



HAL
open science

Déterminisme de la respiration de l'écosystème dans l'étude du bilan de carbone d'une hêtraie de plaine

Jérôme Ngao

► **To cite this version:**

Jérôme Ngao. Déterminisme de la respiration de l'écosystème dans l'étude du bilan de carbone d'une hêtraie de plaine. Sylviculture, foresterie. Université Henri Poincaré - Nancy 1, 2005. Français. NNT : 2005NAN10150 . tel-01748078

HAL Id: tel-01748078

<https://hal.univ-lorraine.fr/tel-01748078v1>

Submitted on 29 Mar 2018

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.



AVERTISSEMENT

Ce document est le fruit d'un long travail approuvé par le jury de soutenance et mis à disposition de l'ensemble de la communauté universitaire élargie.

Il est soumis à la propriété intellectuelle de l'auteur. Ceci implique une obligation de citation et de référencement lors de l'utilisation de ce document.

D'autre part, toute contrefaçon, plagiat, reproduction illicite encourt une poursuite pénale.

Contact : ddoc-theses-contact@univ-lorraine.fr

LIENS

Code de la Propriété Intellectuelle. articles L 122. 4

Code de la Propriété Intellectuelle. articles L 335.2- L 335.10

http://www.cfcopies.com/V2/leg/leg_droi.php

<http://www.culture.gouv.fr/culture/infos-pratiques/droits/protection.htm>

S.C.D. - U.H.P. NANCY 1
BIBLIOTHÈQUE DES SCIENCES
RUE DE LA MAIRIE - B.P. 11
54601 VILLERS LÈS-NANCY Cedex



UMR Ecologie et Ecophysiologie Forestières
Centre INRA de Nancy
54280 Champenoux - France



Université Henri Poincaré Nancy 1
Faculté des Sciences
Domaine scientifique Grignard
54506 Vandœuvre-lès-Nancy - France

UFR Sciences et Techniques Biologiques
Ecole Doctorale Ressources Procédés
Produits Environnement (RP2E)

Thèse

présentée pour l'obtention du titre de

Docteur de l'Université Henri Poincaré Nancy 1

en Biologie Végétale et Forestière

Jérôme NGAO

*Déterminisme de la respiration de
l'écosystème dans l'étude du bilan de carbone
d'une hêtraie de plaine*

Soutenue publiquement le 14 décembre 2005 devant le jury composé de :

Claire Damesin	Professeur, Université Paris XI	<i>Rapporteur</i>
Ivan A. Janssens	Professeur, University of Antwerpen, Belgique	<i>Rapporteur</i>
Valérie Le Dantec	Maître de Conférence, Université Toulouse III	<i>Examineur</i>
Thomas Cordonnier	Ingénieur GREF, ONF Fontainebleau	<i>Examineur</i>
Daniel Epron	Professeur, Université Nancy I	<i>Président du Jury</i>
André Granier	Directeur de Recherche, INRA Nancy	<i>Directeur de thèse</i>

BIBLIOTHEQUE SCIENCES NANCY 1



D 095 172344 7

REMERCIEMENTS

En dépit du temps qui passe, je tiens à remercier toutes les personnes ayant pu perdre du temps, de l'énergie, de la patience, de la bonne humeur, des cheveux (ou gagner des rides et des cernes), une certaine espérance pour la condition humaine, en participant à l'élaboration de cette thèse. Le temps qui ne s'arrête pas ne m'a laissé que peu de marge pour remercier comme il se doit (essayez de vous retrouver!): André-Daniel-Bernard (THE trio of chefs), François & Nanard, Co Ltd. (facile eux!), Oliver, Jean-Marie, Patrick (Vador), Rosine, Yves-Nathalie-Vincenzo (la Phyto style!), Erwin (l'unique), Jean-Marc (Hop là!), Marie-Béa, Pascale, Didier, Laurence (Aïe!Aïe!), Damien (beau gosse!), Claude, Pierre, Jackline, François (bis), Jack (Power) Ranger, Etienne, Claude (bis)... toute l'unité BEF en fait, ainsi que tout le staff INRA Nancy qui m'a rendu la vie si agréable depuis le DEA BF. J'en oublie certainement tellement d'autres, veuillez m'en excuser!

Je remercie également tous ceux et celles qui ont participé à l'élaboration de cette thèse, en particulier les membres des différents comités de thèse (Bernd, Claude Nys, Christophe, Noël et Jean-Marc, Jean-François Dhôte et Patrice Mengin-Lecreux), et surtout le tristement célèbre regroupement de respirateurs de sol, le GERS: Mr le professeur Marc, Michel, Alain, Dominique et Gaëlle (mes frère et sœur de respiration), BIG Kamel, Super Claire, Eric le Grand, Chère Valérie (la Gersoise), et je dois en oublier certainement tant d'autres... Travailler au sein de ce groupe aura été une des expériences les plus agréables et enrichissantes durant cette thèse.

Je tenais à témoigner ma gratitude envers l'Office National des Forêts pour leur soutien durant toute la durée de ma thèse, du financement jusqu'aux contacts de terrain (bureau de Sarrebourg). Merci pour l'intérêt porté à ces travaux.

De même, je remercie profondément les membres du jury pour avoir pris le temps (ô combien précieux!) de lire et discuter ma thèse.

And finally, je tenais à remercier tous les co-thésards, co-galériens post-kébabs, co-stressé(e)s-au-labo, les membres du syndicat virtuel de lutte-contre-l'effet-de-serre-et-de-promotion-du-covoiturage-mixte, des participants au Co-office Partitioning Member Programme, ainsi que les apparitions spectrales d'après 17h30 du bâtiment C (pas de cafés après 17h00!). Sans cette ambiance chaleureuse, le travail de cette thèse n'aura certainement pas eu le même visage. Smacks (priorité aux pitchounettes!)

Le temps est avare (demandez-le au Prince...) et je dois rendre l'antenne. La prochaine drash de Jup' à la prochaine aubrette à brol à septante et un kilomètres au nord des Ardennes belges. Que ce travail soit le témoignage de ces 4 années passées sur les Marches du Bassin Parisien (bientôt, Nancy à 1 heure et demi de Paris, ça sent la banlieue...).

Merci également à toute ma famille qui m'a soutenu sans conditions! Avec (beaucoup) de retard, je te remercie Thi-Tam pour toute ta patience, ton inconscience de mes défauts et de m'avoir supporté et réconforté durant ces années à Nancy. Malgré les apparences, c'est un peu de nous que je grave à travers ces pages.

The first step in the reinforcement process is to identify the behavior that you want to increase. This is often the easiest part, as you are usually looking for a specific action that you would like to see more of. Once you have identified the behavior, the next step is to determine the consequences that will reinforce that behavior. This is where you need to think about what you can do to make the behavior more appealing or rewarding. For example, if you want to increase the number of times your child cleans their room, you might offer a reward or praise each time they do so.

It is important to remember that reinforcement should be used consistently. If you only reinforce a behavior occasionally, the child may not learn that the behavior is always rewarded. Additionally, the reinforcement should be immediate, so that the child can clearly see the connection between the behavior and the reward. Finally, the reinforcement should be meaningful to the child. If the reward is something that the child does not value, it will not be effective.

Another key principle of reinforcement is to start with small steps. If you want to increase a complex behavior, it is best to break it down into smaller, more manageable parts. Reinforcing each small step will help the child build confidence and learn the behavior more easily. For example, if you want to teach a child to write their name, you might start by reinforcing the first letter, then the second letter, and so on.

It is also important to use reinforcement to shape behavior, rather than just to reward it. Shaping involves reinforcing successive approximations of the desired behavior. For example, if you want a child to sit at the table, you might first reinforce them for sitting on the floor, then for sitting on a chair, and finally for sitting at the table. This helps the child learn the behavior in a gradual and controlled way. Additionally, reinforcement can be used to extinguish unwanted behaviors. If a behavior is no longer reinforced, it will eventually stop occurring.

In conclusion, reinforcement is a powerful tool for increasing desired behaviors and decreasing unwanted ones. By using the principles of consistency, immediacy, and meaningfulness, you can effectively reinforce the behaviors you want to see more of. Remember to start with small steps and use reinforcement to shape behavior, rather than just to reward it.

Synthèse

SOMMAIRE

SOMMAIRE	5
R ESUME.....	7
A BSTRACT.....	8
L ISTES	9
Abréviations.....	9
Paramètres.....	9
Tableaux	9
Figures	9
I NTRODUCTION	11
Contexte global: le cycle du carbone face aux changements climatiques.....	11
La respiration de l'écosystème	11
<i>Définitions</i>	11
<i>R_{ECO} et contexte changeant</i>	13
Modèle conceptuel	14
Méthodes de mesures, leurs incertitudes et limites actuelles	16
<i>La respiration de l'écosystème</i>	16
<i>La respiration du sol</i>	17
<i>Estimer les composantes autotrophes et hétérotrophes de la respiration du sol</i>	18
<i>La respiration issue de la décomposition des débris ligneux (R_B)</i>	19
<i>La respiration des parties aériennes</i>	20
P ROBLEMATIQUE - OBJECTIFS.....	21
Au niveau du sol	21
Les débris ligneux.....	21

Hypothèses et objectifs de la thèse	22
M ETHODOLOGIES DE MESURE.....	22
Sites et organisation des mesures	23
Mesure du flux de CO ₂ du sol	23
Expériences de décomposition	27
L ES DETERMINANT DES FLUX DE CO ₂	28
F acteurs climatiques.....	28
<i>Influence de la température</i>	28
<i>Influence du contenu en eau volumique et des précipitations</i>	31
I mportance des composantes de la respiration du sol.....	34
<i>Contribution des différentes composantes à R_{ECO}</i>	34
<i>Variabilité inter-site des composantes de R_S</i>	35
S ensibilité des méthodes de séparation des composantes de R _S	36
<i>Effets des trenched plots sur la décomposition</i>	36
1. La détermination de B ₀	36
2. La constante de décomposition k _R	37
3. Valeur de α _R	38
<i>Décomposition de la litière et des débris ligneux</i>	38
I nfluences des paramètres du sol et du peuplement.....	39
V ariabilité inter-annuelle de R _{ECO}	41
<i>Sensibilité au climat</i>	41
<i>Relation entre GPP et respiration</i>	42
<i>Conséquence d'une éclaircie sur la respiration de l'écosystème</i>	43
1. Biomasse et flux créés par une éclaircie à Hesse	43
2. Conséquence d'une éclaircie sur R _S	43
C ONCLUSIONS - PERSPECTIVES	45
R EFERENCES BIBLIOGRAPHIQUES	47

RESUME

Le but de notre travail a été d'approfondir la connaissance des principaux compartiments participant à respiration d'un écosystème (R_{ECO}) afin d'en dégager les facteurs majeurs influençant sa variabilité dans deux hêtraies (H1 et H2) de la forêt de Hesse. Différents suivis du flux de CO_2 du sol (R_S) ont été initiés, ainsi que des expériences de décomposition de litière de feuilles et de débris ligneux. Ainsi, la respiration du sol autotrophe (R_{Auto}) représente 38% et 42% de R_{ECO} dans les sites H1 et H2 respectivement. La respiration du sol hétérotrophe (R_{Hetero}) représente 14% et 29% de R_{ECO} dans H1 et H2 respectivement. Le flux de CO_2 issu de la décomposition de la nécromasse ligneuse (R_B) contribue à 14% de R_{ECO} dans H1. La contribution annuelle de la décomposition de la litière (R_L) est estimée à 8% de la respiration annuelle total du sol. Pour le site H1, en considérant une valeur annuelle de R_S de $529 \text{ gC m}^{-2} \text{ an}^{-1}$ (2004) et une valeur annuelle de R_{Hetero} de $147 \text{ gC m}^{-2} \text{ an}^{-1}$, la contribution de R_L à R_{Hetero} est ramenée à 29%. Nos résultats confirment que la température du sol est un facteur essentiel influençant grandement la variabilité temporelle des différents flux de CO_2 , mais laisse une grande part de la variabilité (notamment spatiale) à d'autres facteurs susceptibles d'être confondus ou cachés derrière le pattern général imposé par elle. L'effet du contenu volumique en eau du sol (θ_{Surf}) à Hesse est globalement positif sur R_S et R_B , notamment aux faibles valeurs d'humidité. Mais il est plus difficile de prévoir l'effet des variations de θ_{Surf} à plus long terme sur la biomasse microbienne notamment. La variabilité spatiale de R_S peut être décrite à travers la respiration basale normalisée avec des paramètres liés au sol comme la densité apparente ou le rapport C/N du sol superficiel. Les paramètres du peuplement tels que la surface terrière, la densité en nombre tiges ou l'indice de surface foliaire n'expliquent apparemment pas cette variabilité. La biomasse racinaire en elle-même ne permet pas non plus d'expliquer la variabilité spatiale de R_S . Ces différentes approches permettent de mieux cerner les variabilités influençant R_{ECO} et ses composantes. Les limites et incertitudes des méthodes employées durant ce travail sont discutées.

Mots-clefs : autotrophe, carbone, compartiment, contenu en eau, écosystème, flux CO_2 , hétérotrophe, hêtraie, racines, respiration, sol, température, variabilité.

ABSTRACT

The aim of this work was to improve knowledge on the main components of ecosystem respiration (R_{ECO}), and to emphasize the main variables driving its variability within two beech stands of Hesse Forest. Different surveys of soil CO_2 efflux (R_{S}) were initiated, as well as decomposition experiment of leaf litter and woody debris. Thus, autotrophic respiration (R_{Auto}) represented 38% and 42% of R_{ECO} in the H1 and H2 sites, respectively. Heterotrophic respiration represented 14% and 29% of R_{ECO} in the H1 and H2 sites, respectively. CO_2 efflux from woody debris (R_{B}) contributed to 14% of R_{ECO} in H1 site. Annual contribution of leaf litter decomposition (R_{L}) was estimated to 8% of annual R_{S} . For the H1 site, when considering an annual R_{S} value of $529 \text{ g}_C \text{ m}^{-2} \text{ y}^{-1}$ (2004) and an annual R_{Hetero} value of $147 \text{ g}_C \text{ m}^{-2} \text{ y}^{-1}$, contribution of R_{L} to R_{Hetero} was 29%. Our results confirmed that soil temperature was an essential factor having a major influence on temporal variability of CO_2 efflux, but it left a large part of variability that could be explained by confounded or hidden other factors. The effect of soil water content (θ_{Surf}) at Hesse was globally positive on R_{S} and R_{B} , in particular for low values of θ_{Surf} . Spatial variability of R_{S} could be described through the basal respiration rate with soil parameters as soil bulk density or the C-to-N ratio of superficial soil layer. At a first sight, neither stand parameters (basal area, stand density or leaf area index) nor root biomass did not explain spatial variability of R_{S} . These results provided substantial information and allowed a better understanding of variability of R_{ECO} and its components. Limits and uncertainties of methods employed during this work are discussed.

Keywords: autotrophic, beech, carbon, compartment, CO_2 flux, ecosystem, heterotrophic, respiration, root, soil, temperature, variability,

LISTES

Abréviations

CFD-CFS : Chambre Fermée Statique - Chambre Fermée Dynamique
EC : Eddy Covariance (corrélations turbulentes)
GPP : Gross Primary Production (production primaire brute)
MOS: Matière Organique du Sol
NEE : Net Ecosystem Exchange (bilan net de l'écosystème)
 R_{Abg} : Flux de CO₂ des parties aériennes de l'écosystème
 R_{Auto} : Composante autotrophe du flux de CO₂ du sol
 R_B : Flux de CO₂ issu de la décomposition des débris ligneux
 R_D : Flux de CO₂ issu de la décomposition des racines tranchées dans les trenched plots
 R_{ECO} : Flux de CO₂ (ou respiration) de l'écosystème
 R_{Hetero} : Composante hétérotrophe du flux de CO₂ du sol
 R_L : Flux de CO₂ issu de la décomposition de la litière
 R_{MOS} : Flux de CO₂ issu de la décomposition de la MOS
 R_S : Flux total de CO₂ du sol
 R_{TP} : Flux de CO₂ du sol mesuré dans un trenched plot

Paramètres

α_i : Fraction de C perdu du compartiment i (racines, débris ligneux) incorporée dans la MOS
C/N : Rapport du contenu en carbone sur le contenu en azote
CV : Coefficient de variation
 $\delta^{13}C$: Composition isotopique en ¹³C
LAI : Leaf Area Index (indice de surface foliaire)
 k_i : Constante de décomposition d'Olsen du compartiment i (racines, débris ligneux)
 θ_{Surf} : Contenu volumique en eau du sol dans la couche 0-6 cm
 Q_{10} : Facteur de sensibilité à la température
 R_{10} : Flux de CO₂ basal à 10°C
RMSE : Root Mean Square Error (racine carrée de l'erreur résiduelle)
 T_S : Température du sol à -10 cm

Tableaux

Tableau 1 : Valeurs récentes publiées de R_{ECO} et R_S
Tableau 2 : Principales caractéristiques des sites d'études de la forêt de Hesse
Tableau 3 : Principales caractéristiques du protocole de mesure de la respiration du sol
Tableau 4 : Description des placettes de mesure de la respiration du sol
Tableau 5 : Valeurs des paramètres du modèle empirique de R_S , des valeurs annuelles de R_S et leur participation à R_{ECO} pour les mesures effectuées pour l'étude de la variabilité spatiale et de la séparation des composantes de R_S
Tableau 6 : Valeurs des composantes de R_S issu de l'expérience des trenched plots

Figures

Figure 1 : Représentation du bilan de C d'un écosystème forestier

-
- Figure 2 : Valeurs annuelles de NEE, GPP et R_{ECO} à Hesse entre 1996 et 2003
- Figure 3 : Modèle conceptuel des flux et stocks de C dans l'écosystème participant à R_{ECO}
- Figure 4 : Cartes de la forêt de Hesse et localisation des sites d'études
- Figure 5 : Diagramme de la fréquence du vent et modélisation du footprint des mesures par corrélations turbulentes, sur le site H1
- Figure 6 : Exemple d'évolution de R_S et T_S au cours de 24 heures de mesures
- Figure 7 : Comparaison des valeurs de R_S mesurées aux valeurs simulées par le modèle en Q_{10} ou d'Arrhenius
- Figure 8 : Relation entre les résidus de la fonction en Q_{10} et θ_{Surf}
- Figure 9 : Evolution saisonnière de θ_{Surf} mesuré dans une placette contrôle et un trenched plot
- Figure 10 : Effet de faibles pluies (0.5 mm) sur R_S
- Figure 11 : Effet du contenu en eau des débris ligneux sur le flux de CO_2
- Figure 12 : Répartition des différentes composantes au sein de R_{ECO} (2004) dans les sites H1 et H2
- Figure 13 : Analyse de sensibilité du calcul de R_D à l'estimation de la biomasse racinaire, de la constante de décomposition des racines et de la fraction de C perdue sous forme de CO_2
- Figure 14 : Relation en la respiration basale à 10°C et la densité du sol, le rapport C/N de la couche A_0 et le LAI.

INTRODUCTION

Contexte global: le cycle du carbone face aux changements climatiques

L'augmentation globale des températures, attribuée en grande partie à l'augmentation de la concentration atmosphérique en CO_2 (Cox *et al.*, 2000), a relancé ces dernières années l'intérêt porté sur le cycle planétaire du carbone (C). Le protocole de Kyoto pose en effet la question de l'estimation des stocks de C et de leur évolution au cours des prochaines années, notamment dans les écosystèmes terrestres. Cela implique donc de connaître également les flux et les facteurs agissant sur les émissions de CO_2 et de leur augmentation. Parmi les sources de cette augmentation, la consommation des combustibles fossiles (industrie et énergie principalement) émettraient d'ici à 2020 en moyenne de 9.0 à 12.1 gigatonnes de carbone par an ($\text{Gt}_\text{C} \text{ an}^{-1}$, IPCC, 2000) contre $6.3 \pm 0.4 \text{ Gt}_\text{C} \text{ an}^{-1}$ et $2.2 \pm 0.8 \text{ Gt}_\text{C} \text{ an}^{-1}$ par le changement d'utilisation des terres (déboisement en particulier, Dixon *et al.*, 1994) pour la décennie 1990 (IPCC, 2001). Les échanges de CO_2 entre l'atmosphère et les milieux naturels apparaissent donc comme des éléments essentiels interagissant de façon significative à ce contexte de changements globaux. En particulier, les écosystèmes terrestres qui contiennent 2477 Gt_C (IPCC, 2000) absorberaient au niveau planétaire $2 \pm 1 \text{ Gt}_\text{C} \text{ an}^{-1}$ (Falkowsky *et al.*, 2000; IPCC, 2000), même si des incertitudes sur les estimations des stocks de C et de leurs évolutions persistent (Houghton, 2003). La biosphère européenne, en particulier les forêts, les prairies et les zones de tourbière non perturbées, constitue un puits de CO_2 fixant 7% à 12% des émissions européennes de CO_2 d'origine anthropique (Janssens *et al.*, 2001) à l'instar des zones d'Amérique du nord et de l'Asie (Schimel *et al.*, 2001). Ce puits de C européen est depuis les années 1950 en augmentation, avec un plus grand stockage à la fois dans la biomasse des forêts et dans le sol des forêts, prairies et tourbières principalement (Nabuurs *et al.*, 2003). Cela est en grande partie dû à la reprise forestière, la prévention des incendies, un allongement de la saison de végétation, et à la fertilisation par le CO_2 et les dépôts azotés (Schimel *et al.*, 2001). Mais de grandes incertitudes demeurent sur l'évolution de cette séquestration en raison des incertitudes sur l'évolution de la MOS et donc

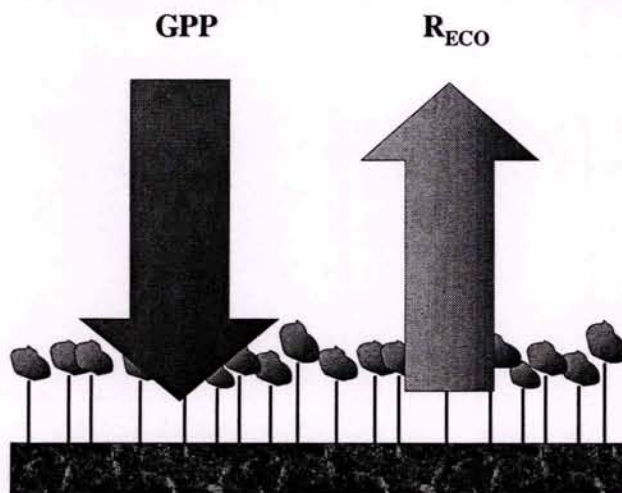


Figure 1. Les deux principaux termes du bilan de carbone (ou net ecosystem exchange, NEE) d'un écosystème: la production primaire brute (ou gross primary production, GPP) et la respiration (R_{ECO}). Par convention, le flux entrant dans l'écosystème est négatif et le flux sortant positif

de la respiration (Liski *et al.*, 2002; Nabuurs *et al.*, 2003). Une accélération de l'augmentation du CO_2 atmosphérique est notamment attendue en raison d'un effet retour du changement climatique sur la force de puits de C des écosystèmes. Certaines simulations prédisent en effet une évolution vers une source nette de C au siècle prochain (Cao et Woodward, 1998; Cox *et al.*, 2000).

La respiration de l'écosystème

Définitions

Le bilan de C ou Net Ecosystem Exchange (NEE), qui traduit la force de puits de C d'un écosystème est la résultante de deux flux de

sens opposés : un flux de CO₂ entrant dans l'écosystème du à l'activité photosynthétique des végétaux (ou Gross Primary Production, GPP) et un flux sortant de l'écosystème appelé communément respiration de l'écosystème (R_{ECO}, Figure 1). Le CO₂ participant à R_{ECO} est produit par les différents compartiments de l'écosystème : le sol, la biomasse sur pied, et les débris ligneux au sol qui sont spécifiques aux écosystèmes forestiers. Une autre perte de C est représentée par le C dissout dans la solution de sol et pouvant sortir de l'écosystème par lessivage, ainsi que l'émission de carbone organique volatile (Randerson *et al.*, 2002). A l'échelle de l'écosystème, le suivi continu des flux de CO₂ au-dessus d'une jeune hêtraie (*Fagus sylvatica* L.) de plaine a permis de quantifier la NEE à -260 g_C m⁻² an⁻¹, avec des valeurs de GPP et de R_{ECO} de -1250 g_C m⁻² an⁻¹ et 990 g_C m⁻² an⁻¹, respectivement, (valeurs de 1997; Granier *et al.*, 2000). Mais ce suivi a également montré que NEE était soumis à une forte variabilité inter-annuelle (de -90 à -560 g_C m⁻² an⁻¹ entre 1996 et 2003, Figure 2). Ces résultats soulignent l'importance des ordres de grandeurs des deux flux par rapport à NEE, qui, en moyenne, avoisinent -660 g_C m⁻² an⁻¹ (GPP), 560 g_C m⁻² an⁻¹ (R_{ECO}) et -100 g_C m⁻² an⁻¹ (NEE) dans les forêts européennes tous types confondues (valeurs moyennes 1996-1998, Valentini *et al.*, 2000). A l'échelle planétaire, la respiration de la biosphère terrestre émet 61 Gt_C an⁻¹ alors que les combustibles fossiles et l'agriculture n'émettent que 6.3 à 8 Gt_C an⁻¹ (Falkowsky *et al.*, 2000; IPCC, 2001). Par conséquent, de faibles variations, naturelles ou induites, des deux flux GPP et R_{ECO} peuvent modifier profondément la force de puits de C d'un écosystème (Cao et Woodward, 1998; Cramer *et al.*, 2001) et donc de la biosphère.

