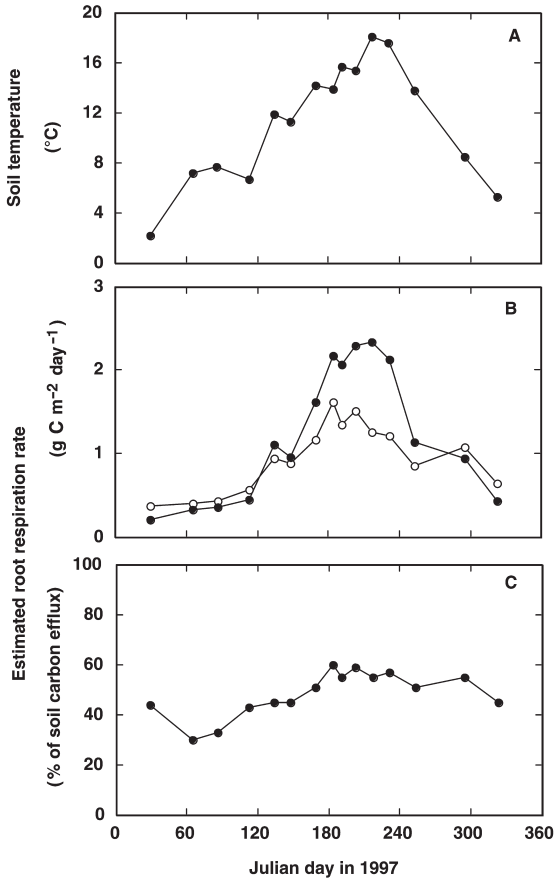

Figure 4. Seasonal courses of (A) soil temperature at 10-cm depth, (B) estimated rhizosphere respiration (●) and temperature-normalized rhizosphere respiration (○), and (C) the contribution of rhizosphere respiration to soil CO_2 efflux. Rhizosphere respiration was normalized to the same soil temperature (10 °C at 10-cm depth) based on a Q_{10} value of 2.2.

Discussion

Our data indicate that the soil organic matter model, based on the SOM sub-model of CENTURY (Parton et al. 1987), can simulate respiratory carbon loss from microbial activity associated with organic matter decomposition at the daily time step. The SOM model is, therefore, a useful tool to calculate

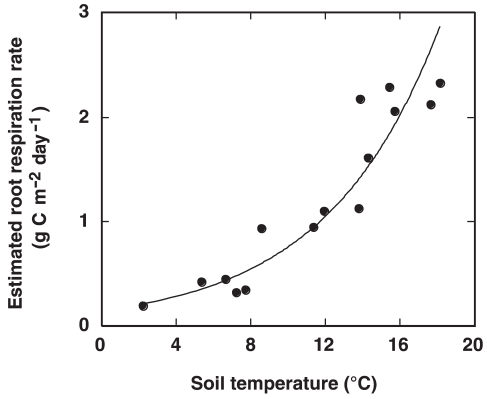

Figure 5. Relationship between estimated rhizosphere respiration and soil temperature at 10-cm depth. An exponential function is fitted through the data (y = 0.228 $e^{0.136x}$; r^2 = 0.86; n = 15).

Table 2. Sensitivity of Q_{10} to rhizosphere respiration and the contribution of rhizosphere respiration to soil CO_2 efflux in response to a 10% increase (or decrease) in litter composition and litter input in the SOM model.

Model parameters	Variation in model parameters	Relative change (%)	
		Q_{10}	Contribution
Leaf litter			
Lignin concentration	+10% (–10%)	0.0 (0.0)	–1.6 (+1.6)
Nitrogen concentration	+10% (–10%)	0.0 (0.0)	+1.6 (–1.9)
Lignin content of structural material	+10% (–10%)	0.0 (0.0)	–0.3 (+0.3)
Litter input	+10% (–10%)	–3.5 (+1.8)	+1.9 (–1.9)
Root litter			
Lignin concentration	+10% (–10%)	0.0 (0.0)	–0.3 (+0.3)
Nitrogen concentration	+10% (–10%)	0.0 (0.0)	–0.3 (+0.3)
Lignin content of structural material	+10% (–10%)	0.0 (0.0)	0.0 (0.0)
Litter input	+10% (–10%)	–1.8 (+1.8)	–0.3 (+0.3)

rhizosphere respiration from daily mean soil CO_2 efflux.

There are few estimates of *in situ* rhizosphere respiration available for comparison with our data. Boone et al. (1998) reported values obtained in an 85-year-old mixed-hardwood forest in Massachusetts from trenched plot data. Their estimates of rhizosphere respiration ranged from 0.2 g C m^{-2} day^{-1} in early spring to 4.3 g C m^{-2} day^{-1} in summer. Because root biomass is thought to increase with increasing stand age (Ewel et al. 1987), higher root biomass in this older site may account for higher maximum values than ours.