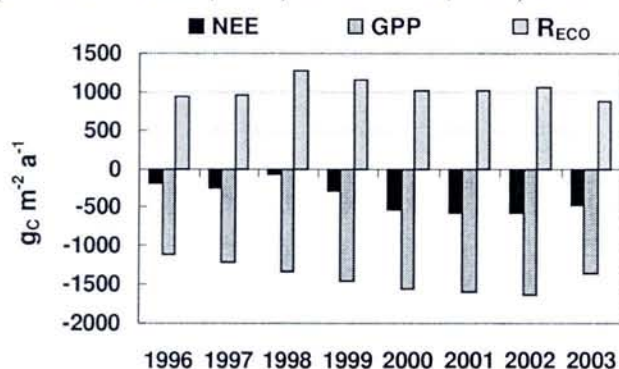


Figure 2. Evolution des différents termes du bilan C mesuré par corrélations turbulentes en forêt de Hesse entre 1996 et 2003 (Granier, comm. pers.)

La NEE varie autant dans l'espace que dans le temps (Granier *et al.*, 2003). Les variations inter-annuelles de NEE (coefficient de variation¹ CV = 50% sur la période 1996-2003) sont au moins autant liées à GPP (CV = 12%) qu'à R_{ECO} (CV = 12%). Par contre, plusieurs études soulignent l'importance de R_{ECO} comme le principal déterminant des variations inter-sites de NEE, dont l'évolution dans le contexte global changeant du réchauffement climatique est incertaine (Liski *et al.*, 1999; Valentini *et al.*, 2000; Grace et Rayment, 2000; Granier *et al.*, 2002). Une des difficultés de l'étude de R_{ECO} réside dans le fait que le flux de CO₂ issue de chaque compartiment est influencé à la fois par les facteurs climatiques (température du sol et de l'air, contenu en eau du sol, précipitations, humidité de surface), les caractéristiques des sites (sol, topographie) et les caractéristiques du peuplement (productivité, allocation, âge, structure, phénologie). Cette multitude de sources et d'interactions souligne la nécessité de mieux quantifier et de mieux comprendre les différents processus impliqués. Ceci constitue un des objectifs majeurs de ce travail.

¹ Le coefficient de variation est défini comme le rapport entre l'écart type et la moyenne d'un échantillon.

Certains modèles globaux de végétation couplés à un scénario d'émission (IS92a, IPCC, 2000) simulent une diminution de la NEE et une augmentation de la respiration au cours du siècle prochain, liées à des modifications de la structures (à travers les propriétés physiologiques, biophysiques, phénologies et biogéochimiques) des peuplements végétaux (Cramer *et al.*, 2001). Outre les influences climatiques, stationnelles ou intrinsèques des peuplements, la respiration de l'écosystème peut aussi être affectée par le mode de sylviculture dans le cas des forêts gérées. Peu d'études ont porté sur les effets de la gestion forestière sur les différents flux de CO₂. Le peu de résultats disponibles révèlent que l'effet d'une éclaircie ou d'une coupe sur la respiration du sol (principal flux étudié) est variable. Une éclaircie (et *a fortiori* une coupe à blanc) réduit la biomasse racinaire mais stimule les communautés microbiennes du sol via les changements microclimatiques en sous-bois tout en modifiant l'état de surface du sol comme la densité apparente (Toland et Zak, 1994; Striegl et Wickland, 1998; Ohashi *et al.*, 2000; Kowalsky *et al.*, 2003; Laporte *et al.*, 2003; Tang *et al.*, 2005c). Yanai *et al.* (2003) soulignent que la récolte de bois induit des modifications des chutes de litières et une diminution du stock de C suite à une accélération de la décomposition des résidus de récolte. Il apparaît donc que la simple coupe d'arbres affecte plusieurs processus en balance pour aboutir à une augmentation ou une diminution de la respiration.

De nombreux travaux tendent à évaluer les variations des processus suite à la modification du régime de gestion ou du climat. Le changement de régime des précipitations prédit par différents modèles globaux se traduirait en Europe par une multiplication des épisodes de sécheresses (IPCC, 2001). Ciais *et al.*, (2005) ont reporté une forte diminution de GPP, associé à une diminution globale de R_{ECO} (toutefois moins prononcée que pour GPP) à travers l'Europe due à la sécheresse de l'été 2003, contribuant à transformer temporairement des zones initialement puits de C en source de C pendant la période estivale.

Une des conséquences de l'augmentation des températures sur les flux de CO₂ est un dégel du permafrost nordique. En effet, les substrats respiratoires immobilisés par le gel sont potentiellement rendus disponibles pour les micro-organismes du sol suite à un réchauffement précoce dû au raccourcissement de la période hivernale ou à un feu, entraînant une augmentation de la respiration du sol, et ainsi transformer une zone initialement puits de C en source de C (O'Neill *et al.*, 2003; Brooks *et al.*, 2004). Une récente synthèse d'études sur le réchauffement artificiel d'écosystèmes *in situ* montre qu'une augmentation de 0.3°C à 6°C induisait significativement une augmentation de la respiration du sol de 20 ± 2%, cette augmentation étant plus forte pour les écosystèmes forestiers (Rustad *et al.*, 2001). Il y a toutefois de fortes incertitudes à cause des variations spatiales et temporelles des projections d'augmentation de température ainsi que le large spectre de processus qui peuvent être potentiellement affectés par la température (Shaver *et al.*, 2000). L'effet de l'augmentation de la température sur la respiration à long-terme reste donc incertain (Grace et Rayment, 2000).

L'effet de l'augmentation de la concentration en CO₂ sur des arbres ou écosystèmes boisés a également été largement étudié, notamment grâce aux dispositifs d'enrichissement en CO₂ FACE (Free Air CO₂ Enrichment). Malgré ces études, il est difficile de donner une tendance générale de l'effet de la seule augmentation de la concentration en CO₂ sur les divers processus des écosystèmes (dont les processus respiratoires) à cause du manque de connaissance des interactions entre la concentration élevée en CO₂ et la fertilité du sol, la sécheresse ou les facteurs biotiques (Karnosky, 2003). Toutefois, il est maintenant avéré que l'augmentation artificielle en CO₂ induit une augmentation du contenu en lignine des tissus végétaux accompagnée d'une diminution du contenu en azote (N), et qui se traduit par un

ralentissement de la décomposition de ces tissus (Ball et Drake, 1997; Coûteaux *et al.*, 1999; Norby *et al.*, 2001).

L'amélioration des connaissances de la respiration d'un écosystème forestier, de part sa nature multiple et son importance dans le cycle du C, représente donc un enjeu important afin d'augmenter la précision des prédictions et des modèles de bilan de C. C'est l'objectif global de la présente thèse dans le cadre du site-atelier de Hesse et du projet européen CARBOEUROPE IP.

Modèle conceptuel

Au cours de cette thèse, nous avons abordé l'étude de R_{ECO} de deux jeunes hêtraies de plaine à travers les différents flux qui la composent et des compartiments associés (Figure 3). Le sol, contenant deux fois plus de C que la végétation (Dixon *et al.*, 1994; Schimel *et al.*, 1995) apparaît comme la principale réserve de C dans les écosystèmes terrestres (IPCC, 2000). Le flux de CO_2 du sol (R_S) est le principal flux de CO_2 participant à R_{ECO} (70% de R_{ECO} en moyenne), et des variations de ce flux peuvent bouleverser le bilan de C (Table 1). Il est donc primordial de connaître son déterminisme. Le flux R_S peut sommairement se décomposer en une composante autotrophe (R_{Auto}) qui regroupe le flux de CO_2 provenant de la respiration racinaire (croissance et maintenance) ainsi que celle des micro-organismes rhizosphériques associées (Hanson *et al.*, 2000). L'autre composante complémentaire de R_S est la respiration hétérotrophe (R_{Hetero}) qui comprend le CO_2 produit au cours de la décomposition de la litière et de la matière organique du sol (MOS). Il est également possible de séparer le flux de CO_2 provenant de la décomposition de la litière *sensu stricto* (R_L) de celle de la MOS (R_{MOS}) (Ewel *et al.*, 1987; Ngao *et al.*, 2005). Le compartiment des débris ligneux est peu souvent pris en compte dans les études de bilan de C, alors que cette nécromasse ligneuse représente un stock de C ainsi qu'une entrée de C dans le sol important, notamment en forêt gérée (Sollins, 1982; Harmon *et al.*, 1986; Jabin *et al.*, 2004). Le CO_2 issu de la décomposition des débris ligneux (R_B), malgré un taux de décomposition généralement plus faible que celle des feuilles, constituerait une composante non négligeable de R_{ECO} . Enfin, la respiration de la biomasse sur pied (R_{Abg}), représentée par les troncs et les branches a également été très peu étudiée. Dans les forêts européennes, R_{Abg} contribue à environ un tiers de R_{ECO} (Janssens *et al.*, 2001; Damesin *et al.*, 2002).

Nous définissons donc R_{ECO} par:

$$R_{ECO} = R_{Auto} + R_{Hetero} + R_B + R_{Abg} \quad (1)$$

$$\text{avec } R_S = R_{Auto} + R_{Hetero} \quad (2)$$

$$R_{Hetero} = R_L + R_{MOS} \quad (3)$$

Dans notre étude, les autres pertes de C autrement que par respiration n'ont pas été abordées. Il s'agit essentiellement du lessivage du C dissout dans la solution de sol. L'exportation du bois de récolte est une autre perte de C pour l'écosystème, et qui, à l'échelle européenne, est relativement faible ($0.096 \text{ Mt}_C \text{ an}^{-1}$) comparée à la biomasse sur pied (6.76 Mt_C) ou au C dans le sol (12.69 Mt_C , Nabuur *et al.*, 2003). Selon les études publiées, la durée de vie des produits forestiers varie entre 1-5 ans (énergie, papier et carton) à 40-150 ans (construction) avec des durées de vie intermédiaires (1-40 ans) pour l'ameublement et l'emballage (Thompson et Matthews, 1989; Buchanan et Levine, 1999).

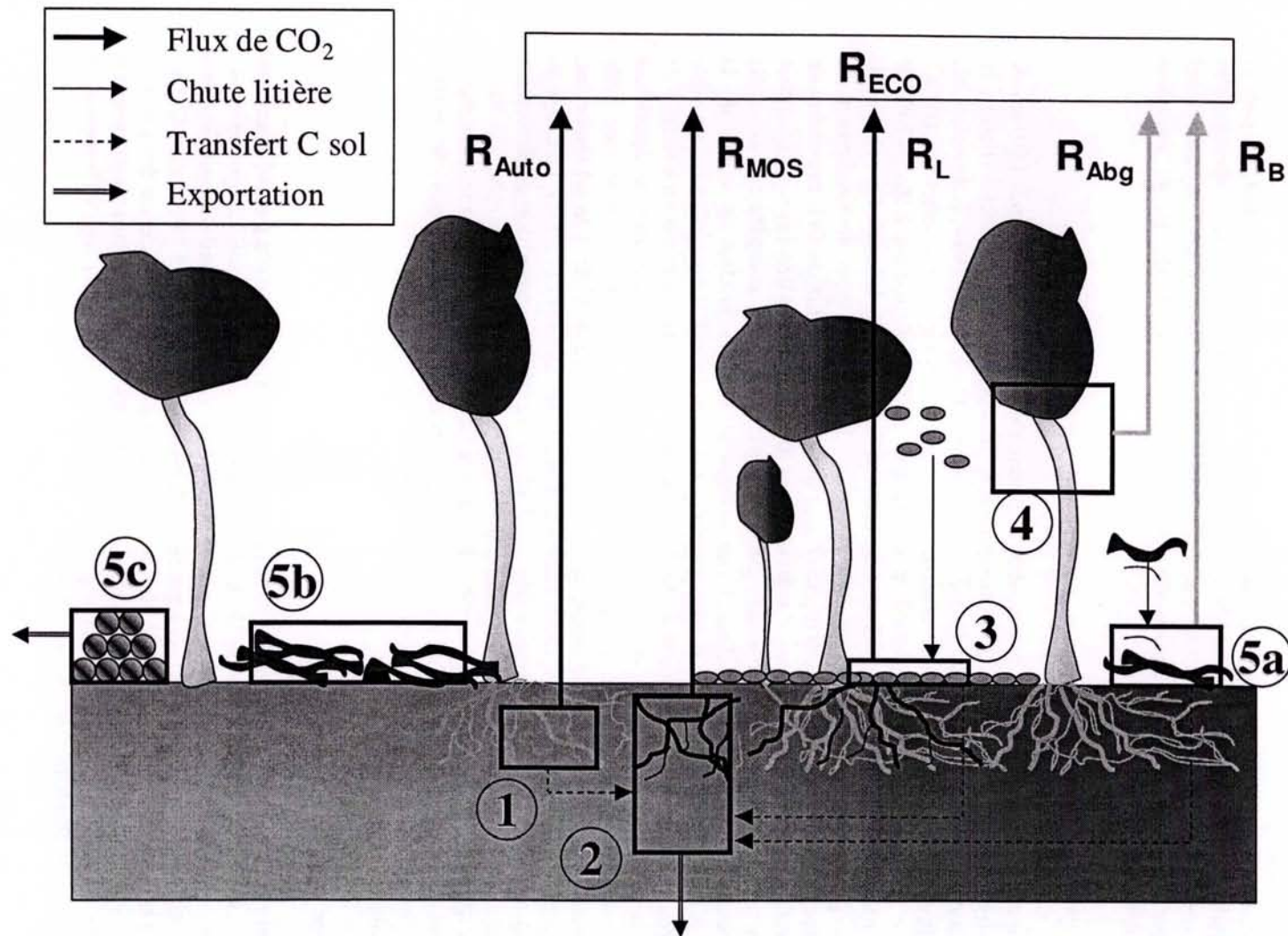


Figure 3. Principaux flux et stocks abordée durant ce travail dans une jeune hêtraie de plaine. Les chiffres indiquent les stocks de C générant les flux associés: 1 = Racines et rhizosphère; 2 = MOS; 3 = Litière; 4 = Biomasse ligneuse aérienne; 5 = nécromasse ligneuse (a: chutes naturelles, b: résidus de coupes, c: produits de récoltes).

Référence	Type	Espèce	Site	Période	R _{ECO}	R _S	%R _{ECO}
Pypker et Fredeen, 2002	FSB	Divers conifères	Colombie-Britannique (Canada)	1999-2000	-	338-466	-
O'Connell <i>et al.</i> , 2003	FB	<i>Picea mariana</i> [Mill.] BSP	SOBS, Saskatchewan (Canada)		-	319-564	-
Zha <i>et al.</i> , 2004	FB	<i>Pinus sylvestris</i> L.	Huhus (Finlande)	1999-2002	591-879	-	-
Reichstein <i>et al.</i> , 2002	FM	<i>Quercus ilex</i> L.	Puéchabon et Castelporziano (France et Italie)	1997-1999	-	-	50*
Bolstad <i>et al.</i> , 2004	FT	Décidues variés	Chequamegon (USA)	1999-2002	1089-1469	809-1194	74-81
Wang <i>et al.</i> , 2004	FB	<i>Pinus sylvestris</i> L.	(Finlande)	2000-2002	565-640	-	42-61 [77-78]**
Granier <i>et al.</i> , 2000	FT	<i>Fagus sylvatica</i> L.	Hesse (France)	1996-1997	793-988	575-663	72-67
Janssens <i>et al.</i> , 2001	F	Boréales à méditerranéennes	Divers (Europe)	1996-1998	1040	660	63
Cette étude	FT	<i>Fagus sylvatica</i> L.	Hesse (France)	2003-2004	884-766	649-589	73-77
Lohila <i>et al.</i> , 2003	C	Diverses	Jokioinen (Finlande)	2000	-	-	46-62**
Allard <i>et Soussana</i> ^a	P	Diverses	Laqueuille (France)	2003-2004	1416-1412	-	-

Tableau 1. Respiration du sol (R_S) et de l'écosystème (R_{ECO}) en g_C m⁻² an⁻¹, et contribution de R_S à R_{ECO} (%R_{ECO}) dans divers types d'écosystèmes (F : Forêt, SB : sub-boréale, B: boréale, M : méditerranéen, T : tempéré, C : culture, P : prairie). * Valeur correspondante à la contribution hétérotrophe de R_S uniquement. ** Valeur de contribution durant la période de végétation [période hors végétation]. ^a Communication personnelle

Méthodes de mesures, leurs incertitudes et limites actuelles

La respiration de l'écosystème

Une des sources de la variabilité des flux mesurés (NEE, GPP, R_{ECO}) réside dans la méthodologie de mesure, à l'instar des estimations des stocks de C (Houghton, 2003). Depuis les années 1996-1998, un ensemble de sites-ateliers intégrés dans un réseau global, FLUXNET (Baldocchi, 2001; Falge *et al.*, 2002) mesure en continu à travers le monde les flux de CO₂ par la méthode des corrélations turbulentes (ou eddy covariance, EC; Baldocchi *et al.*, 1996; Goulden *et al.*, 1996). Le principe général de la méthode repose sur la mesure de la covariance entre la composante verticale de la vitesse du vent et de la variation de la concentration en CO₂ au-dessus du couvert forestier; il faut parfois ajouter au flux mesuré un terme de stockage du CO₂ ainsi que des flux advectifs horizontaux et verticaux (Aubinet *et al.*, 2003). En forêt décidue, si le système mesure en continu le terme NEE, R_{ECO} n'est mesuré que durant la nuit en période feuillée et toute la journée en dehors. Les valeurs de R_{ECO} en phase diurne durant la période de végétation sont extrapolées selon une relation empirique dépendant de la température établie avec les valeurs de R_{ECO} mesurées directement (Aubinet *et al.*, 2003). Par ailleurs, le flux de CO₂ mesuré au-dessus du couvert provient d'une zone plus ou moins étendue appelée "footprint" (Schuepp *et al.* 1990; Schmid, 1994). Cette zone variable à la fois dans l'espace et dans le temps est dépendante de la direction et de la vitesse du vent au-dessus du couvert. Les mesures de flux peuvent varier notablement à très court terme par variations du footprint, comme cela a été montré dans des forêts hétérogènes (Aubinet *et al.*, 2001; 2002). A cette première source de variabilité s'ajoute le problème

délicat des flux nocturnes : une diminution de la turbulence de l'air (à la fois sous et au-dessus du couvert) durant la nuit a souvent été observée (Baldocchi, 2003), induisant une sous-estimation de R_{ECO} dont l'estimation est basée sur les mesures de NEE durant la nuit et les périodes non feuillées pour les essences à feuilles caduques (Aubinet *et al.*, 2002). Malgré ces incertitudes, cette technique standardisée fournit des estimations de bilans de C réalistes qui diffèrent assez bien des mesures d'accroissement en biomasse (Granier *et al.*, 2000; Valentini *et al.*, 2003). Elle s'avère précieuse dans la quantification des variabilités inter-annuelles des flux de C (Granier *et al.*, 2002).

La respiration du sol

Le flux R_S apparaît comme un des termes essentiels du bilan de C, en particulier dans R_{ECO} . Il n'existe pas actuellement de système ni même de méthode de mesure standardisée. En supposant que la diffusion est le mode de transport dominant du flux de CO_2 du sol vers l'atmosphère, différentes techniques ont été développées depuis plusieurs décennies. Deux grands types de méthode co-existent : celles qui mesurent les concentrations de CO_2 en régime transitoire et celles qui mesurent en régime constant (Pumpanen *et al.*, 2004).

Le principal type de méthode en régime transitoire est celle utilisant des chambres fermées. Une première technique consiste à mesurer périodiquement le CO_2 par piégeage et titrage d'une solution d'hydroxyde de sodium à différents moments afin d'en déduire le taux d'augmentation de la concentration en CO_2 (Anderson *et al.*, 1973). Il s'est avéré que cette technique (chambre fermée statique, CFS) sous-estime fortement le flux de CO_2 en raison d'une double diffusion: une diffusion à travers l'interface sol-litière-atmosphère (le flux désiré) mais également une diffusion atmosphère-solution alcaline (Pongracic *et al.*, 1997; Janssens *et al.*, 2000). Malgré la possibilité de couvrir une large variabilité spatiale par un grand nombre d'échantillons, la technique possède une faible résolution temporelle.

Une autre technique plus précise consiste à mesurer l'augmentation de la concentration en CO_2 dans la chambre insérée dans le sol à l'aide d'un analyseur de gaz à infrarouge via une circulation de l'air entre la chambre et l'analyseur (Norman *et al.*, 1992). Cette technique (chambre fermée dynamique, CFD), actuellement très répandue, a une très bonne résolution spatiale et une résolution temporelle correcte dans la description de la variabilité saisonnière (système portable). Une résolution temporelle maximale est obtenue par les systèmes automatiques, mais à faible résolution spatiale (Savage et Davidson, 2003). Il est possible d'utiliser des embases préalablement insérées dans le sol afin de recevoir la chambre sans perturber la mesure par l'insertion dans le sol. Par contre, il existe un risque de coupe des racines fines de surface et de sous-estimation du flux R_S (Hanson *et al.*, 2000; Wang *et al.*, 2005, article 1). Une comparaison de différentes techniques de chambre est présentée par Pumpanen *et al.*, (2004). Malgré les divergences constatées, il a été possible de comparer les données provenant de systèmes différents à condition de les avoir inter-calibrées entre eux, et donc de disposer de facteurs correctifs permettant de passer d'un système à l'autre (Janssens *et al.*, 2000; Pumpanen *et al.*, 2004; Article 1).

Le second type de méthode (mesure en régime constant) regroupe diverses techniques. Les systèmes à chambre ouverte dynamique (COD) mesurent une différence de concentration de CO_2 entre l'intérieur de la chambre et l'atmosphère en tenant compte du débit d'air (Fang et Moncrieff, 1998, Kutsch *et al.*, 2003; Subke *et al.*, 2003). Les systèmes de chambres dynamiques (fermées ou ouvertes) sont confrontés au problème intrinsèque des chambres : posées (ou insérées) au sol, les chambres modifient inmanquablement les conditions naturelles de diffusion du CO_2 et de circulation de l'air (Nay *et al.*, 1994, Davidson *et al.*, 2002). Le risque de fuite n'est également pas à sous-estimer: une étanchéité imparfaite entraîne une différence de pression entre l'intérieur du système et l'extérieur, modifiant le flux

diffusif et provoquant une erreur dans la mesure du flux R_S (Fang et Moncrieff, 1998; Longdoz *et al.*, 2000). Il est également possible de calculer le flux R_S en se basant sur des mesures de gradient de concentration et d'en déduire le flux via un coefficient de diffusion selon le milieu de mesure (sol ou air, Russell *et al.*, 1998; Tang *et al.*, 2005b). Enfin, des mesures de R_S en utilisant la méthode EC au sol (Janssens *et al.*, 2000) est limitée par la faible turbulence en sous-bois (Lankreijer *et al.*, 2003).

Estimer les composantes autotrophes et hétérotrophes de la respiration du sol

Quelle que soit la technique utilisée, la séparation des composantes de R_S se révèle cruciale pour sa compréhension et sa modélisation puisque ces composantes sont issues de processus différents, toutefois interconnectées (Bond-Lamberty *et al.*, 2004), mais ayant leurs régulations propres. Cette séparation permet notamment de mieux cerner le déterminisme de R_S comme par exemple sa sensibilité à la température (Boone *et al.*, 1998; Epron *et al.*, 2001).

Il existe différentes méthodes pour séparer et estimer les composantes autotrophes et hétérotrophes de R_S . Les mesures directes de respiration racinaire s'effectuent soit sur un échantillon de racines ou de sol sans racines (Thierron et Laudelout, 1996; Pregitzer *et al.*, 1998), soit par mesure directe *in situ* sur une racine en place (Bouma *et al.*, 1997; Kutsch *et al.*, 2001). Récemment, une pratique nouvelle consiste à écorcer le phloème des arbres (ou girdling) sur une grande superficie forestière afin de supprimer l'apport des photosynthétats aux racines (Hogberg *et al.*, 2001; Bhupinderpal-Singh *et al.*, 2003). Cette méthode est relativement locale et ponctuelle, ne permettant pas d'effectuer plusieurs estimations dans un même peuplement.

Les méthodes isotopiques (^{13}C et ^{14}C) permettant la séparation des flux R_{Auto} et R_{Hetero} reposent sur la différence de composition isotopique en ^{13}C ($\delta^{13}\text{C}$) du CO_2 de ces deux flux (Balesdent et Balabane, 1996; Bowling *et al.*, 2001; Ehleringer *et al.*, 2000). La différence ^{13}C du CO_2 respiré peut d'abord être exploitée dans le cas de successions de plantes C3/C4. En effet, le type photosynthétiques C3 se distingue par une plus grande discrimination isotopique durant la photosynthèse aboutissant à une valeur de $\delta^{13}\text{C}$ du CO_2 respiré d'environ -28‰ contre -12‰ pour les plantes C4, alors que le $\delta^{13}\text{C}$ de l'air est de -8‰ (Balesdent et Balabane, 1996; Hanson *et al.*, 2000). La différence de ^{13}C a également été utilisée dans des expériences de fumigation de CO_2 (installations FACE) qui emploient du CO_2 industriel. Cela a comme conséquence d'appauvrir le C assimilé en ^{13}C ($\delta^{13}\text{C} = -41‰$ à $-50‰$ pour des plantes en C3) et donc à un appauvrissement du CO_2 respiré par le compartiment autotrophe (Hanson *et al.*, 2000; Article 2). Toutefois, l'utilisation des abondances naturelles limite la distinction $R_{\text{Auto}}/R_{\text{Hetero}}$ à cause d'une trop faible écart entre le $\delta^{13}\text{C}$ des différents compartiments. Le signal $\delta^{13}\text{C}$ peut également être couplé à la méthode de girdling qui accentue les différences en composition isotopiques entre les deux sources (Ekblad et Hogberg 2001; Formanek et Ambus, 2004). Signalons enfin l'isotope radioactif ^{14}C qui est souvent utilisé comme traceur métabolique de l'activité des micro-organismes du sol (rhizosphérique ou non) ou celle photosynthétique des plantes par des approches de type pulse ou pulse-chase par application de ^{14}C -glucose (pour les micro-organismes, Nguyen et Guckert, 2001) ou de $^{14}\text{CO}_2$ (pour les plantes, Kuzyakov, 2002).

Une autre méthode permettant de séparer les composantes R_{Auto} et R_{Hetero} est celle de l'exclusion racinaire par tranchage ou *trenched plot*. Elle consiste à creuser une tranchée autour d'une surface dépourvue d'arbres qui aboutit, au même titre que le girdling, à supprimer l'apport en photosynthétats des racines à l'intérieur des *trenched plot*, et supprimant ainsi R_{Auto} . Cette méthode peut être facilement mise en place sur de petites surfaces (Hart et Sollins, 1998; Rochette *et al.*, 1999; Epron *et al.*, 1999; Hanson *et al.*, 2000; Rey *et al.*, 2002; Lee *et al.*, 2003; Bond-Lamberty *et al.*, 2004a; Lavigne *et al.*, 2003, 2004; Jiang *et al.*, 2005).

R_{Auto} est déduite par soustraction d'un flux R_S mesuré sur un sol témoin et d'un flux mesuré dans un *trenched plot* (R_{TP}) : $R_{\text{Auto}} = R_S - R_{\text{TP}}$. Cette méthode a permis des estimations réalistes en accord avec les valeurs de la littérature, même si des corrections sont nécessaires afin de prendre en compte:

1. Le flux de CO_2 additionnel provenant de la décomposition des racines coupées par le tranchage (R_D , Epron *et al.*, 1999; Lavigne, *et al.*, 2003; Lee *et al.*, 2003; Bond-Lamberty *et al.*, 2004) selon:

$$R_{\text{Auto}} = R_S - (R_{\text{TP}} - R_D) \text{ où } R_{\text{TP}} - R_D = R_{\text{Hetero}} \quad (4)$$

Le terme R_D peut être estimé en calculant la décomposition de la biomasse racinaire initiale présente dans le *trenched plot*, via un modèle de décomposition qui prédit la perte de masse en fonction du temps et un facteur déterminant la fraction partant sous forme de CO_2 durant la perte de masse (Nakane *et al.*, 1983).

2. La suppression du turnover des racines fines dans les *trenched plots* (Nakane *et al.*, 1983, Lee *et al.*, 2003). Sur le site de Hesse, ce turnover est faible et peut donc être négligé (Epron *et al.*, 1999).

3. Le changement de l'humidité du sol causé par la suppression de l'évapotranspiration et ses effets sur la décomposition de la MOS (Epron *et al.*, 1999).

La prise en compte de ces corrections permet d'améliorer la précision des estimations des composantes de R_S .

Enfin, l'estimation de la respiration issue de la décomposition de la litière R_L a été très peu entreprise (Bowden *et al.*, 1993) alors que la litière contribue fortement à la variabilité spatiale de R_S (Fang *et al.*, 1998; Longdoz *et al.*, 2000; Epron *et al.*, 2004). La respiration de la litière a été évaluée en manipulant des quantités de litière par Bowden *et al.* (1993) alors qu'Ewel *et al.* (1987) confrontent les données de respiration du sol à des données de décomposition. Durant cet thèse, une nouvelle méthode a été développée en comparant *in situ* les $\delta^{13}\text{C}$ du CO_2 issu de surfaces de sol couvertes de litières naturelles ($\delta^{13}\text{C} = -30\text{‰}$) ou couvertes de litière appauvrie en ^{13}C ($\delta^{13}\text{C} = -50\text{‰}$). En exploitant cette différence grâce au principe de conservation de masse (Balesdent, 1991; Cheng, 1996; Rochette *et al.*, 1999; Hanson *et al.*, 2000) et un modèle linéaire de mélange isotopique, il a été possible de déterminer la contribution de la décomposition de la litière à la respiration du sol R_L/R_S ainsi que sa variation saisonnière (Article 2).

La respiration issue de la décomposition des débris ligneux (R_B)

Les différentes études portant sur la décomposition de ce stock de C concernent à la fois les débris naturels (comprenant les fines branches comme parfois les arbres tombées à terre) et les résidus d'éclaircie (Harmon *et al.*, 1984). Les études se font principalement par des inventaires de débris ligneux: la perte de masse est estimée par la mesure de la densité du bois dont la valeur initiale est supposée connue (Chambers *et al.*, 2000). Alternativement, ces inventaires sont effectués dans des parcelles dont on connaît la date du dernier événement producteur de débris ligneux comme les récoltes ou les éclaircies (Mattson *et al.*, 1987; Chen *et al.*, 2001; Fraver *et al.*, 2002; Ganjegunte *et al.*, 2004), une tempête ou un incendie (Bond-Lamberty *et al.*, 2003). Les chronoséquences offrent à ce titre un terrain pratique grâce à l'historique connue des parcelles (Foster et Lang, 1982; Chen *et al.*, 2001; Idol *et al.*, 2001). Il s'agit donc d'un travail rétrospectif, en basant les estimations de perte de masse sur la mesure de la densité du bois dont la valeur initiale est supposée connue (Harmon *et al.*, 1986; Kankrina *et al.*, 2002).

Un autre type d'approche consiste à réaliser des expériences de décomposition *in situ* au cours desquelles des échantillons de bois sont mis à décomposer pour plus ou moins longtemps (Frangi *et al.*, 1997; Brown *et al.*, 1995; McColl et Powers, 2003). Ces expériences

permettent de contrôler précisément certains facteurs comme le diamètre ou la longueur des échantillons afin de ne pas multiplier les facteurs explicatifs, tout en permettant de montrer des variations de perte de C à l'échelle de temps des interventions sylvicoles.

Le flux de CO₂ issu de la décomposition de la nécromasse ligneuse (R_B) a été très peu étudié, à la fois *in vitro* et *in situ*. Marra et Edmonds (1994) ont mesuré le flux de CO₂ issu de troncs tombés à terre en utilisant des CFS à chaux sodée comme piège à CO₂. Des incubations en conditions contrôlées ont montré l'influence de la température et de l'humidité sur la respiration de matériels ligneux (Boddy, 1983; Chen *et al.*; 2001; Wang *et al.*, 2003). Malgré leur importance, encore trop peu d'études concernent la respiration des débris ligneux et leur déterminisme.

La respiration des parties aériennes

La respiration des parties aériennes (R_{Abg}) est aussi une composante importante de R_{ECO}. Elle peut être déduite du bilan de C indirectement comme $R_{Abg} = R_{ECO} - S_R$ (Granier *et al.*, 2000). Il est également possible de l'estimer avec des mesures *in vivo* (Ceshia *et al.* 2002; Damesin *et al.*, 2003; Gielen *et al.*, 2003; Bolstad *et al.*, 2004) par des mesures d'échanges gazeux en s'assurant de distinguer les troncs et les branches qui peuvent avoir des flux de respiration différents (Damesin *et al.*, 2002). L'une des principales difficultés d'intégration de R_{Abg} (mais également R_B) à l'échelle de la parcelle est la détermination de la surface ou du volume total des organes aériens. L'établissement de tarifs donnant la surface et/ou volume des arbres s'avère donc nécessaire, pour être ensuite intégré dans les calculs de flux à l'échelle de la parcelle.

PROBLEMATIQUE - OBJECTIFS

L'étude approfondie de R_{ECO} est confrontée à une diversité des processus intervenant ou influençant le flux de CO_2 à l'échelle de l'écosystème. Ainsi, différentes problématiques ont été identifiées.

Au niveau du sol

La variabilité temporelle de R_S , qui est pour une grande part corrélée avec les variables micro-climatiques (température du sol, contenu volumique du sol en eau), commence à être bien documentée. Une autre source de variabilité concerne la mesure de R_S elle-même. Les questions concernant la précision des mesures, les différentes méthodes de mesure (portant à la fois sur les systèmes de mesures et sur le protocole utilisé) et la démarche d'un suivi dans le temps, font encore l'objet de discussions (Lankreijer *et al.*, 2003; Pumpanen *et al.*, 2004). Ces questions d'ordre méthodologique limitent ainsi la connaissance des mécanismes.

La variabilité spatiale, à différentes échelles, et son déterminisme restent quant à elle encore mal connue. Les déterminants de cette variabilité ne sont pas forcément les mêmes à l'échelle de la parcelle et à l'échelle régionale. D'une part, la connaissance des facteurs les plus influents à l'échelle intra-site permettrait d'estimer R_S dans une zone concordante à celle prise en compte pour la mesure de R_{ECO} (=footprint des mesures de flux turbulents). D'autre part, dans la perspective de comparaisons inter-sites, une estimation correcte du flux moyen n'est possible qu'en ayant intégré la variabilité spatiale de la parcelle, supposant ainsi une prise en compte des paramètres pouvant influencer R_S et variant spatialement. Pour parvenir à cette description, une prise en compte de la variabilité saisonnière de R_S est nécessaire car les déterminants de cette variabilité temporelle ne le sont pas forcément spatialement.

La séparation des composantes de R_S (R_{Auto} , R_{Hetero} , R_L) et de leur déterminisme se révèle cruciale pour la modélisation de R_S puisque ces composantes sont issues de processus différents, ayant leurs régulations propres et des substrats différents. Ainsi, peu d'études visant à quantifier le flux de CO_2 issu de la décomposition de la litière fraîche (et son évolution saisonnière) sont disponibles. De même, il a été montré que la contribution des racines est prépondérante dans R_S , à la fois au niveau quantitatif et au niveau des régulations par les déterminants. La séparation de R_{Auto} et R_{Hetero} semble devenir une étape nécessaire dans l'amélioration de la compréhension des mécanismes pilotant R_S , et la technique des *trenched plots* offre cette possibilité. Mais alors que la pratique cette technique se développe (Bond-Lamberty *et al.*, 2004), il est nécessaire d'améliorer la connaissance des conséquences de cette technique. Ces informations permettraient en outre de mieux paramétrer les modèles de bilan de C.

Les débris ligneux

Il existe peu d'informations concernant l'importance et la dynamique de décomposition des débris ligneux d'essences européennes, le hêtre en particulier. Il est néanmoins probable que ces matériaux se décomposent plus lentement que les feuilles par exemple, en raison de la faible qualité du substrat ligneux. Dans les forêts gérées, les interventions sylvicoles, en particuliers les coupes (d'éclaircies principalement, mais aussi d'exploitation) modifient de manière très brutale et rapide les propriétés du couvert, ce qui entraîne une modification de l'activité photosynthétique en réponse au changement du climat lumineux (par une variation brusque du LAI). De même, et selon leur intensité, les éclaircies ont aussi comme conséquence de modifier brutalement le microclimat au sol (essentiellement température et

humidité), et avoir une influence sur R_S (Laporte *et al.*, 2003; Concilio *et al.*, 2005; Tang *et al.*, 2005c). Les débris issus des éclaircies constituent un apport brutal de C en décomposition, qui participerait ainsi à la variabilité spatiale de R_{ECO} et à celle du stockage de C dans le sol. Mais une question reste à ouverte : Quelle est la dynamique du C des débris ligneux issus des coupes d'éclaircies une fois à terre? La connaissance de la dynamique de décomposition des matériaux ligneux et de leurs différentes voies de production permettraient d'établir le bilan en C de ce compartiment, et la gestion des débris de coupe pourrait jouer un rôle dans la variabilité inter-annuelle de R_{ECO} .

Hypothèses et objectifs de la thèse

Ces différentes questions sont ainsi posées en considérant implicitement notre modèle proposé (Figure 3). Notre étude repose donc sur le principe de compartimentation de l'écosystème forestier en autant de stocks de carbone produisant chacun un flux de CO_2 . Ainsi, la principale hypothèse sur laquelle se fonde notre démarche est que la variabilité du flux R_{ECO} est principalement due à la variabilité, tant spatiale que temporelle, de ses compartiments et de leur contribution en terme de flux de CO_2 . Une seconde hypothèse est que les interventions sylvicoles influencent les stocks et les flux de carbone, et qu'un changement d'itinéraire sylvicole peut entraîner une modification du fonctionnement carboné de l'écosystème. **Le but de notre travail est d'approfondir la connaissance des principaux compartiments participant à R_{ECO} afin d'en dégager les facteurs majeurs du déterminisme influençant sa variabilité.** Pour cela, la séparation des différentes composantes a été entreprise afin de préciser:

1. La description de la variabilité saisonnière de R_S réalisée à travers un suivi durant 2 ans. En raison de l'importance de R_S dans R_{ECO} (Tableau 1), ce suivi nous a permis d'estimer des valeurs annuelles de R_S .

2. La variabilité spatiale de R_S abordée à différentes échelles. Une approche géostatistique préliminaire a permis une investigation à une échelle fine. Par la suite, un suivi à l'échelle de la parcelle forestière a précisé l'influence de certaines caractéristiques du sol et du peuplement sur R_S .

3. La séparation entre la composante autotrophe (racines + rhizosphère) et hétérotrophe (décomposition de la litière et de MOS) de R_S . Une expérience de décomposition de litière appauvrie en ^{13}C a été menée pour estimer la contribution de la décomposition de la litière à R_S , alors que la contribution autotrophe/hétérotrophe a été estimée par une expérience de *trenched plots*.

4. La quantification du flux de CO_2 issu du bois (necromasse ligneuse ou biomasse aérienne). Une expérience de décomposition menée durant 2 ans *in situ* en utilisant des résidus de coupes a permis d'estimer la perte de C via la décomposition. Une réévaluation des tarifs de biomasse lors d'une éclaircie réelle nous a offert l'opportunité d'extrapoler la perte de C des résidus de coupe à l'échelle du peuplement.

Ces résultats sont replacés dans un contexte plus large, notamment en discutant des variations inter-annuelles et de l'effet de la gestion sylvicole sur ces flux.

METHODOLOGIES DE MESURE

Cette partie méthodologique donne une description relativement succincte des différentes approches et mesures entreprises durant la thèse. Pour des informations plus précises, le lecteur est invité à se reporter à la section des articles s'y rapportant.

Sites et organisation des mesures

Les mesures ont été faites dans les parcelles 215 (H2) et 217 (H1) de la forêt domaniale de Hesse (Moselle, France). Le tableau 2 présente les principales caractéristiques des deux sites. Ces parcelles accueillent chacune un site-atelier intégré au projet européen CARBOEUROPE IP (Figure 4) avec, au centre de chaque site, une tour à flux dotée d'un système EC mesurant en continu les flux de CO₂, H₂O et d'énergie (Granier *et al.*, 2000). Les vents dominants sont orientés sud-ouest / nord-est (Figure 5a et 5b). En 1999, un réseau de 182 placettes a été mis en place selon un quadrillage de 50 m x 50 m dans les parcelles 217, 218, 221 et 222 afin d'étudier la variabilité spatiale des caractéristiques du sol et du peuplement (Bouriaud *et al.*, 2003). Afin de bénéficier des informations disponibles sur chacune des placettes (LAI et type de sol notamment), lorsque cela fut nécessaire, le choix de placettes a été fait selon ce quadrillage. D'autre part, l'étude des composantes de R_S oriente le choix des placettes vers celles se situant dans la zone de footprint (Figure 5b). Ce dernier point est relativement important pour la partie consacrée à la variabilité spatiale de R_S. Pour le site H1, les zones d'études ont été privilégiées dans l'axe sud-ouest / nord-est jusqu'à une distance maximum de 300 m de la tour à flux. Pour le site H2, l'emplacement des mesures et travaux se situent au maximum à 100 m de la tour à flux. Par ailleurs, une étude géostatistique préliminaire a permis de conclure qu'il n'y a pas de structure spatiale de R_S à l'échelle de 10 m (Voir ci-après) : ainsi, les mesures prises au pas d'un mètre dans une placette dont la surface n'excède pas 100 m² à 150 m² ne sont pas autocorrélées.

Mesure du flux de CO₂ du sol

Les mesures du flux de CO₂ du sol ont été menées avec un système CFD Licor 6200 composé d'un analyseur de gaz infrarouge Li-6252 (Licor, Lincoln, USA) relié à une chambre Li 6000-9. Le système ne présente pas de fuite détectable par la mesure de différence de pression entre l'intérieur et l'extérieur de la chambre (Article 1). En outre, il a été comparé à d'autres systèmes CFD et, avec le protocole employé (Tableau 3), il peut être considéré comme fiable tout au long de l'étude.

L'échantillonnage de R_S s'est effectué dans 9 placettes disposées, selon les besoins (i) soit en fonction du type de sol et du LAI dans la zone de footprint (étude de la variabilité spatiale, Article 5), (ii) soit à l'intérieur de placettes tranchées ou non (séparation des composantes autotrophes et hétérotrophes, Article 4) à proximité des sites-ateliers. Dans les deux cas, les placettes n'excèdent jamais 50 m². Hormis à l'intérieur des *trenched plots* où la place fait relativement défaut, les embases sont distantes d'un mètre les uns des autres selon deux transects aléatoires. Les mesures menées dans le cadre de l'étude de la variabilité spatiale ou de la séparation des composantes de R_S se basent sur le même pas de temps: Elles ont été effectuées depuis juillet 2003 à janvier 2005 au pas de temps de 2 semaines afin de capter la majeure partie de la variabilité saisonnière. Des mesures préalables montrent qu'il n'y a pas de variations significatives de R_S au cours d'un cycle de 24 heures (Figure 6).

Des mesures en continu de la température du sol sont faites par 5 et 4 thermocouples cuivre-constantan dans H1 et H2, respectivement. Les données sont acquises toutes les 10 s et des moyennes semi-horaires sont enregistrées (Model CR7 datalogger, Campbell Scientific, Courtaboeuf, France). Des mesures en continu du contenu volumique en eau du sol à -10 cm sont effectuées par un système TDR (time-domain reflectometry) TRASE (SoilMoisture Equipment Corp., Santa Barbara, USA). Les données sont acquises toutes les heures. Un thermocouple cuivre-constantan (M. Yernaux, Faculté agronomique de Gembloux, Belgique) mesure la température du sol à -10 cm de profondeur (T_S), alors que une sonde ThetaProbe ML2x (Delta-T Device, Cambridge, GB) mesure le contenu volumique en eau du sol de la

		H1	H2
Localisation (Tour)		48°40'27"N, 7°03'53"E	48°40'40"N, 7°04'05"E
Pente		< 3%	<3%
Altitude (m)		305	300
Température moyenne annuelle (°C)	2003		10.8
	2004		9.7
Précipitations annuelles (mm)	2003		660
	2004		913
Age (ans)		35	≤ 20
Densité (tiges ha ⁻¹)		3450	17938
Surface terrière (m ² ha ⁻¹) et	2003	25.24 (1.11)	14.52 (1.92)
accroissement (m ² ha ⁻¹ an ⁻¹)	2004	26.2 (0.94)	16.63 (2.11)
Biomasse aérienne totale (t _{MS} ha ⁻¹) et	2003	130.37 (7.08)	47.42 (7.95)
accroissement (t _{MS} ha ⁻¹ an ⁻¹)	2004	136.33 (5.96)	56.22 (8.80)
Hauteur moyenne (m)	2005	15.1	8.7
Type de sol		Stagnic luvisol*	Luvisol*
Humus		Oligo-mull à méso-mull	Oligo-mull
Espèces (% surface terrière)		<i>Fagus sylvatica</i> L. (> 90%), <i>Fagus sylvatica</i> L. (63%), <i>Carpinus betulus</i> L., <i>Betula pendula</i> Roth, <i>Quercus petraea</i> (Matt.) Lielb. et <i>petraea</i> (Matt.) Liebl., <i>Larix decidua</i> Mill., <i>Picea abies</i> L. (2%), <i>Betula pendula</i> Roth (1%)	
Chute de litière (gC m ⁻²)	2003	180	-
	2004	171	159
Densité apparente du sol à -10 cm (g cm ⁻³)		1.18	1.15

Tableau 2. Caractéristiques générales des sites d'études. * Classification FAO.

Caractéristique	Valeur
Durée de la mesure (s)	60
Temps attente après la pose de la chambre (s)	15
Durée entre deux mesures (s)	> 60
Contact sol-chambre	embase PVC (Ø110 mm)
Piège à chaux sodée	Non
nombre de mesure/point	1

Tableau 3. Paramètres de mesure de R_S avec le système Licor 6200.

couche 0-6 cm (θ_{Surf}) en même temps que chaque mesure de R_S. Les données de T_S et θ_{Surf} sont utilisées comme variables explicatives dans un modèle empirique:

$$R_S = R_{10} Q_{10} \frac{T_S - 10}{10} e^{-e(a - b \theta_{\text{Surf}})} \quad (5)$$

Où R₁₀ est la respiration standardisée à 10°C, Q₁₀ le facteur par lequel le flux est multiplié lors d'une variation de 10°C, permettant d'exprimer la sensibilité de R_S à la température, a et b sont les paramètres de la fonction simplifiée de Gompertz (Janssens *et al.*, 2001). R₁₀ et Q₁₀ définissent la fonction de température alors que a et b définissent la fonction de contenu en eau. Ces deux fonctions ont été choisies parmi d'autres en fonction d'un R² maximum, d'une erreur résiduelle (RMSE) minimale et d'une distribution non biaisée des résidus (Voir la partie **Déterminants des Flux de CO₂**). Les valeurs annuelles de R_S sont obtenues en simulant et en

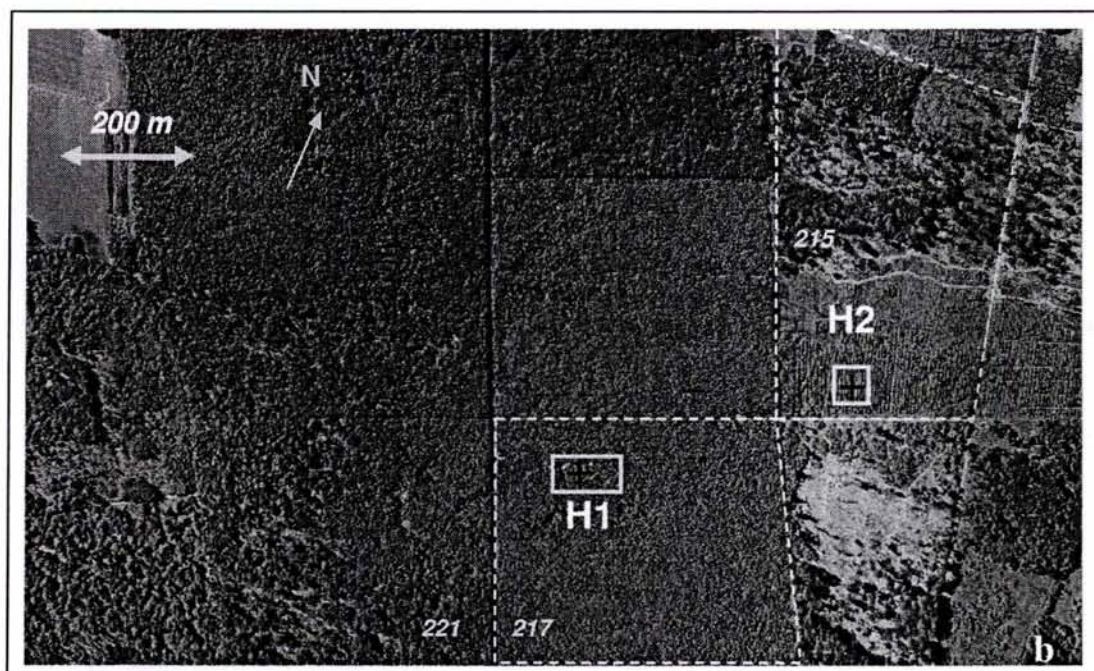
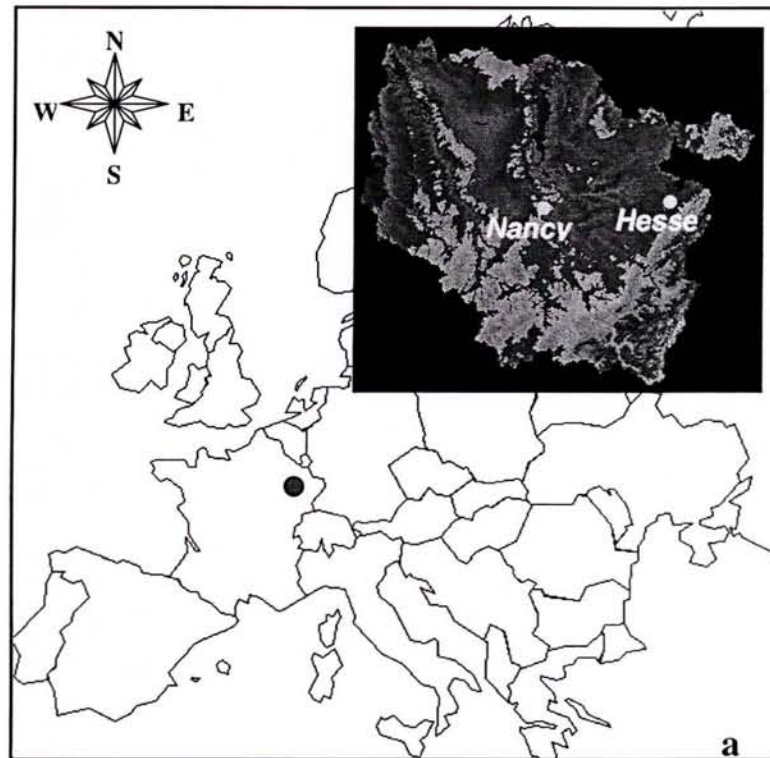


Figure 4. Localisation de la forêt de Hesse (a) et position des deux parcelles après la tempête de décembre 1999 (b, Photographie infrarouge ARAT-CNES, Juin 2000). Les croix indiquent la position des tours à flux.