The high Q_{10} (3.9) observed for *in situ* rhizosphere respiration is consistent with values obtained by Boone et al. (1998) for a mixed hardwood forest, but is much higher than those reported for enzymatic reactions or plant tissue respiration. Excised or excavated roots often exhibit Q_{10} values of approximately 2 (Sowell and Spomer 1986, Cropper and Gholz 1991, Ryan et al. 1996, Bouma et al. 1997, Epron and Badot 1997). Root respiration is required for maintenance, growth and ion uptake (Lambers et al. 1983); therefore, it depends on root biomass and activity. In a young stand, coarse root biomass is not at steady state and is thought to increase throughout the year. In addition, root growth in our stand occurred in late spring and early summer with a maximum growth rate at the beginning of July as observed at rhizotron windows (unpublished data). This contrasted with data from a *Pinus radiata* D. Don stand in New Zealand (Santantonio and Grace 1987), showing that fine root production peaked in early spring then decreased sharply in summer. In addition to increases in root growth and biomass in late spring, energy requirements for ion uptake and transport are thought to reach a maximum during the growing season. Seasonal changes in photosynthate supply to roots may also affect respiration of roots (Hansen and Jensen 1977) and that of associated microorganisms through changes in root exudates (Edwards 1991). Therefore, our Q_{10} parameter may confound the effects of temperature and of changes in root biomass and root and shoot activities. To examine this hypothesis, data were normalized to the same soil temperature (10 °C at 10-cm depth) based on a Q_{10} of 2.2 obtained for excised roots of beech (Epron and Badot 1997). In this case, the lowest values of temperature-normalized rhizosphere respiration were observed from January to March (R_{10} = 0.4 g C m^{-2} day^{-1}), whereas the highest value was observed in early July (R_{10} = 1.6 g C m^{-2} day^{-1}) when fine root growth was at a maximum. The fact that our calculated R_{10} remained higher in late summer (0.8–1.2 g C m^{-2} day^{-1}) than in early spring is consistent with the pattern of root and shoot activities and with yearly root biomass increment.

Microbial respiration (i.e., soil CO_2 efflux from the "no roots" subplots, Figure 2A) exhibited a lower temperature sensitivity than rhizosphere respiration, with a Q_{10} of 2.3 when plotted against soil temperature at 10-cm depth (data not shown). Boone et al. (1998) reported similar differences in temperature sensitivity of root and microbial respiration. The reason for this discrepancy is unclear, but it is possible that the positive effect of high temperature on microbial respiration in summer can be offset by the negative effects of mild drought. Severe drought is thought to alter the metabolism of both microorganisms and roots, whereas mild drought is known to reduce microbial respiration by limiting the diffusion of soluble organic substrates within the soil (Skopp et al. 1990).

Apparently, rhizosphere respiration has a higher temperature sensitivity than microbial respiration, which would explain the greater contribution of root respiration to total soil CO_2 efflux in summer than during the remainder of the year. This is in agreement with a previous study showing that an empirical model of soil CO_2 efflux is improved by including seasonal variation in root activity (Hanson et al. 1993). Differences between root and microbial population phenology may also account for the observed seasonal changes in the contribution of root respiration to total soil CO_2 efflux. Our estimates of the contribution of rhizosphere respiration to soil CO_2 efflux ranged from 30 to 60%, with an annual mean of 52%. This value is slightly lower than that obtained by subtracting the annual soil CO_2 efflux recorded for "no roots" subplots from that recorded for the main plot on the same site (60%, Epron et al. 1999*b*) or for a 29-year-old slash pine (*Pinus elliottii* Engelm.) plantation in Florida (62%, Ewel et al. 1987). But it is similar to those estimated by comparing soil

respiration before and after clear-felling in an 80-year-old Japanese red pine (*Pinus densiflora* Siebold & Zucc.) stand and in a 102-year-old oak (*Quercus* sp.) forest (51%, Nakane et al. 1983, 1996). In a temperate mixed hardwood forest in Massachusetts, the contribution of root respiration ranged from 33% when the decomposition of roots killed by trenching was neglected, to 49% of soil CO_2 efflux when the decomposition of dead roots was taken into account (Bowden et al. 1993). For younger trees, Lin et al. (1999) analyzed the stable isotope ratios of carbon and oxygen in CO_2 efflux and found that rhizosphere respiration accounted for about 23–32% of soil respiration in 4-year-old Douglas-fir seedlings grown in reconstituted forest soil in terracosms.

In conclusion, our study confirmed that rhizosphere respiration is a major component of soil CO_2 efflux. The size of this component varied throughout the year, with a maximum in early summer corresponding with a maximum in root growth. Soil temperature accounted for most of the variation in rhizosphere respiration. Drought effects on root respiration were not observed in this study. Soil water deficit is known to reduce respiration rate of fine roots (Gansert 1994, Burton et al. 1998), but the effects of drought-induced decreases in root respiration on soil CO_2 efflux and forest carbon budgets have not yet been described. Our methods will be suitable for sites subject to drought, provided that the soil organic matter decomposition model is validated over a wider range of soil water contents.

Acknowledgments

This work was supported by the European programme Euroflux (ENV4-CT95-0078) and by the Office National des Forêts (ONF). The District Urbain du Pays de Montbéliard (DUPM) is also acknowledged for financial support.

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