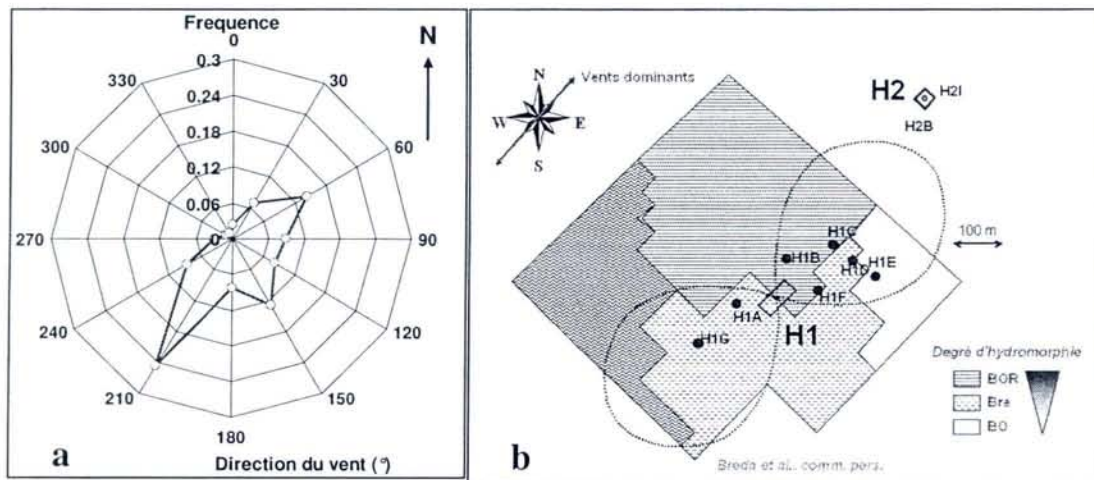


Figure 5. Diagramme en fréquence de la direction des vents mesurée en haut de la tour H1 en 2004 (a) et répartition des placettes de mesure (b). Les zones délimitées par les traits pointillés représentent la zone supposée de footprint de la tour à flux du site H1. Les placettes ont été établies sur trois principaux types de sol (BOR, Bra et BO) qui se différencient par leur degré d'hydromorphie. La flèche verte indique la direction des vents dominants.

	H1A*	H1B*	H1C	H1D	H1E	H1F	H1G	H2B	H2I
n	7016	7535	4158	3898	3638	3638	7276	17968	17968
G	47.5	35.7	44.3	30.0	45.3	53.9	48.7	16.6	16.6
LAI	6.9	5.6	7.2	5.8	8.1	4	6.9	7.4	7.4
<i>Densité apparente</i>	0.81	0.69	0.88	0.75	0.87	0.75	0.85	0.85	1.02
<i>A_f</i>	8.5	8.1	5.9	5.8	4.7	13.4	9.6	6.8	9.0
<i>Litière</i>	5.0	1.7	3.3	4.1	5.0	3.3	4.2	4.3	1.5
<i>C</i>									
<i>Racines</i>	1.1	1.30	0.8	1.6	1.0	0.7	1.8	1.0	1.2
<i>Sol</i>	24.5	26.0	26.5	22.7	32.1	34.0	31.2	24.5	24.2
<i>Total</i>	41.3	40.3	37.9	36.1	44.0	52.1	51.0	39.7	38.7
<i>A₀</i>	0.37	0.37	0.37	0.15	0.29	0.41	0.19	0.18	0.23
<i>Litière</i>	0.05	0.02	0.03	0.05	0.05	0.04	0.05	0.05	0.03
<i>N</i>									
<i>Racines</i>	0.01	0.02	0.01	0.03	0.01	0.01	0.04	0.02	0.01
<i>Sol</i>	0.36	0.22	0.45	0.23	0.37	0.44	0.29	0.20	0.12
<i>Total</i>	3.8	3.3	3.1	3.3	3.3	4.3	4.2	3.2	3.5

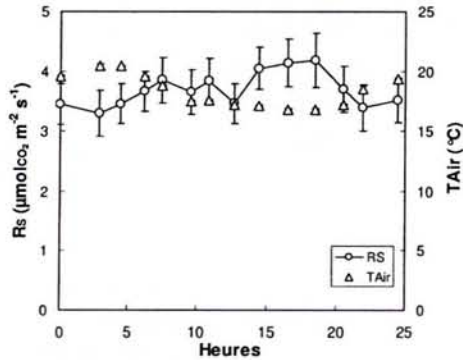
Tableau 4. Principales caractéristiques des placettes impliquées dans l'étude de la variabilité spatiale de R_S . Les placettes du site H1 ne sont pas localisées à l'intérieur du site CARBOEUROPE H1 mais à l'extérieur. Les caractéristiques sont: densité des arbres (n, tiges ha^{-1}), surface terrière (G, $m^2 ha^{-1}$), indice de surface foliaire (LAI, $m^2 m^{-2}$), densité apparente du sol ($g cm^{-3}$), contenus en C et N ($t ha^{-1}$) des différents stocks de l'écosystème participant à R_S . Les placettes indiquées par un * ont été éclaircies précocement en début 2004.

sommant les valeurs journalières de R_S en appliquant l'équation (5) avec les données de température et de contenu en eau mesurées en continu sur le terrain.

La séparation des composantes autotrophes et hétérotrophes de R_S a été réalisée en mesurant le flux de CO_2 du sol dans 2 trenched plots installés dans chaque site. Les trenched plots (TP) et les placettes témoins (CP) dans chaque site sont choisies dans un même environnement en espèce et LAI, et sont distants au maximum de 30 m. Les mesures de R_S ,

T_S et θ_{Surf} sont effectuées au même pas de temps que celles des placettes de suivies sur 12 colliers (H1) et 7-8 colliers (H2) par trenched plot.

Figure 6. Variations de R_S et de la température de l'aire (T_{Air}) au cours d'un cycle de 24 heures. Les barres, lorsqu'elles sont visibles, représentent les intervalles de confiance à 95%.



Expériences de décomposition

Deux expériences de décomposition de litière ont été menées dans le site H1, l'une utilisant une litière de feuilles de hêtre appauvrie en ^{13}C en 2002, l'autre utilisant les débris ligneux d'une éclaircie simulée en février 2003 (Articles 2 et 3, respectivement). La quantité de litière appauvrie simule la chute de litière mesurée en 2001 (161 gC m^{-2}). Des prélèvements d'air analysés pour la détermination du $^{13}\text{CO}_2$ du sol ont été effectués à six dates au cours de 2002, à la fois au-dessus de la litière appauvrie qu'au-dessus d'une zone témoin. La contribution de la litière à R_S est

déduite selon le principe de conservation de masse:

$$R_L/R_S = (\delta - \delta_{\text{BG}})/(\delta_L - \delta_{\text{BG}}) \quad (6)$$

Où δ représente le $\delta^{13}\text{C}$ de la source de CO_2 du sol (sans indice), de la litière (indice L) ou du CO_2 dérivant des processus autre que la décomposition de la litière (indice BG). Alors que δ_L est déterminé sur la matière sèche des feuilles de litière, δ est déterminée par la technique des Keeling plot (Keeling, 1958) qui lie de façon linéaire l'inverse de la concentration en CO_2 et le $\delta^{13}\text{C}$ de l'échantillon d'air. La valeur de δ est l'ordonnée à l'origine de cette relation.

L'expérience de décomposition de débris ligneux détermine de manière destructive la perte de masse de fagots de bois ($75 \text{ cm} \times 40 \text{ cm}$ environ) qui représentent les résidus d'éclaircies. Afin de les préserver des perturbations dues à la faune ou d'éventuels visiteurs, les fagots sont disposés de manière aléatoire à l'intérieur du site-atelier H1 sur une surface de 100 m^2 environ, dans un environnement en LAI, n, type de sol et composition spécifique le plus homogène possible. La perte de masse est suivie par un échantillonnage destructif de 7 fagots environ au pas de temps de deux mois durant 2 ans (2003-2004). Aux mesures de perte de masse s'ajoute une mesure de la densité d'échantillons de bois de chaque fagot récolté. Pour 3 stades de décomposition, plusieurs sous-échantillons ont été mis en incubation dans un système fermé dynamique pour des séries de mesures de flux de CO_2 en fonction de la température de l'air. Pour chaque échantillon, une fonction de température est ajustée (modèle exponentiel Q_{10}) afin de capturer l'effet de la température sur R_B .

LES DETERMINANTS DES FLUX DE CO₂

Le but de notre travail a été d'approfondir la connaissance des principaux compartiments participant à R_{ECO} afin d'en dégager les facteurs majeurs du déterminisme influençant sa variabilité temporelle et spatiale dans le contexte de la forêt de Hesse.

Facteurs climatiques

Nos différentes mesures ont montré une grande variabilité temporelle de R_S à l'échelle saisonnière (Tableau 5). Cette variabilité est pour une grande part expliquée par les variations de température et de contenu en eau du sol. La modélisation de cette variabilité par ces facteurs est indispensable afin de la prendre en compte dans les analyses ultérieures.

Influence de la température

Sur les deux sites de la forêt de Hesse, la température du sol à -10 cm (T_S) est la mieux corrélée temporellement avec R_S (Epron *et al.*, 1999). R_S répond comme attendu de façon exponentielle à T_S. En effet, la température permet à seule d'expliquer, selon les placettes, 40% à 80% (moyenne 46%) de la variabilité saisonnière de R_S avec un modèle empirique en Q₁₀. Il est connu que les modèles à base Q₁₀ sous-estiment le flux aux basses températures, et le surestiment aux températures hautes. En utilisant un modèle basé sur l'équation d'Arrhenius modifiée (Lloyd et Taylor, 1994), les valeurs prédites par ce dernier ne diffèrent pas plus de 10% de celles prédites par le modèle Q₁₀ (Figure 7). Les valeurs annuelles dérivées des deux modèles ne diffèrent pas plus de 8%, soulignant la forte similitude entre les deux modèles empiriques. De plus, la distribution des résidus de la relation à la température seule montre une relation nette avec θ_{Surf} (Figure 8), qui indique une forte relation entre l'humidité et la fonction de température. Cela est en accord avec différentes études qui ont montré que la valeur de Q₁₀ variait avec la gamme de températures considérée, ainsi qu'avec l'humidité (Lloyd et Taylor, 1994; Chen *et al.*, 2000; Wang *et al.*, 2002; Janssens *et al.*, 2003; Curiel Yuste *et al.*, 2003).

Dans notre étude de la variabilité spatiale de R_S, les valeurs de Q₁₀ (Tableau 5, Article 5) restent relativement plus faibles que celles publiées classiquement (Davidson *et al.*, 1998; Buchmann, 2000; Reichstein *et al.*, 2003; Epron *et al.*, 2004a; Hashimoto, 2005). Le facteur Q₁₀ intègre l'effet de la température sur différents processus (respiration de croissance et de maintenance racinaire, décomposition de la litière et de la MOS, évolution de la biomasse microbienne, effet de priming dû à la chute de la litière) qui ont leur propre sensibilité à la température: cela aboutit à des valeurs de Q₁₀ (i) qui sont plus élevées que celles généralement reportées pour des processus physiologiques (Q₁₀ = 2), (ii) et qui peuvent également varier au cours de l'année (Davidson *et al.*, 1998; Janssens et Pilegaard, 2003;

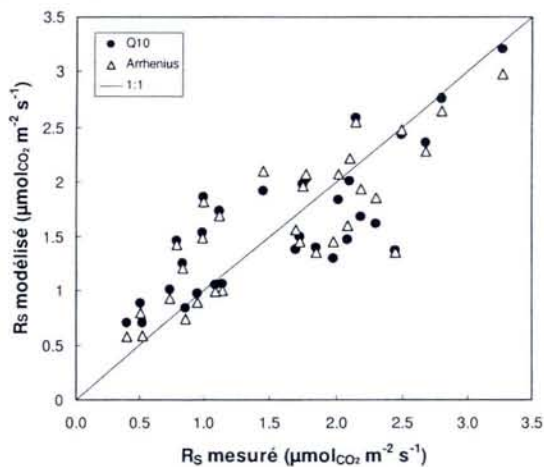


Figure 7. Exemple de relation entre valeurs mesurées de R_S et valeurs prédites par un modèle exponentiel Q₁₀ (ronds pleins) ou par un modèle d'Arrhenius modifié (triangles). Données de la placette H1A (2003-2004).

Placette	Variabilité spatiale									Trenched plot*			
	H1A	H1B	H1C	H1D	H1E	H1F	H1G	H2B	H2I	CPH1	CPH2	TPH1	TPH2
Période	A	A	A	A	A	A	A	B	B	B	B	B	B
R ₁₀	1.63 (0.22)	2.37 (0.35)	1.44 (0.28)	1.62 (0.27)	1.46 (0.30)	2.10 (0.33)	1.78 (0.35)	1.46 (0.21)	1.40 (0.19)	1.39 (0.14)	1.36 (0.08)	0.92 (0.09)	1.08 (0.09)
Q ₁₀	2.49 (0.70)	2.73 (0.76)	2.35 (0.98)	2.40 (0.90)	2.54 (1.00)	2.45 (0.72)	2.89 (1.06)	3.27 (0.88)	2.89 (0.73)	3.14 (0.58)	3.11 (0.29)	2.42 (0.44)	2.51 (0.31)
a	0.97 (1.33)	1.13 (0.77)	1.17 (1.34)	1.34 (1.31)	0.27 (1.02)	0.25 (0.67)	0.89 (0.92)	3.49 (3.65)	1.94 (1.34)	0.96 (1.33)	0.96 (1.33)	0.96 (1.33)	0.96 (1.33)
b	25.30 (23.33)	17.52 (12.48)	21.97 (22.30)	25.54 (24.11)	15.70 (21.16)	14.74 (12.65)	19.56 (18.71)	46.33 (49.01)	24.35 (17.69)	25.30 (23.33)	25.30 (23.33)	25.30 (23.33)	25.30 (23.33)
R ²	0.68	0.75	0.53	0.61	0.66	0.72	0.68	0.90	0.89	0.83	0.68	0.9	0.76
RMSE	0.42	0.50	0.46	0.41	0.38	0.49	0.47	0.29	0.24	0.47	0.32	0.29	0.31
R _{10i}	1.72	2.20	1.38	1.63	1.51	2.15	1.84	1.59	1.36	-	-	-	-
Annuel ₂₀₀₃	599	769	481	567	525	738	640	555	474	-	-	-	-
Annuel ₂₀₀₄	595	763	478	563	521	732	635	550	470	529	528	337	398
% R _{ECO}	0.78	1.00	0.62	0.73	0.68	0.96	0.83	0.72	0.61	0.69	0.69	0.44	0.52

Tableau 5. Les mesures de flux de CO₂ du sol ont été menées sur 2 périodes en fonction de la placette (A : 2003-2004, B : 2004 uniquement). Les paramètres R₁₀ (μmol_{CO2} m⁻² s⁻¹), Q₁₀, a et b de l'équation 5, le coefficient de détermination (R²), la racine carrée de l'erreur résiduelle (RMSE) sont calculés pour le modèle ajusté aux données par placette séparément, à la fois pour l'étude de la variabilité spatiale et pour les trenched plots. Lorsque le modèle est ajusté sur la totalité des données de la variabilité spatiale, seule le R₁₀ (appelé R_{10i}) est variable d'une placette à l'autre, les autres paramètres étant ajustés pour l'ensemble des placettes (Q₁₀ = 2.70; a = 0.87; b = 18.06; R² = 0.69; RMSE = 0.45). Le flux de respiration annuel pour 2004 ("Annuel₂₀₀₄", g_C m⁻² an⁻¹) est calculé pour chaque placette en utilisant l'ajustement sur l'ensemble des données. Pour les trenched plots, les paramètres R₁₀ et Q₁₀ sont ajustés par placettes sur les données de la période A. Les valeurs de a et b sont celles de la placette H1A ajustées sur la période A durant laquelle l'effet de θ_{surf} est mieux modélisée et d'inclure de corriger l'humidité trop forte des trenched plots (Voir "Influence du contenu en eau du sol"). Les valeurs annuelles de 2004 ont été reportées par rapport à R_{ECO} de 2004 (%R_{ECO}). Les valeurs entre parenthèses correspondent aux intervalles de confiance à 95%. * Voir également le Tableau 6 pour les détails des flux annuels.

Curiel Yuste *et al.*, 2004).

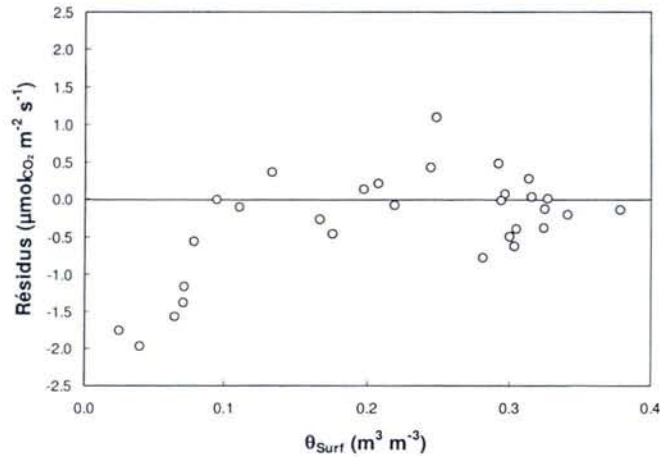


Figure 8. Relation entre les résidus de la relation de température et le contenu en eau du sol (θ_{Surf}). Donnée de la placette H1A.

Notre étude sur les trenched plots montrent un Q_{10} plus élevé dans les placettes contrôles (Tableau 5, Article 4), même si Bååth et Wallander (2003) montrent qu'en microcosme les deux composantes ont le même Q_{10} . Plusieurs auteurs ont souligné le rôle des racines dans la sensibilité de R_S à la température. Les racines seraient ainsi plus sensibles à la température que la décomposition de la MOS, se traduisant par un Q_{10} plus haut pour la composante autotrophe de R_S que pour la composante hétérotrophe (Boone *et al.*, 1998; Epron *et al.*, 2001, Lavigne *et al.*, 2003; Reichstein *et al.*, 2005), alors que Tang *et al.* (2005b) suggèrent l'inverse: ceci serait principalement dû à une acclimatation des racines aux conditions méditerranéennes de leur site, surtout durant la saison de végétation combinant fortes températures et faibles contenus en eau du sol. Notre étude semble donc confirmer les travaux précédemment cités. De plus, la sensibilité à la température ne semble pas différer spatialement entre les placettes ni entre les sites H1 et H2, alors que l'exclusion racinaire entraîne une diminution du Q_{10} . Parallèlement, nous n'avons pas pu montrer de différences significatives de biomasse racinaire dans la couche 0-15 cm entre placettes (Tableau 4). Nos données tendent donc bien à confirmer que la sensibilité à la température captée par nos mesures serait en forte relation avec la dynamique des racines. De plus, les valeurs plus élevées de Q_{10} dans les placettes contrôles témoigneraient d'une combinaison de la hausse de la température et du pic de croissance racinaire au cours de la saison qui ne se retrouve pas dans les trenched plots.

Les valeurs de Q_{10} de respiration de la nécromasse, établies pour les échantillons maintenus à humidité de terrain, est plus faible que celles concernant R_S (Q_{10} situés entre 1.21 et 2.4). Ces valeurs sont en accord avec celles de Chen *et al.* (2000) et Wang *et al.* (2003). Ces auteurs ont également montré que comme pour R_S , le facteur Q_{10} variait à la fois en fonction de la gamme de température et avec l'humidité de l'échantillon. Dans notre étude, il existe une grande variabilité de cette réponse à la température entre les échantillons de bois (Article 3). Ni le diamètre de l'échantillon, la classe de décomposition via l'infradensité du bois ou le contenu volumique en eau des échantillons n'ont pu expliquer cette variabilité, alors qu'à une température donnée, la respiration du bois est différente selon le diamètre de l'échantillon. Hicks et Harmon, 2002 ont pourtant montré que l'infradensité pouvait influencer

la diffusivité de l'O₂ qui est un important régulateur des processus physiologiques impliqués dans la décomposition et la production du CO₂. Une première possibilité pouvant expliquer ces valeurs de Q₁₀ serait que le niveau d'humidité (celle du terrain) est juste suffisant pour un fonctionnement métabolique "de base". A ce niveau, le flux de CO₂ serait plus contrôlé par l'humidité que par la température, comme certains auteurs l'ont montré pour R_S durant des périodes ou dans des sites soumis à un stress hydrique (Davidson *et al.*, 1998; Epron *et al.*, 1999; Reth *et al.*, 2005). Une seconde hypothèse concernerait une variabilité entre échantillons du degré de colonisation par les micro-organismes saprotrophes, la biomasse et/ou l'activité microbienne (Hicks *et al.*, 2003).

Nos résultats confirment donc qu'à l'échelle de notre étude, la température est un facteur essentiel influençant grandement la variabilité temporelle des différents flux de CO₂, mais laisse une grande part de la variabilité (notamment spatiale) à d'autres facteurs susceptibles d'être confondus ou cachés derrière le pattern général imposé par elle.

Influence du contenu en eau volumique et des précipitations

Le contenu en eau du sol est, après la température, la seconde variable abiotique la plus influente sur les flux de CO₂ (Janssens *et al.*, 2003; Wang *et al.*, 2003), et sont dans beaucoup de cas en interaction comme nous l'avons suggéré précédemment. Durant notre étude, θ_{Surf} était directement corrélé à T_S. Les mesures estivales, en particulier celles durant la canicule de l'été 2003, ont permis de préciser l'influence du contenu en eau du sol (θ_{Surf}) sur l'évolution saisonnière de R_S (Article 4 et 5). La fonction de Gompertz (Janssens *et al.*, 2001), qui décrit la réponse de R_S à θ_{Surf} , ne permettrait de reproduire l'évolution de R_S dans nos placettes que dans des gammes de θ_{Surf} se situant entre 0.2 m³ m⁻³ (valeur au-delà de laquelle θ_{Surf} n'est pas limitant) et 0.07 m³ m⁻³, valeur en dessous de laquelle la forme mathématique de la fonction ne reproduit plus des variations de R_S. Cependant, cette très faible valeur de θ_{Surf} n'est atteinte que durant 2 campagnes de mesures et durant une période de deux semaines maximum par an. Ainsi, pour l'ensemble du jeu de données, la prise en compte de θ_{Surf} a grandement amélioré les performances du modèle empirique comme dans d'autres études (Rey *et al.*, 2002; Curiel Yuste *et al.*, 2003; Epron *et al.*, 2004b) puisqu'en moyenne 23% de la variance saisonnière observée est expliquée par ce facteur.

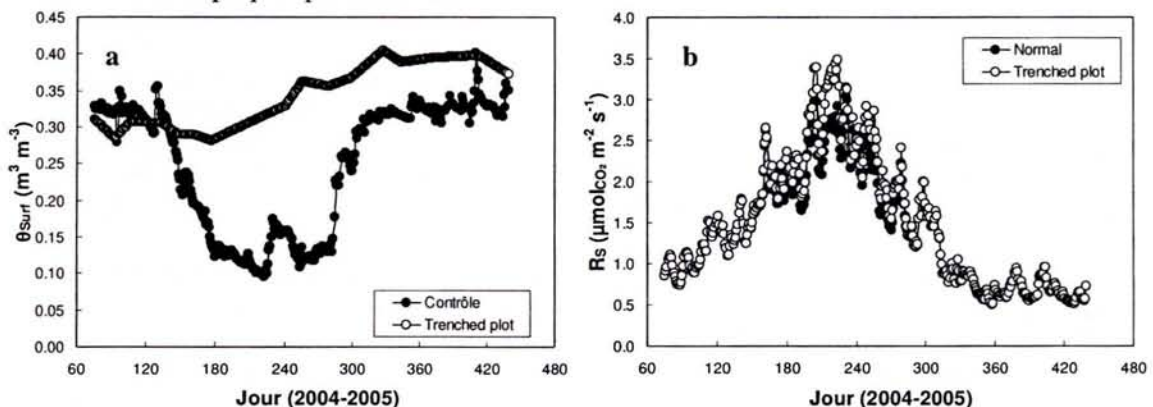


Figure 9. (a) Evolution saisonnière du contenu volumique en eau du sol (θ_{Surf}) dans une parcelle contrôle et dans un trenced plot et (b) évolution de la respiration du sol (R_S) simulée avec l'équation (5) avec les contenus en eau de sol contrôles (Normal) ou des trenced plots. Données de la placette H1A (CPH1).

Durant l'expérience des trenced plots, la suppression de l'évapotranspiration par le tranchage des racines a maintenu une humidité du sol relativement élevée (Figure 9a). Cet

écart d'humidité n'a pas induit directement de différences de biomasse microbienne pouvant expliquer les différences du flux de CO₂ du sol entre le trenched plot et la placette contrôle. Différents auteurs ont montré que les variations saisonnières de θ_{Surf} modifiaient les structures microfongiques ainsi que les biomasses microbiennes (Schimel *et al.*, 1999; McLean et Huhta, 2000). Li *et al.* (2005) ont observé une diminution de la biomasse bactérienne et fongique dans un trenched plot par rapport à une placette témoin, mais n'ont pas mesuré l'humidité du sol. Selon les auteurs, la suppression de l'allocation de C provoquée par le tranchage des racines expliquerait cette diminution de biomasse microbienne. Par ailleurs, les valeurs annuelles de R_S calculées en utilisant les valeurs de θ_{Surf} mesurées dans les trenched plots seraient 5 à 14% supérieures aux valeurs annuelles de R_S calculées avec les valeurs de θ_{Surf} mesurées dans les placettes contrôles (Figure 9b).

Alors que l'écart maximum des températures du sol entre placettes n'est que de 2°C, les valeurs de θ_{Surf} sont pour certaines dates relativement variables d'une placette à l'autre (de 0.02 m³ m⁻³ à 0.1 m³ m⁻³ sur l'ensemble des mesures), mais aucune hiérarchisation n'a pu être établie en fonction du type de sol ou de la densité apparente du sol.

En considérant l'ensemble de ces résultats, il apparaît qu'un modèle empirique ne prenant en compte que l'effet de T_S et θ_{Surf} ne reproduit pas complètement toutes les variations

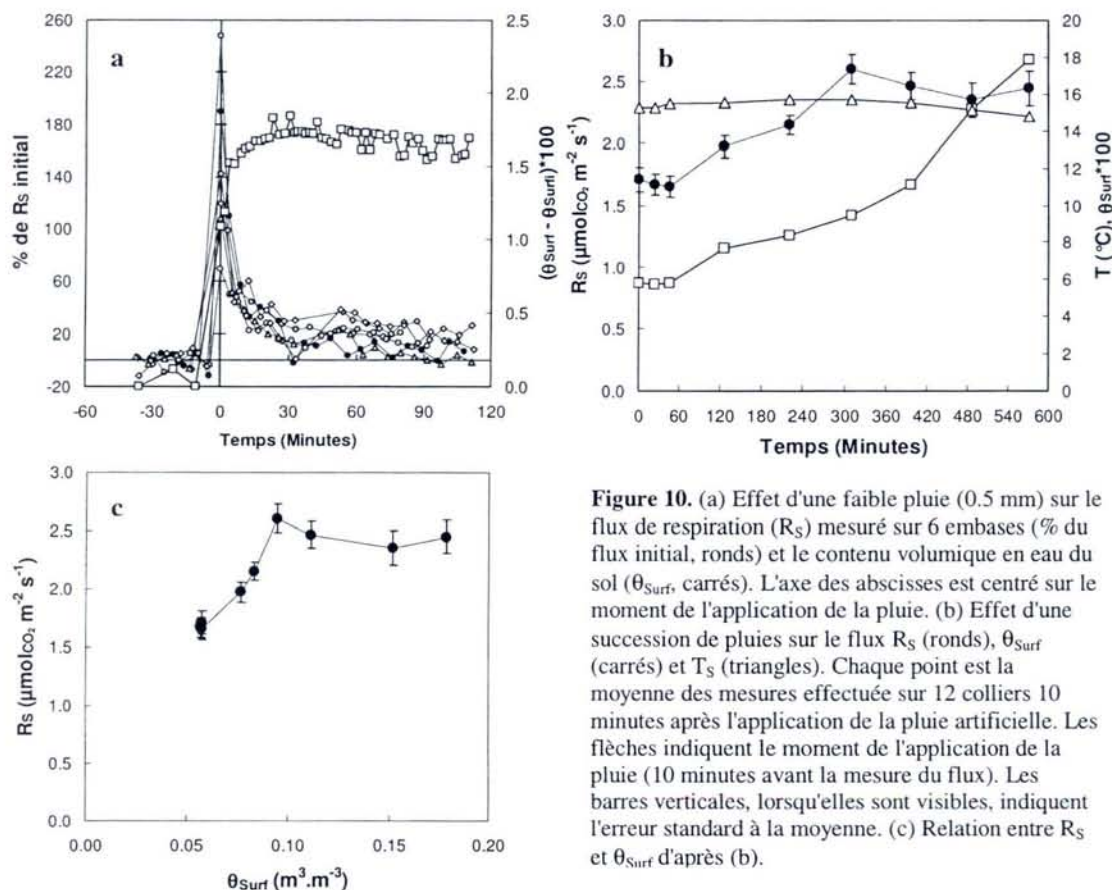


Figure 10. (a) Effet d'une faible pluie (0.5 mm) sur le flux de respiration (R_S) mesuré sur 6 embases (% du flux initial, ronds) et le contenu volumique en eau du sol (θ_{Surf} , carrés). L'axe des abscisses est centré sur le moment de l'application de la pluie. (b) Effet d'une succession de pluies sur le flux R_S (ronds), θ_{Surf} (carrés) et T_S (triangles). Chaque point est la moyenne des mesures effectuée sur 12 colliers 10 minutes après l'application de la pluie artificielle. Les flèches indiquent le moment de l'application de la pluie (10 minutes avant la mesure du flux). Les barres verticales, lorsqu'elles sont visibles, indiquent l'erreur standard à la moyenne. (c) Relation entre R_S et θ_{Surf} d'après (b).

saisonniers de R_S . La valeur de R^2 (0.69, Tableau 4) montre que le modèle empirique explique 69% de la variabilité. Des processus tel qu'une augmentation de la respiration suite à une pluie (Rey *et al.*, 2002; Curiel Yuste *et al.*, 2003; Lee *et al.*, 2004) ou l'effet de priming (augmentation rapide de l'activité respiratoire suite à un apport de C facilement assimilable,

Fontaine *et al.*, 2003; Kuzyakov *et al.*, 2002) consécutif au lessivage des litières fraîchement tombées au sol en automne (Ibrahima *et al.*, 1995; Subke *et al.*, 2004) ont été mis en évidence et participeraient à la variabilité saisonnière de R_S . L'effet de très faibles pluies (< 1 mm) a été suivi sur un sol relativement sec ($0.05 \text{ m}^3 \text{ m}^{-3}$) qui a été préservé des précipitations durant 3 mois par un toit en PVC. Une première série de mesures a été menée suite à une seule pluie (0.5 mm) afin de voir l'effet direct de la pluie sur R_S (Figure 10a), puis une succession de pluies a été appliquée à intervalle régulier (Figure 10b). Ainsi, une pluie de faible amplitude a induit une augmentation transitoire de R_S (+ 60% à +250% du flux initial). De plus, l'augmentation progressive de θ_{surf} jusqu'à environ $0.1 \text{ m}^3 \text{ m}^{-3}$ a induit une augmentation de R_S mais qui, au delà de $0.1 \text{ m}^3 \text{ m}^{-3}$ semble s'arrêter (Figure 10c). Une des hypothèses expliquant les mécanismes de ces pulses serait une excitation quasi-instantanée des micro-organismes des horizons superficiels (litière et couche A_0 du sol minéral) qui minéralisent rapidement des composés labiles intra-cellulaires, ces composés étant libérés dans le sol suite à une rupture des parois cellulaires bactériennes consécutive à l'augmentation rapide du potentiel hydrique du sol (Birch, 1958; Kieft *et al.*, 1987; Reichstein *et al.*, 2002; Fierer et Schimel, 2003). Une autre possibilité serait un déplacement par l'eau de pluie du CO_2 contenu dans les couches superficielles, comme le ferait l'insertion d'une chambre de respiration directement dans le sol (Article 1). La pluie peut donc entraîner sur un sol sec de fortes variations de R_S à très court terme mais répété durant la saison. Pour modéliser cet effet, il est nécessaire d'effectuer des mesures dans d'autres conditions de θ_{surf} et disposer d'une plus grande gamme de précipitations appliquées.

Notre étude sur la respiration du bois (Article 3) n'a pas pu conclure à un effet éventuel de l'humidité des échantillons sur la variabilité des respirations basales à 10°C (R_{10}). Par contre, en ne considérant qu'un seul échantillon à la fois, nous pouvons mettre en évidence une relation linéaire entre le R_{10} et le contenu volumique en eau de l'échantillon (Figure 11a), en accord avec Chen *et al.* (2000). D'autre part, la diminution du contenu en eau des échantillons a provoqué une diminution des valeurs de R_{10} (Figure 11b). Une hypothèse pour expliquer cette diminution serait une limitation de la respiration par la disponibilité en substrats (Hick *et al.*, 2003) dont les mouvements dans les tissus des débris ligneux, comme pour les pores du sol, sont restreints aux valeurs de potentiels hydriques très basses (Wilson et Griffin, 1975).

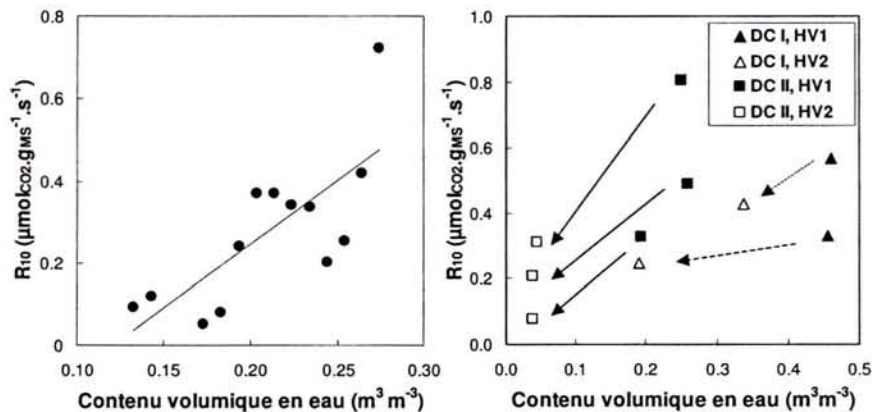


Figure 11. (a) Relation entre la respiration basale à 10°C (R_{10}) d'un échantillon de bois et son contenu volumique en eau interpolé linéairement au cours d'une succession de 13 cycles de température entre 4°C et 34°C . L'équation de la relation globale est $R_{10} = 3.11[\text{Contenu en eau}] - 0.38$ ($R^2 = 0.57$). (b) Evolution du R_{10} pour des échantillons à humidité initiale de terrain (HV1, symboles pleins) et des mêmes échantillons séchés à l'étuve (HV2, symboles ouverts) à 65°C durant 24 heures. Les flèches indiquent l'évolution du R_{10} .

L'effet du contenu volumique en eau à Hesse est globalement positif sur les flux de respiration (R_S et R_B), notamment aux faibles valeurs d'humidité. A très court terme, l'augmentation de θ_{surf} induit une augmentation de la disponibilité en substrat immédiat (effet pulse de CO_2), alors qu'il est plus difficile de prévoir l'effet des variations de θ_{surf} à plus long terme sur la biomasse microbienne. Une étude des variations de l'activité microbienne permettrait de mieux comprendre ces interactions, notamment aux fortes valeurs d'humidité, en conditions d'hydromorphie qui sont présentes à faible profondeur (-35 cm dans le sol le plus hydromorphe).

Importance des composantes de la respiration du sol

Contribution des différentes composantes à R_{ECO}

Notre étude est en accord avec la littérature sur le fait que R_S est la composante majeure de R_{ECO} (Tableau 5, Article 5). En moyenne sur l'ensemble de nos placettes (sans prendre en compte le footprint de la mesure de R_{ECO}), R_S contribue à 80% et 65% de R_{ECO} dans les sites H1 et H2, respectivement. Ces valeurs sont conformes à celles récemment publiées (Tableau 1), mais la prise en compte du footprint dans cette comparaison est primordiale compte tenu de grande variabilité spatiale dans le site H1 (Tableau 5).

	H1		H2	
	CP	TP	CP	TP
R ($\text{g}_C \text{ m}^{-2} \text{ an}^{-1}$)	529	337	528	398
R_D ($\text{g}_C \text{ m}^{-2} \text{ an}^{-1}$)	-	189	-	183
R_{Auto} ($\text{g}_C \text{ m}^{-2} \text{ an}^{-1}$)	381	-	312	-
R_{Hetero} ($\text{g}_C \text{ m}^{-2} \text{ an}^{-1}$)	148	-	216	-
R_{Auto} (%)	72	-	59	-
COD ($\mu\text{g}_C \cdot \text{g}^{-1}$)	132 (5)	125 (5)	167 (8)*	150 (15)*

Tableau 6. Valeurs annuelles (2004) de la respiration sol (R) mesurée dans les trenched plots (TP) ou dans les placettes témoins (CP), du flux de CO_2 issu de la décomposition des racines des tranchées (R_D , équation 4), de la composante autotrophe de R_S (R_{Auto}) et de sa contribution à R_S . Les valeurs de carbone organique dissout (COD) sont également données (Article 4).

Déterminée dans l'article 4, la composante autotrophe de R_S est de 72% et 59% dans H1 et H2, respectivement (Tableau 6). Rappelons que R_{Auto} est calculée par différences (équation 4), et que les valeurs de flux annuels des placettes contrôles et tranchées (termes R_S et R_{TP} , Tableau 4) sont inférieures d'environ $100 \text{ g}_C \text{ m}^{-2} \text{ an}^{-1}$ à celles reportées par Epron *et al.* (1999) mais pour des flux de CO_2 issus de la décomposition des racines (terme R_D) équivalentes. Cette comparaison est toutefois à considérer avec précautions car les deux études ont été menées sur deux zones différant probablement dans leur profil d'enracinement. Plus largement, Bond-Lamberty *et al.* (2004) recense 56 sites dans lesquels R_{Auto} et R_{Hetero} ont été déterminés par diverses techniques. Dans cette revue, l'exclusion racinaire est utilisée dans 20 des 56 sites dont Hesse étant le seul site répertorié dans le groupe tempéré chaud. Par rapport à cette synthèse, nos valeurs de R_{Auto} sont supérieures et semblent être en partie dues aux corrections apportées (décomposition des racines tranchées principalement) que seules 3 autres études répertoriées prennent en compte. En effet, en ignorant ces corrections, nos estimations de la contribution de R_{Auto} à R_S (35% et 22% dans H1 et H2, respectivement) sont situées dans l'intervalle de confiance à 95% de la relation R_S / contribution R_{Auto} proposée par Bond-Lamberty *et al.* (2004). Notre étude confirme donc l'importance de ces corrections pour une estimation non biaisée des composantes de R_S par trenched plot.

Respectivement dans H1 et H2, R_{Auto} représente 38% et 42% de R_{ECO} et R_{Hetero} représente 14% et 29% de R_{ECO} (Figure 12). Ces résultats montrent la part importante que représentent

les composantes de R_S dans R_{ECO} . Reichstein *et al.* (2002) ont montré par la méthode EC dans des sites méditerranéens que R_{Hetero} représente 50% de R_{ECO} . Le flux R_B contribue à 8% de R_{ECO} dans H1 (Article 3). La contribution annuelle de R_L a été estimée à 8% de la valeur annuelle de R_S (Article 2). De même, la contribution annuelle de R_L à R_{Hetero} avait été estimée à 20% dans l'hypothèse d'un rapport R_{Auto}/R_{Hetero} de 60:40. Pour le site H1, en considérant une valeur annuelle de R_S de $529 \text{ gC m}^{-2} \text{ an}^{-1}$ (2004) et une valeur annuelle de R_{Hetero} de $147 \text{ gC m}^{-2} \text{ an}^{-1}$, la contribution de R_L à R_{Hetero} est ramené à 29%, ce qui reste comparable aux résultats de Bowden *et al.* (1993) et Rey *et al.* (2002). La fraction restante ($333 \text{ gC m}^{-2} \text{ an}^{-1}$ et $215 \text{ gC m}^{-2} \text{ an}^{-1}$ dans H1 et H2, respectivement) représenterait 33% et 29% de R_{ECO} et serait attribuée à la respiration des parties aériennes R_{Abg} , ce qui est en accord avec les estimations directes effectuées par Damesin *et al.* (2002) sur H1.

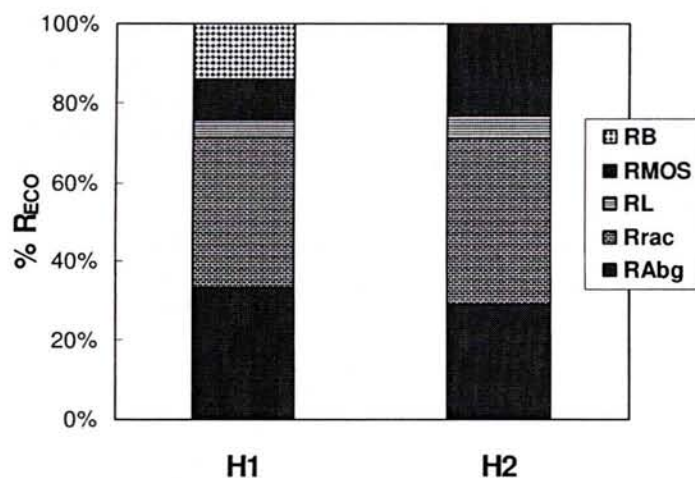


Figure 12. Répartitions des différents flux par rapport à R_{ECO} dans H1 ($1002 \text{ gC m}^{-2} \text{ an}^{-1}$) et H2 ($743 \text{ gC m}^{-2} \text{ an}^{-1}$) en 2004. La contribution de R_S ($R_{Auto} + R_L + R_{MOS}$) à R_{ECO} est de l'ordre de 69% (H1) et 71%. Pour cette répartition, les valeurs utilisées proviennent des expériences de trenched plots, de la décomposition des litières et des débris ligneux pour l'année 2004.

Variabilité inter-site des composantes de R_S

Nos résultats montrent une différence inter-site de R_{Auto} et de sa contribution à R_{ECO} qui peut s'expliquer par plusieurs hypothèses. Jiang *et al.* (2005) suggèrent une augmentation de R_{Hetero} et une diminution de R_{Auto} avec l'âge alors que d'autres auteurs tendraient à montrer que R_{Auto} augmenterait avec l'âge du site via l'augmentation de la surface ou la biomasse racinaire chez les peuplements adultes non matures (Gough *et al.*, 2004; Bond-Lamberty *et al.*, 2004; Claus et George, 2005). Nos données de biomasse racinaire provenant à la fois des trenched plots et des placettes de variabilité spatiale (Tableau 4, Article 4 et 5) ne diffèrent pas significativement entre les sites, ne permettant donc pas d'expliquer (i) les différences de respiration autotrophe entre H1 et H2, ni (ii) la variabilité spatiale des valeurs de R_{10i} pour cette parcelle de la forêt de Hesse (Tableau 5), contrairement à d'autres auteurs (Stoyan *et al.*, 2000; Reth *et al.*, 2005; Sørensen et Buchmann, 2005).

Une autre hypothèse serait la relation possible entre R_{Auto} et la productivité du peuplement, comme le tendent à montrer les récentes études qui établissent le lien entre GPP et R_S via une allocation rapide des assimilats récents aux racines (Högberg *et al.*, 2001; Janssens *et al.*, 2001; Cardon *et al.*, 2002; Högberg *et al.*, 2002; Tang *et al.*, 2005a). Le plus fort accroissement en biomasse totale (aérienne et racinaire, LeGoff et Ottorini, 2001) calculé pour H2 ($8.8 \text{ tMS ha}^{-1} \text{ an}^{-1}$) que pour H1 ($5.0 \text{ tMS ha}^{-1} \text{ an}^{-1}$) ne s'accorde pas avec une plus faible valeur de R_{Auto} dans cette parcelle, même si une plus forte allocation de C aux racines pourrait

être envisagée (Bond-Lamberty *et al.*, 2004). Cette relation entre R_{Auto} et la productivité du peuplement a jusqu'à présent été montrée à une échelle plus large (variabilité intersite, Janssens *et al.*, 2001) et participerait à la variabilité inter-annuelle de R_S (Voir la partie **Variabilité inter-annuelle** ci-dessous).

Alternativement, une plus faible respiration autotrophe dans H2 équivaut à une plus forte respiration hétérotrophe. La plus forte teneur en carbone organique dissout (COD) dans la placette contrôle de H2 que celui de H1 (Article 4) suggérerait une plus forte activité microbienne pouvant concorder avec la plus forte valeur de R_{Hetero} . La respiration du sol est souvent liée à la quantité de chute de litière qui stimulerait et alimenterait la composante hétérotrophe de R_S (Raich et Nadelhoffer, 1989; Longdoz *et al.*, 2000; Reichstein *et al.*, 2003). Dans la revue de Bond-Lamberty *et al.* (2004), R_{Hetero} est positivement corrélé avec les entrées de détritiques (= chutes de litière et productivité des racines fines). En 2004, les chutes de litière étaient de 171 gC m^{-2} et 159 gC m^{-2} dans H1 et H2 respectivement. D'où, selon les résultats de Bond-Lamberty *et al.* (2004), la plus grande contribution hétérotrophe du site H2 serait expliquée plutôt par une plus grande productivité des racines fines que par la différence de chute de litière.

Sensibilité des méthodes de séparation des composantes de R_S

Les méthodes utilisées pour séparer les composantes de R_S et R_{ECO} reposent sur certaines hypothèses qui sont parfois ignorées ou sous-entendues, sans toutefois en connaître l'impact sur le calcul final.

Effets des trenched plots sur la décomposition

La méthode des trenched plots a permis la quantification des principales composantes de R_S . Cependant plusieurs hypothèses sont implicitement faites, et certains effets ne sont pas pris en compte dans certains travaux utilisant cette méthode (Hart et Sollins, 1998; Rochette *et al.*, 1999; Rey *et al.*, 2002; Jiang *et al.*, 2005). Dans une revue portant sur la séparation des composantes autotrophe et hétérotrophe, Hanson *et al.* (2000) soulignent la nécessité d'apporter des corrections sur les estimations des composantes. Une première correction concerne la différence de contenu en eau du sol induit par la suppression de l'évapotranspiration dans les trenched plots. Cette différence peut être en partie prise en compte au niveau des flux annuels en utilisant les valeurs de T_S et θ_{Surf} enregistrées en conditions naturelles pour les simulations de flux journaliers des placettes contrôles comme des placettes témoins (Epron *et al.*, 1999; Rey *et al.*, 2002). (voir la partie **Influence du contenu en eau du sol**, Figure 9).

Une seconde correction concerne la prise en compte du flux de CO_2 additionnel (R_D) provenant de la décomposition des racines coupées par le tranchage (Epron *et al.*, 1999; Lavigne, *et al.*, 2003; Lee *et al.*, 2003; Bond-Lamberty *et al.*, 2004) selon:

$$R_D = (1 - \alpha_R) B_0 (1 - e^{-k_R t}) \quad (7)$$

Où α_R est la fraction de C incorporée dans la MOS durant la décomposition, B_0 la biomasse racinaire initiale totale à l'intérieur du trenched plot (gC m^{-2}), t le temps (an) et k_R la constante de décomposition des racines (an^{-1}). La détermination du flux R_D implique au moins 3 sources d'incertitude:

1. La détermination de B_0

Une étude de sensibilité faisant varier B_0 dans son intervalle de confiance à 95% montre que le calcul de R_{Auto} (équation 4) y est très sensible (Figure 13a). Cette sensibilité est avant tout liée à l'incertitude sur la valeur de la biomasse racinaire qui a été déterminée par 8 carottes de sol dans chaque site au moment de l'établissement des trenched plots (Article 4). Il

existe une seconde incertitude sur l'estimation de B_0 lorsque la biomasse estimée à partir des carottes est rapportée sur l'ensemble du profil de sol. D'après Epron *et al.* (1999), la biomasse racinaire estimée par les carottes de sol représente 45% de la biomasse totale. Nous avons appliqué ce facteur correctif afin de tenir compte à la fois de la distribution verticale des racines et de la proximité des arbres. Malgré le fait que notre étude se situe dans la même parcelle que ces auteurs, il est possible que le profil d'enracinement soit différent: le facteur de

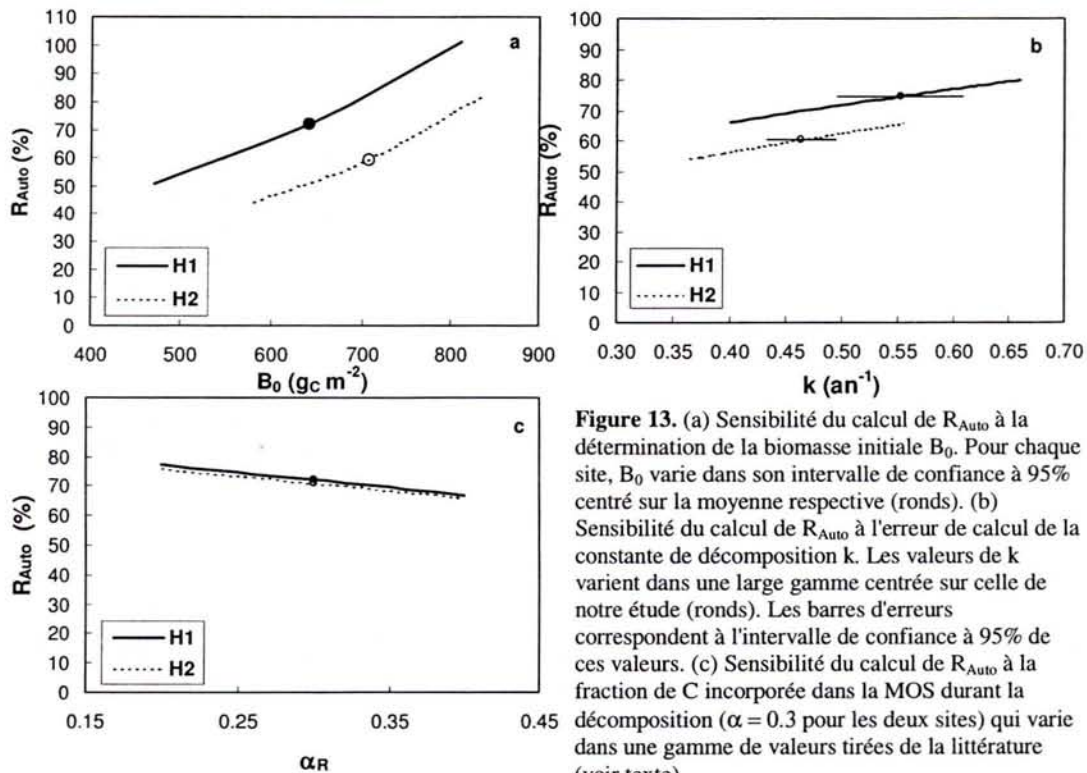


Figure 13. (a) Sensibilité du calcul de R_{Auto} à la détermination de la biomasse initiale B_0 . Pour chaque site, B_0 varie dans son intervalle de confiance à 95% centré sur la moyenne respective (ronds). (b) Sensibilité du calcul de R_{Auto} à l'erreur de calcul de la constante de décomposition k . Les valeurs de k varient dans une large gamme centrée sur celle de notre étude (ronds). Les barres d'erreurs correspondent à l'intervalle de confiance à 95% de ces valeurs. (c) Sensibilité du calcul de R_{Auto} à la fraction de C incorporée dans la MOS durant la décomposition ($\alpha = 0.3$ pour les deux sites) qui varie dans une gamme de valeurs tirées de la littérature (voir texte).

correction appliqué serait plus élevé à cause d'un enracinement plus superficiel due à une hydromorphie plus superficielle sur nos placettes (Y. Lefèvre, INRA Nancy, comm. pers.).

2. La constante de décomposition k_R

Une analyse de sensibilité montre que l'incertitude sur la constante de décomposition des racines (k_R) a un impact relativement moyen sur le calcul de R_{Auto} (Figure 13b) lorsque k_R varie dans une large gamme dont les valeurs proviennent de différents modèles (Dewar, 1991; Liski *et al.*, 2005). L'impact de cette incertitude est par contre très faible à l'intérieur de l'intervalle de confiance à 95% de k_R ¹: une erreur de $\pm 10\%$ sur la valeur de k_R entraîne une erreur de $\pm 3\%$ en contribution de R_{Auto} pour la parcelle H1, et une erreur de $\pm 2\%$ sur la valeur de k_R entraîne une erreur de $\pm 2\%$ en contribution de R_{Auto} dans la parcelle H2. Cela nous indique que malgré la grande variabilité des racines, l'estimation de la constante de décomposition est relativement robuste, et que le calcul du terme R_{Auto} est très peu sensible à ce paramètre.

¹ L'intervalle de confiance de k_R a été calculé sur 100 couples de valeurs de biomasse initiale et finale dans leur intervalle de confiance respectif, centré sur leur moyenne respective et assumant une distribution normale.

3. Valeur de α_R

Une autre étude de sensibilité montre qu'une erreur non négligeable est faite lorsqu'on considère la fraction α_R (Figure 13c). En effet, dans une gamme située entre 0.22 (Jenkinson, 1990) et 0.4 (Parton *et al.*, 1987), R_{Auto} variait d'environ $\pm 5\%$ en contribution. La valeur de 0.3 pour la décomposition des racines, située entre ces deux valeurs, semble cohérente avec celle de 0.2 déterminée pour la décomposition de litière de feuilles de hêtre (Article 1), ainsi qu'avec l'étude de Ladd *et al.* (1995) qui ont déterminé une fraction respirée durant la décomposition $(1 - \alpha_R)$ de 0.75 grâce à l'utilisation de ^{14}C -glucose.

La prise en compte du flux R_D , qui représente 56% et 46% du flux de CO_2 issu des trenched plots, permet une correction de R_{Auto} passant de 35% et 22% (H1 et H2 respectivement) à 72% et 59% soit une correction de +37%, alors que la plupart des auteurs effectuant cette correction modifient leur estimation de 1% à 23% (Ohashi *et al.*, 2000; Lavigne *et al.*, 2003; Lee *et al.*, 2003; Bond-Lamberty *et al.*, 2004). Ces résultats soulignent donc les précautions à prendre lors de ces corrections, en particulier la détermination de la biomasse racinaire à laquelle les calculs de R_{Auto} sont très sensibles.

Décomposition de la litière et des débris ligneux

La contribution de la décomposition de la litière (R_L) a été estimée en comparant le $\delta^{13}\text{C}$ issu de litière de feuilles contrôles (naturelles) et celui de litière de feuilles appauvries en ^{13}C (Article 2). En 2002, la contribution de R_L varie de 2.8% en printemps à environ 11.4% en été, et diminue juste avant la chute des feuilles en automne. Les valeurs annuelles de R_S et R_L sont de $980 \text{ g}_C \text{ m}^{-2}$ et $80 \text{ g}_C \text{ m}^{-2}$, respectivement. Annuellement, la contribution de la décomposition de la litière fraîche a été de 8% de R_S , et 80% de la perte total C. L'autre fraction qui entre dans la MOS (20% de la perte total de C), représente seulement $20 \text{ g}_C \text{ m}^{-2}$.

La principale hypothèse faite durant cette expérience est que le taux de décomposition de la litière contrôle et celle de la litière appauvrie sont identiques. Il a été montré que le fractionnement isotopique durant la décomposition était équivalent pour les deux types de litières bien qu'elles diffèrent entre elles par un plus grand rapport C/N des litières contrôle (58 contre 34 pour les litières appauvries). Cette différence du rapport C/N implique un taux de décomposition moins élevé de cette litière (Swift *et al.*, 1979; Berg *et al.*, 2000). La prise en compte de cette différence dans les calculs amène à une diminution du rapport R_L/R_S de 25% (Article 2).

La décomposition des débris ligneux est basée sur une hypothèse implicite selon laquelle tous les échantillons se décomposent de la même façon et à la même vitesse. La variabilité des mesures de respiration en conditions contrôlées suggère qu'il existe une variabilité dans le taux de colonisation et donc du taux de décomposition (Article 3). La valeur de k_B atteint $0.24 \pm 0.02 \text{ an}^{-1}$ lorsqu'elle est calculée sur l'ensemble des données de perte de masse et non plus sur les valeurs moyennes. Cette valeur de k_B permet d'estimer le flux R_B à $60 \text{ g}_C \text{ m}^{-2} \text{ an}^{-1}$, en assumant une fraction α_B de C perdu durant la décomposition sous forme de CO_2 de 0.8 (Dewar, 1991). Les incertitudes de cette valeur de R_B portent sur 2 aspects. La première incertitude concerne la dynamique de décomposition des échantillons, reflétée par la constante de décomposition k_B . Le modèle de décomposition sous-jacent (Olsen, 1967) est bien ajusté aux données ($R^2 = 0.95$), et l'intervalle de confiance à 95% de k_B (0.02 an^{-1}) est relativement faible (< 10%). Il semble donc que le modèle utilisé est bien adapté, comme l'ont montré diverses études (Harmon *et al.*, 1986). Un second aspect concerne la fraction de α_B de C perdu durant la décomposition sous forme de CO_2 . Cette dernière influençant linéairement la respiration annuelle, son choix est donc important sur le calcul final. Liski *et al.* (2005) utilisent dans le modèle YASSO une valeur de 0.2 pour les fractions de masse d'un pool

passant dans un autre pool plus résistant à la décomposition, équivalent à une fraction perdue sous forme de CO₂ de 0.8. Il semblerait que cette valeur soit adaptée pour les stades de décomposition relativement précoce et durant lesquelles la fragmentation du matériau n'est pas amorcée (Harmon *et al.*, 1986). Les estimations de R_B par les mesures directes de flux de CO₂ issu d'échantillons de bois sont très supérieures aux valeurs de pertes de masse (160 g_C m⁻² an⁻¹ contre 60 g_C m⁻² an⁻¹, Article 3). Cette différence peut être attribuée aux gammes de températures simulées lors des incubations (4°C-34°C) qui ne correspondraient pas à celles rencontrées sur le terrain. Les faibles températures (< 4°C) peuvent en particulier durer sur le terrain plusieurs mois et limiter l'activité microbienne du bois en décomposition.

Au-delà de la simple quantification des flux autotrophe et hétérotrophe, la séparation de ces deux composantes a permis d'évaluer l'impact de certains facteurs sur les flux de CO₂. Nous avons pu notamment souligner que les modifications induites par les trenched plots (humidité du sol, décomposition des racines et biomasse microbienne) et par les expériences de décomposition ont été évaluées et corrigées afin d'améliorer l'estimation des composantes de R_{ECO}. Enfin, malgré leur importance quantitative, la biomasse des racines ne permet pas, à l'échelle de notre étude, d'expliquer la variabilité spatiale de R_S, ni de la contribution de R_{Auto} à R_S, alors que des travaux futurs permettraient de vérifier si, plus que la biomasse, l'activité microbienne contrôlerait la variabilité spatiale de la composante hétérotrophe de R_S.

Influences des paramètres du sol et du peuplement

Les paramètres abordés durant l'étude de la variabilité spatiale sont la densité apparente du sol, la hauteur de la couche A₁ (qui représente la couche minérale incorporant la matière

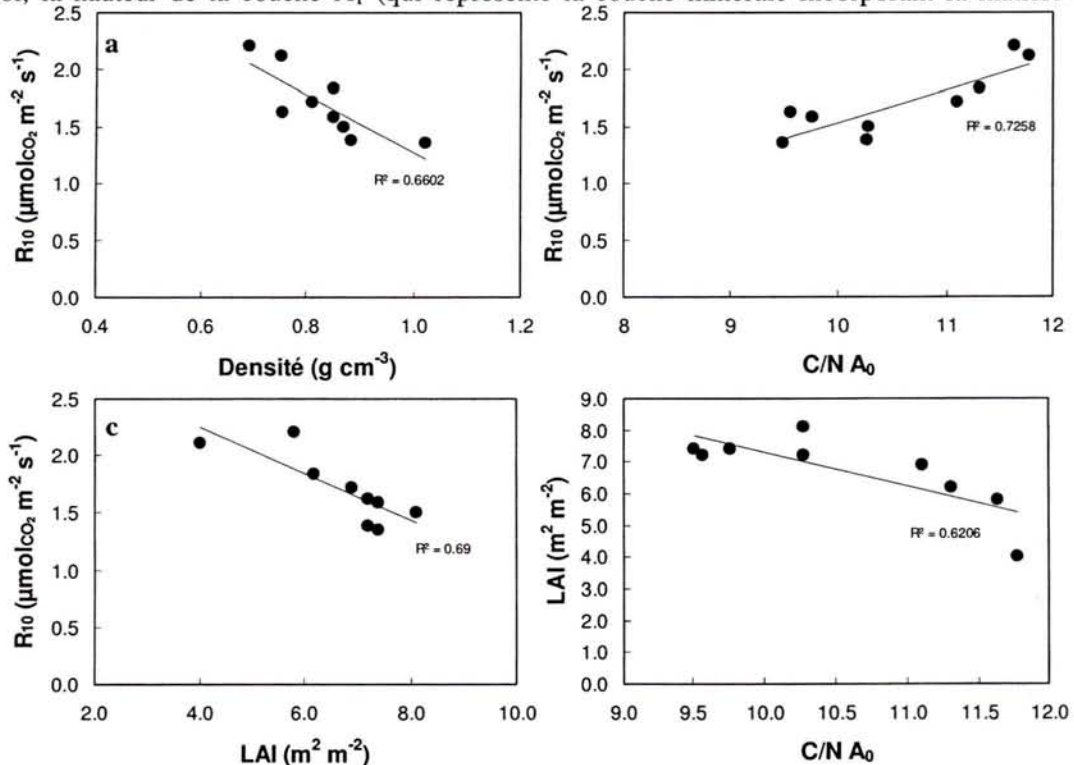


Figure 14. Relation entre la respiration basale à 10°C (R₁₀) et (a) la densité apparente du sol, (b) le rapport C/N de la couche A₁, et (c) l'indice de surface foliaire de 2004 (LAI). (d) Relation entre le LAI et l'indice de surface foliaire. Chaque point représente une valeur par placette. Les relations linéaires sont significatives au niveau p = 0.05.

organique provenant des couches humiques de la litière ou couche O), le C et l'azote (N) contenu dans la litière de feuilles, la couche A₁ et dans la MOS autre que A₁ (Tableau 4, Article 5). Ces paramètres déterminés dans chaque placette ont été analysés par corrélation avec le paramètre R_{10i} afin d'expliquer la variabilité spatiale de R_S après avoir pris en compte la plus grande partie de la variabilité saisonnière, comme cela a été fait par Reichstein *et al.* (2003) à une échelle plus globale. Ainsi, le paramètre R_{10i} est significativement et négativement corrélé à la densité apparente du sol et positivement corrélé au rapport C/N de la couche A₁ (Figure 14a et b) sans que ces deux paramètres soient corrélés entre eux (Article 5). Jordan *et al.* (2003) suggèrent que la compaction du sol induit une plus grande perte de N microbien tout en réduisant l'activité microbienne par réduction l'activité acide phosphatase. Cela est compatible avec la forte corrélation entre le R_{10i} et le rapport C/N de la couche A₁. Nous pouvons formuler l'hypothèse suivante: moins il y a de N, plus les microbes doivent minéraliser la MOS pour assurer un approvisionnement adéquat en N, ce qui est compatible avec les travaux de Kang *et al.* (2003). De plus, la densité serait inversement liée au degré d'hydromorphie du sol (via les types de sol des placettes): une plus grande activité des racines, des microorganismes mais également des vers de terre (bioturbation) se développerait pour contrebalancer l'anoxie temporaire qui s'établit lorsque la nappe d'eau remonte dans les sols les plus hydromorphes, induisant finalement une plus faible densité apparente dans les horizons de surface.

En faisant le parallèle avec la densité du sol, l'évolution de la production de CO₂ au cours de la décomposition serait soumise à un compromis entre les fortes densités (= bois pas ou peu décomposé) qui présentent une diffusivité de O₂ limitée et un faible contenu en eau mais riche en substrats facilement décomposables, et les plus faibles densités (= décomposition avancée du bois) qui seraient limitées par la qualité des substrats respiratoires (Progar *et al.*, 2000; Hicks et Harmon, 2002; Wang *et al.*, 2002; Hicks *et al.*, 2003).

Les valeurs de R_{10i} sont également corrélées négativement avec les valeurs de LAI de 2004 (Figure 14c). Reichstein *et al.* (2003) décrivent une relation positive entre la respiration du sol avec le LAI, ce qui est *a priori* attendu. D'autre part, le LAI est fortement corrélé avec le rapport C/N de la couche A₁ (Figure 14d). Une analyse de corrélation partielle incluant la densité, le rapport C/N de A₁ et le LAI confirme la relation uniquement entre le LAI et le rapport C/N.

Le R_{10i} peut être ainsi prédit par un modèle linéaire simple:

$$R_{10i} = -1.47 [\text{densité}] + 0.19 [C/N] \quad (8)$$

en ne retenant que la densité et le rapport C/N de A₁. Ce modèle permet d'expliquer 87% de la variabilité observée du R_{10i} (p = 0.0022). Au-delà de l'intérêt de prédire le paramètre R_{10i} dans le but d'estimer la respiration basale ou annuelle d'une placette quelconque, ce résultat permet de mettre en relation la variabilité spatiale d'une respiration normalisée avec un facteur lié à la diffusion et un autre facteur lié à la production du CO₂, même si la densité peut également influencer indirectement les processus de production du CO₂.

Dans le cadre de la forêt de Hesse, la variabilité spatiale de R_S peut être décrite à travers la respiration basale normalisée avec des paramètres liés au sol comme la densité apparente et le rapport C/N du sol superficiel. Les paramètres du peuplement tels que la surface terrière, la densité en nombre tiges ou l'indice de surface foliaire n'expliquent apparemment pas cette variabilité. La biomasse racinaire en elle-même ne permet pas non plus d'expliquer la variabilité spatiale de R_S, mais l'expérience des *trenched plots* suggère plutôt un taux de production de débris racinaires plus important permettant une respiration hétérotrophe plus importante.

Variabilité inter-annuelle de R_{ECO}

Notre étude a confirmé que les processus responsables des flux de CO_2 sont soumis à des fluctuations opérant à différentes échelles spatiales et temporelles. La variabilité saisonnière des facteurs climatiques explique la majeure partie des variations des flux de CO_2 du sol à l'échelle de l'année (Epron *et al.*, 1999, 2001). A une échelle temporelle plus large, les variations inter-annuelles des flux de CO_2 sont cruciales pour les projections des changements futurs des écosystèmes (Hui *et al.*, 2003). Différentes études ont montré une relation directe entre la variabilité du climat et celle des flux de CO_2 . Raich *et al.*, 2002 ont montré une relation entre la variabilité inter-annuelle des flux de CO_2 et les variations de températures globales. De manière indirecte, les variations climatiques pourraient également influencer les flux de CO_2 par un allongement de la durée de saison de végétation et modifier l'activité photosynthétique (Griffis *et al.*, 2003; Norby et Luo, 2004; Badeck *et al.*, 2004), qui est connue pour être l'un des déterminants de la respiration du sol (Craine *et al.*, 1999; Högberg *et al.*, 2001; Kuziyakov et Cheng, 2001; Cardon *et al.*, 2002). Enfin, les travaux de gestion forestière et/ou de la perturbation des sols participent également à la variabilité inter-annuelle de R_{ECO} (IPCC, 2001; Granier *et al.*, 2003; Epron *et al.*, 2004, Concilio *et al.*, 2005).

La réponse à long-terme des écosystèmes face à cet environnement changeant ne peut être comprise qu'à travers une vision multi-échelles, à la fois saisonnière comme nous l'avons vu mais également à l'échelle inter-annuelle.

Sensibilité au climat

La comparaison des deux années de mesures de R_S (2003 et 2004) effectuées durant cette thèse aurait été intéressante dans la perspective par exemple d'évaluer l'impact de la sécheresse 2003 sur les composantes de R_{ECO} . Mais cette comparaison est délicate du fait d'une période de mesures incomplète en 2003. La figure 2 montre une large variation inter-annuelle de NEE entre 1996 et 2003 (site H1) se traduisant par un coefficient de variation durant la période 1996-2003 d'environ 50% pour NEE, 12% pour GPP et R_{ECO} . Les variations inter-annuelles sont généralement attribuées aux variables climatiques comme les températures moyennes de l'air et les rayonnements photosynthétiquement actifs (PAR) durant le printemps et l'été, les précipitations estivales et le déficit de saturation en vapeur d'eau (Aubinet *et al.*, 2002; Wang *et al.*, 2004, Zha *et al.*, 2004). Dans notre étude, les valeurs annuelles de R_{ECO} ont été plus fortes en 2004 ($1002 \text{ gC m}^{-2} \text{ an}^{-1}$) par rapport à 2003 (884 gC m^{-2}), et pouvant être expliquées par le fait que 2003 avait été une année plus sèche (Tableau 1), en particulier durant la période estivale (Ciais *et al.*, 2005). Epron *et al.* (2004a) ont calculé que 67% de la variabilité inter-annuelle de la respiration du sol entre 1996 et 2001 en forêt de Hesse était attribuée à la température moyenne et les précipitations estivales, en accord avec Wang *et al.* (2004) et Zha *et al.* (2004). La température moyenne en 2003 était supérieure qu'en 2004, en particulier durant les mois de juin à août durant lesquels les écarts entre les deux années pouvaient aller jusqu'à $+4^\circ\text{C}$. Nos valeurs annuelles de R_S en 2003 et 2004 sont très proches malgré la différence de pluviométrie (écarts $< 10 \text{ gC m}^{-2} \text{ an}^{-1}$, Tableau 5), même si globalement, les valeurs de 2004 sont inférieures à celle de 2003, ce qui est en accord avec R_{ECO} . Ces observations, ne pouvant pas être expliquées par les effets directs de la variabilité climatique, amèneraient l'hypothèse d'un changement fonctionnel de l'écosystème. Cette notion, introduite par Hui *et al.* (2003), regroupe tous les effets indirects de la variabilité climatique (saisonnière et inter-annuelle). Dans notre étude, ce changement fonctionnelle pourrait être une altération de la balance GPP / R_{ECO} , en relation avec une diminution de GPP à cause de la sécheresse de l'été 2003 ainsi que de l'éclaircie d'une partie de la parcelle début 2004 (Voir ci-après).

Un effet direct de variations climatiques (variations de température, de l'humidité du sol ou des précipitations) semblerait expliquer une partie de la variabilité inter-annuelle de R_{ECO} et de R_S . Mais ces deux flux ne sont les seuls à être influencés par le climat: d'autres processus (comme GPP) ont été influencés et pourraient participer indirectement aux variations inter-annuelles des flux de respiration.

Relation entre GPP et respiration

Différentes études ont montré des variations inter-sites et inter-annuelles de NEE, R_{ECO} et de GPP (Janssens *et al.*, 2001; Falge *et al.*, 2002; Granier *et al.*, 2003). En dépit des nombreuses études menées, il reste de grandes incertitudes sur l'évolution de la respiration avec l'augmentation de la température. Certaines études tendent notamment à montrer que la décomposition de la MOS serait insensible aux variations de température (Liski *et al.*, 1999; Grace et Rayment, 2000). Griffis *et al.* (2003) montrent par contre une augmentation inter-annuelle de GPP en réponse à une plus longue saison de végétation.

Il est maintenant connu que R_{Auto} est directement lié à l'activité photosynthétique des plantes via l'allocation rapide des photosynthétats (Craine *et al.*, 1999; Kuzyakov et Cheng, 2001; Cardon *et al.*, 2002) qui intervient entre 2-6 heures à 1-6 jours (Kuzyakov et Cheng, 2001; Ekblad *et al.*, 2005; Tang *et al.*, 2005a). De même, la sensibilité de R_S à la température semblerait être due plus aux racines qu'aux micro-organismes responsables de la décomposition de la MOS (Boone *et al.*, 1998; Epron *et al.*, 2001; Lavigne *et al.*, 2003). Cette sensibilité reflèterait une forte influence de la température sur la photosynthèse au cours de la saison de végétation, période durant laquelle la contribution autotrophe est la plus élevée (Hanson *et al.*, 2000; Epron *et al.*, 2001; Lee *et al.*, 2003; Jiang *et al.*, 2005). Les études utilisant le signal $\delta^{13}CO_2$ ont déterminé que R_{Auto} et R_S sont régulés par les déterminants contrôlant la photosynthèse comme le déficit de saturation en vapeur d'eau, le PAR, la température de l'air ou le stress hydrique du sol (Bowling *et al.*, 2001, 2002; Fessenden et Ehleringer, 2003; Ekblad *et al.*, 2001, 2005).

La productivité des écosystèmes, dépendante de la photosynthèse, influencerait l'allocation de C vers les compartiments souterrains, et donc R_S (Janssens *et al.*, 2001). Les productions annuelles de litière, de racines fines et d'exudats racinaires sont soumises à l'activité photosynthétique et donc à ses fluctuations. Cela suppose néanmoins que R_{Auto} soit dépendante de l'allocation des photosynthétats (cf. plus haut) et que R_{Hetero} soit issue de la décomposition de la MO "jeune" (litière de l'année et racines fines, Janssens *et al.*, 2001). Les revues de Raich et Nadelhofer (1989), puis de Davidson *et al.* (2002) montrent que l'allocation de C vers les compartiments souterrains résulte directement de la différence entre R_S et les chutes de litière, que nous pouvons supposer être dépendantes de la productivité aérienne. Cela suppose également un état plus ou moins stable de la quantité de C dans sol, ce qui n'est peut être pas valable pour de jeunes forêts en croissance (Davidson *et al.*, 2002). En reprenant l'équation de Davidson *et al.* (2002)¹ et les valeurs de chutes de litière (Tableau 2), la valeur annuelle de R_S atteindrait 791 $g_C m^{-2} an^{-1}$ (H1 2003), 765 $g_C m^{-2} an^{-1}$ (H1 2004) et 732 $g_C m^{-2} an^{-1}$ (H2 2004). Ces valeurs sont supérieures à celles que nous avons mesuré (Tableau 5). D'autre part, la relation entre la productivité et le flux de CO_2 du sol est abordée par Bond-Lamberty *et al.* (2004) qui suggèrent une relation globale entre R_{Auto} et R_{Hetero} (Voir partie "**Importance des composantes de la respiration du sol**"). Ils montrent également une relation positive entre R_{Hetero} et l'entrée de détritiques composés des chutes de

¹ Annual $R_S = 287 + 2.80$ [Annual Litterfall] pour toutes forêts (jeunes et matures) confondues

litière et des racines fines mortes. Selon cette relation¹ et en ne considérant dans les détritiques que la chute de litière, R_{Hetero} à H1 et H2 atteindrait $364 \text{ g}_C \text{ m}^{-2} \text{ an}^{-1}$ et $357 \text{ g}_C \text{ m}^{-2} \text{ an}^{-1}$, respectivement. Ces estimations sont également supérieures à celle estimées par les tranchés plots (Tableau 6). Les relations entre les chutes de litière et R_S et R_{Hetero} proposées par les deux études (Davidson *et al.*, 2002; Bond-Lamberty *et al.*, 2004) ne semblent pas applicables au site de Hesse durant notre étude. Ces relations globales sont en effet valables pour des situations à l'équilibre, ce qui n'est sans doute pas le cas à Hesse (peuplement jeunes, interventions sylvicoles fréquentes).

Les variations de GPP semblent donc diriger plus ou moins directement les patrons d'allocations de C au sol et aboutir au final à fortement influencer les composantes autotrophe et hétérotrophe de R_S . Une meilleure compréhension de ces variations d'allocation (directes via les racines ou indirectes via la litière) et leur interaction avec les variations climatiques permettrait une avancée vers un modèle conceptuel intégrant les flux de C entrants et sortant d'un écosystème. Le flux R_{Hetero} semble être découplé de cette relation GPP-respiration, rappelant par la même que ce flux est régulé par d'autres mécanismes. De plus, ces variations soumises aux variations inter-annuelles du climat peuvent être masquées par de brusques interventions sylvicoles, dont les conséquences sont encore variables et mal connues.

Conséquence d'une éclaircie sur la respiration de l'écosystème

1. Biomasse et flux créés par une éclaircie à Hesse

L'éclaircie effectuée à Hesse (H1) en hiver 2005 a diminué la surface terrière de $25.93 \text{ m}^2 \text{ ha}^{-1}$ en 2004 à $19.24 \text{ m}^2 \text{ ha}^{-1}$. La densité a diminué de $3450 \text{ tiges ha}^{-1}$ à $3073 \text{ tiges ha}^{-1}$ (Bréda *et al.*, INRA Nancy, comm. pers.). La biomasse de débris ligneux laissée sur le terrain est de $410 \text{ g}_C \text{ m}^{-2}$ (Article 3). En utilisant les tarifs de biomasse de LeGoff et Ottorini (2001), la biomasse racinaire totale laissée suite à l'éclaircie atteint $390 \text{ g}_C \text{ m}^{-2}$. Ces valeurs sont relativement importantes notamment en comparaison avec le stock de débris ligneux déjà en place² ($167 \pm 47 \text{ g}_C \text{ m}^{-2}$), les chutes de litière de feuilles³ ($180 \text{ g}_C \text{ m}^{-2}$, site H1 en 2004, proche des valeurs données par Lebreton *et al.*, 2001) ou les chutes naturelles de fines branches⁴ ($17 \pm 13 \text{ g}_C \text{ m}^{-2}$, moyenne 1999-2003 dans H1). Dans l'article 3, nous avons estimé que la décomposition des débris ligneux (R_B) issus de l'éclaircie participerait à 8% de R_{ECO} . En utilisant les constantes de décomposition déterminées par Epron *et al.* (1999) pour les racines fines ($< 2\text{mm} = 0.38$) et pour les racines grossières ($> 2\text{mm} = 0.22$), ainsi que la fraction α_R de 0.3 (Article 4), nous obtenons un flux de CO_2 provenant de la décomposition des racines mortes d'environ $58 \text{ g}_C \text{ m}^{-2} \text{ an}^{-1}$ pour la première année de décomposition (inclus dans le flux R_S). Ces résultats soulignent ainsi la magnitude des entrées de C dans le sol suite à une éclaircie normale, et qui, par décomposition, sont susceptible de participer de manière significative à R_{ECO} .

2. Conséquence d'une éclaircie sur R_S

Différentes études ont montré que l'impact d'une éclaircie sur R_S est variable, entraînant une diminution, une augmentation ou une stabilisation de R_S . Il a été montré

¹ $R_{\text{Hetero}} = 253.49 + 0.61 \text{ Detritus}$; Les détritiques étant composés des chutes de litière et des racines fines mortes

² Les débris ligneux en place ont été récoltés dans 19 placettes ($4 \times 4 \text{ m}^2$) couvrant la gamme de LAI et de densité du site H1.

³ Récoltés dans 54 bacs à litière ($0.25 \times 0.25 \text{ m}^2$) réparties sur une surface de 0.6 ha (Granier *et al.*, 2000)

⁴ Idem

qu'une éclaircie réduit la biomasse racinaire (vivante) à court terme, tout en stimulant les communautés microbiennes du sol par des changements microclimatiques (augmentation de l'éclairement au sol et des précipitations incidentes) ou induit une recolonisation par les racines des arbres non éclaircis des niches laissées libres (Toland et Zak, 1994; Striegl et Wickland, 1998; Ohashi *et al.*, 2000; Kowalsky *et al.*, 2003; Laporte *et al.*, 2003; Epron *et al.*, 2004a; Tang *et al.*, 2005). Yanai *et al.* (2003) soulignent que la récolte de bois induit des modifications des chutes de litières et une diminution du stock de C du sol suite à une accélération de la décomposition des résidus de récolte. Dans le site H1, 2 placettes ont été éclaircies précocement début 2004 (Tableau 4). En comparant les campagnes de mesures estivales et automnales de 2003 à celles de 2004¹, les valeurs moyennes de R_S diffèrent significativement entre les deux années mais sans suivre une tendance claire. Dans cette analyse, l'effet de l'éclaircie sur R_S n'apparaît donc pas clairement. Bouriaud (2003) a montré des changements brusques et importants des propriétés du couvert (chute du LAI et de l'indice de densité relative) suite à l'éclaircie de 1998/1999. En utilisant le modèle CASTANEA (Dufrêne *et al.*, 2005), il montre que la diminution brutale de la surface d'interception durant l'année de l'éclaircie entraîne un effet dépressif transitoire sur GPP, aboutissant à une diminution de R_{Auto} . Mais les conséquences d'une telle diminution sur la dynamique racinaire sont mal connues. A la suite de la même éclaircie que celle discutée par Bouriaud (2003), Epron *et al.* (2004a) ont souligné une forte augmentation de R_S en 1999 en comparaison avec la période 1996-2001. L'expérience des *trenched plots*, dont le but initial était de couper les racines, équivaut finalement à une coupe à blanc (très localisée), tant par l'effet du tranchage sur le contenu en eau du sol (Toland et Zak, 1994, Laporte *et al.*, 2003) que par la suppression de la recolonisation du *trenched plot* par les racines (*idem* suite à une coupe à blanc). La diminution globale de la respiration dans les *trenched plots*, malgré une part importante de R_D (Article 4), spéculerait en faveur d'une stimulation de la croissance racinaire à la suite de l'éclaircie en 1999. Ainsi, nos observations de R_S en 2003 et 2004 suggéreraient qu'une augmentation de R_S suite à une éclaircie, tel qu'il a été suggéré par Epron *et al.* (2004), est amoindrie par l'effet retard de la sécheresse 2003 sur R_S .

Il est donc encore difficile de conclure quant un effet précis d'une éclaircie sur les flux de CO_2 à court et moyen terme, d'autant que ces dernières se succèdent environ tous les 5 ans sur notre site et pourraient donc être en interactions avec les variations inter-annuelles du climat à ce pas de temps. Il apparaît aussi que selon la nature de ces interactions, une part importante de cette influence passe par la productivité du peuplement, renforçant le lien existant entre R_S et GPP.

¹ Les campagnes ne diffèrent pas de plus de 4 jours (jours juliens). Données de l'Article 5.

CONCLUSIONS - PERSPECTIVES

Notre étude avait pour but de séparer les différentes composantes de R_{ECO} dans le but de dégager les facteurs principaux influençant sa variabilité à travers celle de ses composantes. L'une des caractéristiques de cette étude a été le constant souci du changement d'échelle, à la fois spatiale et temporelle. La combinaison d'une échelle temporelle saisonnière et de l'échelle spatiale de la parcelle forestière a présenté des avantages, notamment dans la quantification des flux, mais également des inconvénients, en particulier des contraintes techniques.

Sur le site de Hesse, la variabilité saisonnière de R_S est bien expliquée par les variations de température et de contenu en eau du sol. Cette prise en compte à travers un modèle empirique permet de s'affranchir des variations saisonnières. Mais le fait que la majorité de la variabilité saisonnière de R_S soit expliquée par les variations microclimatiques (température et contenu en eau du sol) devient un résultat de plus en plus établi, et n'en constitue pas moins qu'une simplification voire un masquage d'une partie de la variabilité saisonnière et des processus sous-jacents. Toutefois, nos mesures confirmeraient une plus grande sensibilité à la température de R_S que R_{Hetero} uniquement. L'intégration d'évènements se produisant à court terme, comme les précipitations et surtout les processus phénologiques (racinaires et microbiennes) aux modèles empiriques de R_S constituent un challenge dans l'amélioration des connaissances de R_S .

La variabilité spatiale de R_S à l'échelle de la parcelle forestière est corrélée à la variabilité spatiale de certaines caractéristiques liées à la diffusion du CO_2 et à sa production dans le sol superficiel. Malgré leur importance quantitative, la biomasse des racines ne permettent pas, à l'échelle de notre étude, d'expliquer la variabilité spatiale de R_S à l'échelle intra ou inter-parcellaire, peut-être en raison d'une trop faible gamme de variation dans notre zone de mesure. Ainsi, la variabilité spatiale de R_S semblerait être due plus à la composante hétérotrophe qu'à la composante autotrophe. Ces résultats posent le problème de l'échantillonnage de R_S dans une zone quelconque et de l'extrapolation à une échelle spatiale plus grande : à quelle échelle peut-on considérer nos mesures de R_S comme représentatives de l'unité de surface considérée? Dans notre étude, nos placettes de mesure de R_S ont été choisies en fonction des mesures de R_{ECO} couvrent une zone spatialement relativement hétérogène.

En séparant ces deux composantes de R_S , notre étude a permis de confirmer la part importante de la contribution des racines et de la rhizosphère dans R_S et R_{ECO} . Et malgré cette importance, les données de biomasse racinaire de nos deux sites ne permettent pas d'en expliquer les différences de R_{Auto} . Des avancées sont attendues dans la caractérisation de la dynamique saisonnière et la variabilité spatiale des racines pour pouvoir vérifier l'impact des variations climatiques sur R_S et le lien probable avec GPP. La composante R_{Hetero} participe également de façon importante à R_{ECO} . Les différentes corrections apportées pour estimer R_{Auto} ont souligné l'importance quantitative de la décomposition de MO nouvelle (les racines nouvellement coupées), à l'instar de la litière de feuilles. La discussion des différences de R_{Auto} et R_{Hetero} (et des corrections) observées entre sites H1 et H2 ont soulevé, outre le problème des racines et de leur détermination précise, la question des processus dirigeant R_{Hetero} . Cette même interrogation est également posée pour la variabilité des mesures de R_B . Il apparaît donc primordial de coupler les mesures de R_{Hetero} et R_B avec des approches à une échelle plus fine et de déterminer si, plus que la biomasse, l'activité microbienne contrôlerait la variabilité spatiale de ces flux. Bien qu'en conditions naturelles (hors *trenched plots*) R_{Hetero} soit conceptuellement corrélé à l'allocation des photosynthétats (directement via la mortalité des racines, indirectement via la production de litière), ses mécanismes sont encore mal

connus. Il serait intéressant par exemple d'approfondir les connaissances des substrats respiratoires et de l'enchaînement des processus respiratoires dans le sol. L'utilisation des méthodes isotopiques offre de grandes perspectives dans ce domaine. La réalisation des "Keeling plots" permettant de déterminer la signature isotopique de CO₂ respiré nous a par exemple permis de quantifier la variabilité saisonnière de R_L ainsi que la fraction de C perdu sous forme de CO₂ lors de la décomposition. Des avancées identiques sont attendues dans l'étude de la décomposition des débris ligneux permettant de vérifier ou non les hypothèses faites lors d'estimation de R_B.

D'un point de vue méthodologique, durant ce travail, plusieurs approches originales ou récentes ont été abordées et évaluées dans leur imprécisions et incertitudes. Les mesures de R_S, bien que très largement pratiquées et étudiées, sont indispensables pour estimer correctement les différentes composantes du bilan de C de l'écosystème. Le développement des comparaisons des systèmes de mesures s'avère une étape de départ indispensable dans le cadre, par exemple, d'études travaillant à une large échelle spatiale (comparaison de sites différents) et utilisant différents systèmes de mesures. De même, la comparaison de R_S et de sa participation de R_{ECO} n'est pas triviale. Nous avons montré que R_S se révéla très variable spatialement. Une meilleure estimation de la contribution de R_S à R_{ECO} nécessite la modélisation du footprint des mesures de flux par corrélations turbulentes. Nous avons également montré que la séparation de R_{Auto} et R_{Hetero} nécessite des corrections indispensables pour des estimations non biaisées de ces flux, en particulier la détermination de la biomasse racinaire à laquelle les calculs sont très sensibles.

Les valeurs annuelles de R_S, déterminées durant notre étude, ne permettent pas de discriminer les effets de la sécheresse et de l'éclaircie pour établir une certaine hiérarchie des facteurs, soulignant l'intérêt des suivis à moyen et long termes des flux de CO₂. Par ailleurs, le suivi de R_S dans des zones d'éclaircies locales mais réparties dans l'ensemble d'une parcelle permettraient enfin de préciser les conséquences de ces travaux forestiers sur les flux de CO₂ du sol. L'association de simulations issues de modèles de sylviculture avec des simulations de modèles de fonctionnement carboné des écosystèmes permettraient d'évaluer l'impact de la gestion sylvicole de façon précise sur le bilan de C et le potentiel de stockage de C d'un écosystème forestier.

En perspective à plus long-terme, notre étude soulignerait la nécessité de l'émergence de modèles conceptuels ou appliqués qui permettraient de renforcer le lien déjà esquissé par les études récentes entre les flux de respiration et la photosynthèse.

REFERENCES BIBLIOGRAPHIQUES

- Anderson J.M. (1973). Carbon dioxide evolution from two temperate deciduous woodland soils. *Journal of Applied Ecology* 10: 361-378.
- Aubinet M., Heinesch B. and Longdoz B. (2002). Estimation of the carbon sequestration by a heterogeneous forest: night flux corrections, heterogeneity of the site and inter-annual variability. *Global Change Biology* 8: 1053-1071.
- Aubinet M., Heinesch B. and Yernaux M. (2003). Horizontal and vertical CO₂ advection in a sloping forest. *Boundary-Layer Meteorology* 108: 397-417.
- Baath E. and Wallander H. (2003). Soil and rhizosphere microorganisms have the same Q₁₀ for respiration in a model system. *Global Change Biology* 9: 1788-1791.
- Badeck, F. W., A. Bondeau, K. Bottcher, D. Doktor, W. Lucht, J. Schaber and S. Sitch (2004). Responses of spring phenology to climate change. *New Phytologist* 162: 295-309.
- Baldocchi D., Valentini R., Running S., Oechels W. and Dahlman R. (1996). Strategies for measuring and modelling carbon dioxide and water vapour fluxes over terrestrial ecosystems. *Global Change Biology* 2: 159-168.
- Baldocchi D. *et al.* (2001). FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bulletin of the American Meteorological Society* 82: 2415-2434.
- Ball S. and Drake B. (1997). Short-term decomposition of litter produced by plants grown in ambient and elevated atmospheric CO₂ concentrations. *Global Change Biology* 3: 29-35.
- Baldocchi D. (2003). Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biology* 9: 479-492.
- Balesdent J. and Balabane M. (1996). Major contribution of roots to soil carbon storage inferred from maize cultivated soils. *Soil Biology Biochemistry* 28: 1261-1263.
- Berg B. (2000). Litter decomposition and organic matter turnover in northern forest soils. *Forest Ecology Management* 133: 13-22.
- Bhupinderpal S., Nordgren A., Lofvenius M. O., Hogberg M. N., Mellander P. E. and Hogberg P. (2003). Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year. *Plant Cell and Environment* 26: 1287-1296.
- Bhupinderpal-Singh, Nordgren A., Löfvenius M.O., Högberg M.N., Mellander P.E. and Hogberg P. (2003). Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year. *Plant Cell Environment* 26: 1287-1296.
- Birch H. (1958). The effect of soil drying on humus decomposition and nitrogen availability. *Plant soil* 10: 9-31.
- Boddy L. (1983). Carbon dioxide release from decomposing wood: effect of water content and temperature. *Soil Biology Biochemistry* 15: 501-510.
- Bolstad P. V., Davis K. J., Martin J., Cook B. D. and Wang W. (2004). Component and whole-system respiration fluxes in northern deciduous forests. *Tree Physiology* 24: 493-504.
- Bond-Lamberty B., Wang C. K. and Gower S. T. (2004). A global relationship between the heterotrophic and autotrophic components of soil respiration? *Global Change Biology* 10: 1756-1766.

-
- Bond-Lamberty B., Wang C. and Gower S.T. (2003). Annual carbon flux from woody debris for a boreal black spruce fire chronosequence. *Journal of Geophysical Research* 108: 9 pp.
- Boone R.D., Nadelhoffer K.J., Canary J.D. and Kaye J.P. (1998). Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature* 396: 570-572.
- Borken W., Xu Y. J., Davidson E. A. and Beese A. (2002). Site and temporal variation of soil respiration in European beech, Norway spruce, and Scots pine forests. *Global Change Biology* 8: 1205-1216.
- Bouma T.J., Nielsen K.L., Eissenstat D.M. and Lynch J.P. (1997). Estimating respiration of roots in soil: interaction with soil CO₂, soil temperature and soil water content. *Plant Soil* 195: 221-232.
- Bouriaud O. (2003). Analyse fonctionnelle de la productivité du hêtre : Influence des conditions de milieu, de la structure du peuplement et du couvert, effets de l'éclaircie. ENGREF, Nancy, 320 pp.
- Bouriaud O., Soudani K. and Bréda N. (2003). Leaf area index from litter collection: impact of specific leaf area variability within a beech stand. *Canadian Journal remote sensing* 29: 371-380.
- Bowden R.D., Nadelhoffer K.J., Boone R.D., Melillo J.M. and Garrison J.B. (1993). Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. *Canadian Journal of Forest Research* 23: 1402-1407.
- Bowling D.R., Tans P.P. and Monson R.K. (2001). Partitioning net ecosystem carbon exchange with isotopic fluxes of CO₂. *Global Change Biology* 7: 127-145.
- Bowling D.R., McDowell N.G., Bond B.J., Law B.E. and Ehleringer J.R. (2002). ¹³C content of ecosystem respiration is linked to precipitation and vapor pressure deficit. *Oecologia* 131: 113-124.
- Brooks P.D., McKnight D. and Elder K. (2004). Carbon limitation of soil respiration under winter snowpacks: potential feedbacks between growing season and winter carbon fluxes. *Global Change Biology* 11: 231-238.
- Brown S., Mo J., McPherson J.K. and Bell D.T. (1995). Decomposition of woody debris in Western Australian forests. *Canadian Journal of Forest Research* 26: 954-966.
- Buchanan A.H. and Levine S.B. (1999). Wood-based building materials and atmospheric carbon emissions. *Environmental Science and Policy* 2: 427-437.
- Buchmann N. (2000). Biotic and abiotic factors controlling soil respiration rates in *Picea abies* stands. *Soil Biology Biochemistry* 32: 1625-1635.
- Cao M. and Woodward F.I. (1998). Dynamic responses of terrestrial ecosystem carbon cycling to global climate change. *Nature* 393: 249-252.
- Cardon Z.G., Czaja A.D., Funk J.L. and Vitt P.L. (2002). Periodic carbon flushing to root of *Quercus rubra* saplings affects soil respiration and rhizosphere microbial biomass. *Oecologia* 133: 215-223.
- Ceschia E., Damesin C., Lebaube S., Pontaville J. Y. and Dufrêne E. (2002). Spatial and seasonal variations in stem respiration of beech trees (*Fagus sylvatica*). *Annals of Forest Science* 59: 801-812.
- Chambers J.Q., Higuchi N., Schimel J.P., Ferreira L.V. and Melack J.M. (2000). Decomposition and carbon cycling of dead trees in tropical forests of central Amazon. *Oecologia* 122: 380-388.
- Chen H., Harmon M.E. and Griffiths R.P. (2001). Decomposition and nitrogen release from decomposing woody roots in coniferous forests of the Pacific Northwest: a chronosequence approach. *Canadian Journal of Forest Research* 31: 246-260.
- Chen H., Harmon M.E., Griffiths R.P. and Hicks W. (2000). Effects of temperature and moisture on carbon respired from decomposing woody roots. *Forest Ecology and Management* 138: 51-64.

Cheng W. (1996). Measurement of rhizosphere respiration and organic matter decomposition using natural ^{13}C . *Plant Soil* 183: 263-268.

Ciais P., Reichstein M., Granier A., Ogée J., Allard V., Aubinet M., Buchmann N., Bernhofer C., Carrara A., Chevallier F., De Noblet N., Friend A., Friedlingstein P., Gründwald T., Heinesch B., Keronen P., Knohl A., Krinner G., Lousteau D., Manca G., Matteucci G., Miglietta F., Ourcival J.M., Papale D., Pilegaard K., Rambal S., Seufert G., Soussana J.F., Sanz M.J., Schulze E.D., Vesala T. and Valentini R. (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* doi: 10.1038/nature03972.

Concilio A., Ma S., Li Q., LeMoine J., Chen J., North M., Moorhead D. and Jensen R. (2005). Soil respiration response to prescribed burning and thinning in a mixed-conifer and hardwood forests. *Canadian Journal of Forest Research* 35: 1581-1591.

Coûteaux M.M., Kurz C., Bottner P. and Raschi A. (1999). Influence of increased atmospheric CO_2 concentration on quality of plant material and litter decomposition *Tree Physiology* 19: 301-311.

Cox P. M., Betts R.A., Jones C.D., Spall S.A. and Totterdell I.J. (2000). Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408: 184-187.

Craine J.M., Wedin D.A. and Chapin F.S. (1999). Predominance of ecophysiological controls on soil CO_2 flux in a Minnesota grassland. *Plant Soil* 207:77-86.

Cramer W., Bondeau A., Woodward F.I., Prentice I.C., Betts R.A., Brovkin V., Cox P.M., Fisher V., Foley J.A., Friend A.D., Kucharick C., Lomas M.R., Ramankutty N., Sitch S., Smith B., White A. and Young-Molling C. (2001). Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. *Global Change Biology* 7: 357-373.

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

Damesin C. and Lelarge C. (2003). Carbon isotope composition of current-year shoots from *Fagus sylvatica* in relation to growth, respiration and use of reserves. *Plant Cell and Environment* 26: 207-219.

Davidson E.A., Belk E. and 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 Biology* 4: 217-227.

Davidson E.A., Savage K., Bolstad P., Clark D.A., Curtis P.S., Ellsworth D.S., Hanson P.J., Law B.E., Luo Y., Pregitzer K.S., Randolph J.C. and Zak D. (2002). Belowground carbon allocation in forests estimated from litterfall and IRGA-based soil respiration measurements. *Agriculture and Forest Meteorology* 113: 39-51.

Dewar R. (1991). Analytical model of carbon storage in the trees, soils, and wood products of managed forests. *Tree Physiology* 8: 239-258.

Dixon R.K., Brown S., Houghton R.A., Solomon A.M., Trexler M.C. and Wisniewski J. (1994). Carbon pool and flux global forest ecosystem. *Science* 263: 185-190.

Ehleringer J.R., Buchmann N. and Flanagan L.B. (2000). Carbon isotope ratios in belowground carbon cycle processes. *Ecological Applications* 10: 412-422.

Ekblad A. and Hogberg P. (2001). Natural abundance of ^{13}C in CO_2 respired from forest soils reveals speed of link between tree photosynthesis and root respiration. *Oecologia* 127: 305-308.

Ekblad A., Boström B., Holm A. and Comstedt D. (2005). Forest soil respiration rate and $\delta^{13}\text{C}$ is regulated by recent above ground weather conditions. *Oecologia* 143: 136-142.

Epron D., Farque L., Lucot E. and Badot P.M. (1999). Soil CO_2 efflux in a beech forest: the contribution of root respiration. *Annals of Forest Science* 56: 289-295.

Epron D., Ngao G. and Granier A. (2004a). Interannual variation of soil respiration in a beech forest ecosystem over a six-year study. *Annals of Forest Science* 61: 499-505.

Epron D., Nouvellon Y., Roupsar O., Mouvondy W., Mabiata A., Saint-Andre L., Joffre R., Jourdan C., Bonnefond J.M., Berbigier P. and Hamel O. (2004b). Spatial and temporal variations of soil respiration in a Eucalyptus plantation in Congo. *Forest Ecology and Management* 204: 149-160.

Ewel K.C., Cropper W.P. and Gholz H.L. (1987). Soil CO₂ evolution in Florida slash pine plantations. I. Changes through time. *Canadian Journal of Forest Research* 17: 325-329.

Falge E., Baldocchi D., Tenhunen J., Aubinet M., Bakwin P., Berbigier P., Bernhofer C., Burba G., Clement R., Davis K. J., Elbers J. A., Goldstein A. H., Grelle A., Granier A., Guomundsson J., Hollinger D., Kowalski A. S., Katul G., Law B. E., Malhi Y., Meyers T., Monson R. K., Munger J. W., Oechel W., Paw K. T., Pilegaard K., Rannik U., Rebmann C., Suyker A., Valentini R., Wilson K. and Wofsy S. (2002). Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agricultural and Forest Meteorology* 113: 53-74.

Falkowski P., Scholes R.J., Boyle E., Canfield D., Elser J., Gruber N., Hibbard K., Högberg P., Linder S., Mackenzie F.T., Moore III B., Pedersen T., Rosenthal Y., Seitzinger S., Smetacek V. and Steffen W. (2000). The global carbon cycle: A test of our knowledge of earth as a system. *Science* 290: 291-296.

Fang C. and Moncrieff J.B. (1998). An open-top chamber for measuring soil respiration and the influence of pressure difference on CO₂ efflux measurement. *Functional Ecology* 12: 319-325.

Fessenden, J. E. and Ehleringer J.R. (2003). Temporal variation in delta C-13 of ecosystem respiration in the Pacific Northwest: links to moisture stress. *Oecologia* 136: 129-136.

Fierer N. and Schimel J.P. (2003). A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. *Soil Science Society of America Journal* 67: 798-805.

Fontaine S., Mariotti A. and Abbadie L. (2003). The priming effect of organic matter: a question of microbial competition? *Soil Biology and Biochemistry* 35: 837-843.

Formànek P. and Ambus P. (2004). Assessing the use of δ¹³C natural abundance in separation of root and microbial respiration in a Danish beech (*Fagus sylvatica* L.) forest. *Rapid Communications Mass Spectrometry* 18: 1-6.

Foster J.R. and Lang G.E. (1982). Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. *Canadian Journal of Forest Research* 12: 617-626.

Frangi J.L., Richter L.L., Barrera M.D. and Aloggia M. (1997). Decomposition of *Nothofagus* fallen woody debris in forests of Tierra del Fuego, Argentina. *Canadian Journal of Forest Research* 27: 1095-1102.

Fraver S., Wagner R.G. and Day M. (2002). Dynamics of coarse woody debris following gap harvesting in the Acadian forest of central Maine, U.S.A. *Canadian Journal of Forest Research* 32: 2094-2105.

Ganjegunte G.K., Condrón L.M., Clinton P.W., Davis M.R. and Mahieu N. (2004). Decomposition and nutrient release from radiata pine (*Pinus radiata*) coarse woody debris. *Forest Ecology and Management* 187: 197-211.

Gielen B., Scarascia-Mugnozza G. and Ceulemans R. (2003). Stem respiration of *Populus* species in the third year of free-air CO₂ enrichment. *Physiologia Plantarum* 117: 500-507.

Gough C. M. and Seiler J. R. (2004). The influence of environmental, soil carbon, root, and stand characteristics on soil CO₂ efflux in loblolly pine (*Pinus taeda* L.) plantations located on the South Carolina Coastal Plain. *Forest Ecology and Management* 191: 353-363.

-
- Goulden M.L., Munger J.W., Fan S.M., Daube B.C. and Wofsy S.C. (1996). Measurements of carbon sequestration by long-term eddy covariance: methods and critical evaluation of accuracy. *Global Change Biology* 2: 169-182.
- Grace J. and Rayment M. (2000). Respiration in the balance. *Nature* 404: 819-820.
- Granier A., Aubinet M., Epron D., E. F., Gudmundsson J., Jensen N. O., Köstner B., Matteucci G., Pilegaard K., Schmidt M. and Tenhunen J. (2003). Deciduous forests: carbon and water fluxes, balances and ecophysiological determinants In: Fluxes of carbon, water and energy of European forests. Valentini R. (Ed.) Ecological studies. 163 Berlin, 270p.
- Granier A., Pilegaard K. and Jensen N. O. (2002). Similar net ecosystem exchange of beech stands located in France and Denmark. *Agricultural and Forest Meteorology* 114: 75-82.
- Granier A., Ceschia E., Damesin C., Dufrene E., Epron D., Gross P., Lebaude S., Le Dantec V., Le Goff N., Lemoine L., Lucot E., Ottorini J.M., Pontailler J.Y. and Saugier B. (2000). The carbon balance of a young Beech forest. *Functional Ecology* 14: 312-325.
- Griffis, T.J., Black T.A., Morgenstern K., Barr A.G., Nesic Z., Drewitt G.B., Gaumont-Guay D. and McCaughey J.H. (2003). Ecophysiological controls on the carbon balances of three southern boreal forests. *Agricultural and Forest Meteorology* 117: 53-71.
- H**anson P.J., Edwards N.T., Garten C.T. and Andrews J.A. (2000). Separating root and soil microbial contribution to soil respiration: A review of methods and observations. *Biogeochemistry* 48: 115-146.
- Harmon M.E., Franklin J.F., Swanson F.J., Sollins P., Gregory S.U., Lattin J.D., Anderson N.H., Cline S.P., Aumen N.G., Sedell J.R., Lienkaemper G.W., Cromack K. and Cummins K.W. (1986). Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15: 133-302.
- Hart S.C. and Sollins P. (1998). Soil carbon and nitrogen pools and processes in an old-growth conifer forest 13 years after trenching. *Canadian journal of forest research* 28: 1261-1265.
- Hashimoto S. (2005). Q₁₀ values of soil respiration in Japanese forests. *Journal Forest Research* 10: 409-413.
- Hicks W.T. and Harmon M.E. (2002). Diffusion and seasonal dynamics of O₂ in woody debris from the Pacific Northwest, USA. *Plant Soil* 243: 67-79.
- Hicks W.T., Harmon M.E. and Griffiths R.P. (2003). Abiotic controls on nitrogen fixation and respiration in selected woody debris from the Pacific Northwest, USA. *Ecoscience* 10: 66-73.
- Högberg P., Nordgren A. and Agren G. I. (2002). Carbon allocation between tree root growth and root respiration in boreal pine forest. *Oecologia* 132: 579-581.
- Högberg P., Nordgren A., Buchmann N., Taylor A.F.S, Ekblad A., Hogberg M.N., Nyberg G., Ottoson-Löfvenius M. and Read D.J. (2001). Large scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411: 789-792.
- Houghton R. A. (2003). Why are estimates of the terrestrial carbon balance so different? *Global Change Biology* 9: 500-509.
- Hui, D. and G. Katul (2003). Partition interannual variability in net ecosystem exchange between climatic variability and functional change. *Tree Physiology* 23: 433-442.
- I**brahimia A., Joffre R. and Gillon D (1995). Changes in litter during the initial leaching phase: an experiment on the leaf litter of Mediterranean species. *Soil Biology Biochemistry* 27: 931-939.
- Idol T.W., Figler R.A., Pope P.E. and Ponder Jr F. (2001). Characterization of coarse woody debris across a 100 year chronosequence of upland oak-hickory forests. *Forest Ecology and Management* 149: 153-161.

IPCC (2000). L'utilisation des terres, le changement d'affectation des terres et la foresterie. Nairobi, GIEC: 24.

IPCC (2001). The carbon cycle and atmospheric carbon dioxide. In: Climate change 2001: The scientific basis. Contribution of working group I to the third assessment report of the Intergovernmental Panel on Climate Change. Houghton H.J. Cambridge, Cambridge University Press: 183-238.

Janssens I.A., Kowalski A.S., Longdoz B. and Ceulemans R. (2000). Assessing forest soil CO₂ efflux: an *in situ* comparison of four techniques. *Tree Physiology* 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., Gudmundson J., Minerbi S., Berbigier P., Ibrom A., Moncrieff J.B., Aubinet M., Bernhofer C., Jensen N.O., Vesala T., Granier A., Schulze E.D., Lindroth A., Dolman A.J., Jarvis P.G., Ceulemans R. and Valentini R. (2001). Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology* 7: 269-278.

Janssens I. A., Dore S., Epron D., Lankreijer H., Buchmann N., Longdoz B., Brossaud J. and Montagnani L. (2003). Climatic influences on seasonal and spatial differences in soil CO₂ efflux. In: Fluxes of carbon, water and energy of European forests. Valentini R. (Ed.) Ecological studies. 163 Berlin, 270p.

Janssens I. A. and Pilegaard K. (2003). Large seasonal changes in Q₁₀ of soil respiration in a beech forest. *Global Change Biology* 9: 911-918.

Jiang L., Shi F., Lli B., Chen J. and Chen J. (2005). Separating rhizosphere respiration from total respiration in two larch plantation in northeastern China. *Tree Physiology* 25: 1187-1195.

Jordan D., Ponder F. and Hubbard V.C. (2003). Effects of soil compaction, forest leaf litter and nitrogen fertilizer on two oak species and microbial activity. *Applied Soil Ecology* 23: 33-41.

Kang S.Y., Doh S., Lee D., Jin V.L. and Kimball J.S. (2003). Topographic and climatic controls on soil respiration in six temperate mixed-hardwood forest slopes, Korea. *Global Change Biology* 9: 1427-1437.

Kankrina O.N., Harmon M.E., Kukuev Y.A., Treyfeld R. F., Kashpor N.N., Kresnov V.G., Skudin V.M., Protasov N.A., Yatskov M., Spycher G. and Povarov E.D. (2002). Coarse woody debris in forest regions of Russia. *Canadian Journal of Forest Research* 32: 768-778.

Karnosky D.F. (2003). Impacts of elevated atmospheric CO₂ on forest trees and forest ecosystems: knowledge gaps. *Environment International* 29: 161-169.

Keeling C.D. (1958). The concentration and isotopic abundances of atmospheric carbon dioxide in rural areas. *Geochim. Cosmochim. Acta* 13: 322-334.

Kieft T., Soroker E. and Firestone M. (1987.). Microbial biomass response to a rapid increase in water potential when dry soil is wetted. *Soil Biology Biochemistry* 19: 119-126.

Kowalski S., Sartore M., Burlett R., Berbigier P. and Loustau D. (2003). The annual carbon budget of a French pine forest (*Pinus pinaster*) following harvest. *Global Change Biology* 9: 1051-1065.

Kutsch W., Liu C., Hormann G. and Herbst M. (2005). Spatial heterogeneity of ecosystem carbon fluxes in a broadleaved forest in Northern Germany. *Global Change Biology* 11: 710-88.

Kutsch W.L., Staack A., Wötzel J., Middelhoff U. and Kappen L. (2001). Field measurements of root respiration and total soil respiration in an alder forest. *New Phytologist* 150: 157-168.

Kuzyakov Y. and Cheng W. (2001). Photosynthesis controls of rhizosphere respiration and organic matter decomposition. *Soil Biology Biochemistry* 33: 1915-1925.

Kuzyakov Y. (2002). Separating microbial respiration of exudates from root respiration in non-sterile soils: a comparison of four methods. *Soil Biology Biochemistry* 34: 1621-1631.

-
- Ladd J.N., Amato M., Grace P.R. and Van Veen J.A. (1995). Simulation of ^{14}C turnover through the microbial biomass in soils incubated with ^{14}C -labelled plant residues. *Soil Biology and Biochemistry* 27: 777-783.
- Lankreijer L.A., Janssens I.A., Buchmann N., Longdoz B., Epron D. and Dore S. (2003). Measurement of soil respiration. In: Fluxes of carbon, water and energy of European forests. Valentini R. (Ed.) Ecological studies. 163 Berlin, 270p.
- Laporte M.F., Duchesne L.C. and Morrison I.K. (2003). Effect of clearcutting, selection cutting, shelterwood cutting and microsites on soil surface CO_2 efflux in a tolerant hardwood ecosystem of northern Ontario. *Forest Ecology and Management* 174: 565-575.
- Lavigne M.B., Boutin R., Foster R.J., Goodine G., Bernier P.Y. and Robitaille G. (2003). Soil respiration responses to temperature are controlled more by roots than by decomposition in balsam fir ecosystems. *Canadian Journal of Forest Research* 33: 1744-1753.
- Lavigne M.B., Foster R.J. and Goodine G. (2004). Seasonal and annual changes in soil respiration in relation to soil temperature, water potential and trenching. *Tree Physiology* 24: 415-424.
- Lebret M., Nys C. and Forgeard F. (2001). Litter production in an Atlantic beech (*Fagus sylvatica* L.) time sequence. *Annals of Forest Science* 58: 755-768.
- Lee M. S., Nakane K., Nakatsubo T. and Koizumi H. (2003). Seasonal changes in the contribution of root respiration to total soil respiration in a cool-temperate deciduous forest. *Plant and Soil* 255: 311-318.
- Lee X., Wu H. J., Sigler J., Oishi C. and Siccama T. (2004). Rapid and transient response of soil respiration to rain. *Global Change Biology* 10: 1017-1026.
- Le Goff, N. and J.-M. Ottorini (2001). Root biomass and biomass increment in a beech (*Fagus sylvatica* L.) stand in North-East France. *Annals of Forest Science* 58: 1-13.
- Li Y., Xu M., Zou X. and Xia Y. (2005). Soil CO_2 efflux and fungal and bacterial biomass in a plantation and a secondary forest in wet tropics in Puerto Rico. *Plant and Soil* 268: 151-160.
- Liski J., Perruchoud D. and Karjalainen T. (2002). Increasing carbon stocks in the forest soils of western Europe. *Forest Ecology and Management* 169: 159-175.
- Liski J., Iilvesniemi H., Mäkelä A. and Westman C.J. (1999). CO_2 emission from soil in response to climatic warming are overestimated - The decomposition of old soil organic matter is tolerant of temperature. *Ambio* 28: 171-180.
- Liski J., Palosuo T., Peltoniemi M. and Sievänen R. (2005). Carbon and decomposition model Yasso for forest soils. *Ecological Modelling*, *In press*.
- Lloyd J. and Taylor J.A. (1994). On the temperature dependence of soil respiration. *Functional Ecology* 8: 315-323.
- Lohila A., Aurela M., Regina K. and Laurila T. (2003). Soil and total ecosystem respiration in agricultural fields: effect of soil and crop type. *Plant and Soil* 251: 303-317.
- Longdoz B., Yernaux M. and Aubinet M. (2000). Soil CO_2 efflux measurements in a mixed forest: impact of chamber disturbances, spatial variability and seasonal evolution. *Global Change Biology* 6: 907-917.
- Marra J.L. and Edmonds R.L. (1994). Coarse woody debris and forest floor respiration in an old-growth coniferous forest on the Olympic Peninsula, Washington, USA. *Canadian Journal of Forest Research* 24: 1811-1817.
- Mattson K.J., Swank W.T. and Waide J.B. (1987). Decomposition of woody debris in a regenerating, clear-cut forest in the Southern Appalachians. *Canadian Journal of Forest Research* 17: 712-721.

McColl J.G. and Powers R.F. (2003). Decomposition of small woody debris of California red fir: mass loss and elemental content over 17 years. *Soil Science Society of America Journal* 67: 1227-1233.

McLean M.A. and Huhta V. (2000). Temporal and spatial fluctuations in moisture affect humus microfungus community structure in microcosms. *Biology and Fertility of Soils* 32: 114-119.

Nabuurs G. J., Schelhaas M. J., Mohren G. M. J. and Field C. B. (2003). Temporal evolution of the European forest sector carbon sink from 1950 to 1999. *Global Change Biology* 9: 152-160.

Nakane K., Yamamoto M. and Tsubota H. (1983). Estimation of root respiration rate in a mature forest ecosystem. *Japanese Journal of Ecology* 33: 397-408.

Nay S.M., Mattson K.G. and Bormann B.T. (1994). Biases of chamber methods for measuring soil CO₂ efflux demonstrated with a laboratory apparatus. *Ecology* 75: 2460-2463.

Ngao J., Epron D., Brechet C. and Granier A. (2005). Estimating the contribution of leaf litter decomposition to soil CO₂ efflux in a beech forest using ¹³C depleted litter. *Global Change Biology* 11: 1768-1776.

Norby R.J., Cotrufo M.F., Ineson P., O'Neill E.G. and Canadell J.G. (2001). Elevated CO₂, litter chemistry and decomposition: a synthesis. *Oecologia* 127: 153-165.

Norby, R. J. and Y. Q. Luo (2004). Evaluating ecosystem responses to rising atmospheric CO₂ and global warming in a multi-factor world. *New Phytologist* 162:281-293.

Norman J.M., Garcia R. and Verma S.B. (1992). Soil surface CO₂ fluxes and the carbon budget of grassland. *Journal of Geophysical Research* 97: 18845-18853.

Ohashi M., Gyokusen K. and Saito A. (2000). Contribution of root respiration to total soil respiration in a Japanese cedar (*Cryptomeria japonica* D. Don) artificial forest. *Ecological Research* 15: 323-333.

O'Neill K.P., Kasischke E.S. and Richter D.D. (2003). Seasonal and decadal patterns of soil carbon uptake and emission along an age sequence of burned black spruce stands in interior Alaska. *Journal of Geophysical Research-Atmospheres* 108: 8155-8155.

Parton W.J., Schimel D.S., Cole C.V. and Ojima D.S. (1987). Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal* 51: 1173-1179.

Pongracic S., Kirschbaum M.U.F. and Raison R.J. (1997). Comparison of soda lime and infrared gas analysis techniques for in situ measurement of forest soil respiration. *Canadian Journal of Forest Research* 27: 1890-1895.

Progar R.A., Schowalter T.D., Freitag C.M. and Morell J.J. (2000). Respiration from coarse woody debris as affected by moisture and saprotroph functional diversity in Western Oregon. *Oecologia* 124:426-431.

Pregitzer K.S., Lakowski M.J., Burton A.J., Lessard V.C. and Zak D.R. (1998). Variation in sugar maple root respiration with root diameter and soil depth. *Tree Physiology* 18: 665-670.

Pumpanen J., Kolari P., Ilvesniemi H., Minkinen K., Vesala T., Niinisto S., Lohila A., Larmola T., Morero M., Pihlatie M., Janssens I., Yuste J. C., Grunzweig J. M., Reth S., Subke J. A., Savage K., Kutsch W., Ostreg G., Ziegler W., Anthoni P., Lindroth A. and Hari P. (2004). Comparison of different chamber techniques for measuring soil CO₂ efflux. *Agricultural and Forest Meteorology* 123: 159-176.

Pypker T.G. and Fredeen A.L. (2003). Belowground CO₂ efflux from cut blocks of varying ages in sub-boreal British Columbia. *Forest Ecology and Management* 172: 249-259.

Raich J.W. and Nadelhoffer K. J. (1989). Belowground carbon allocation in forest ecosystems: global trends. *Ecology* 70: 1346-1354.

-
- Randerson J. T., Chapin F. S., Harden J. W., Neff J. C. and Harmon M. E. (2002). Net ecosystem production: A comprehensive measure of net carbon accumulation by ecosystems. *Ecological Applications* 12: 937-947.
- Reichstein M., Rey A., Freibauer A., Tenhunen J., Valentini R., Banza J., Casals P., Cheng Y., Grünzweig J.M., Irvine J., Joffre R., Law B.E., Loustau D., Miglietta F., Oechel W., Ourcival J.M., Pereira J.S., Peressotti A., Ponti F., Qi Y., Rambal S., Rayment M., Romanya J., Rossi F., Tedeschi V., Tirone G., Xu M. and Yakir D. (2003). Modeling temporal and large-scale spacial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. *Global Biogeochemical cycles* 17: 1104.
- Reichstein M., Tenhunen J., Rouspard O., Ourcival J. M., Rambal S., Dore S. and Valentini R. (2002). Ecosystem respiration in two Mediterranean evergreen Holm Oak forest: drought effects and decomposition dynamics. *Functional Ecology* 16: 27-39.
- Reichstein M., Tenhunen J. D., Rouspard O., Ourcival J. M., Rambal S., Miglietta F., Peressotti A., Pecchiari M., Tirone G. and Valentini R. (2002). Severe drought effects on ecosystem CO₂ and H₂O fluxes at three Mediterranean evergreen sites: revision of current hypotheses? *Global Change Biology* 8: 999-1017.
- Reichstein M., Subke J.A., Angeli A.C. and Tenhunen J.D. (2005). Does the temperature sensitivity of decomposition of soil organic matter depend upon water content, soil horizon, or incubation time? *Global Change Biology* 11: 1-14.
- Reth S., Reichstein M. and Falge E. (2005). The effect of soil water content, soil temperature, soil pH-value and the root mass on soil CO₂ efflux - A modified model. *Plant and Soil* 268: 21-33.
- Rey A., Pegoraro E., Tedeschi V., Deparri I., Jarvis P. G. and Valentini R. (2002). Annual variation in soil respiration and its components in a coppice oak forest in Central Italy. *Global Change Biology* 8: 851-866.
- Rochette P., Flanagan L.B. and Gregorich E.G. (1999). Separating soil respiration into plant and soil components using analyses of the natural abundance of carbon-13. *Soil Science Society of America Journal* 63: 1207-1213.
- Russell C.A., Voroney R.P., Black T.A., Blanken P.D. and Yang P.C. (1998). Carbon dioxide efflux from the floor of a boreal aspen forest. II. Evaluation of methods - verification by infra-red analysis of a dynamic closed chamber. *Can. J. Soil Sci.* 78: 311-316.
- Rustad L.E., Campbell J.L., Marion G.M., Norby R.J., Mitchell M.J., Hartley G.M., Cornelissen J.H.C. and Gurevitch (2001). A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental warming. *Oecologia* 126: 543-562.
- S**avage K. E. and Davidson E.A. (2003). A comparison of manual and automated systems for soil CO₂ flux measurements: trade-offs between spatial and temporal resolution. *Journal of experimental Botany* 54: 891-899.
- Schimel D.S., House J.I., Hibbard K.A., Bousquet P., Vici P., Peylin P., Braswell B.H., Apps M.J., Baker D., Bondeau A., Canadell J., Churkina G., Cramer W., Denning A.S., Field C.B., Friedlingstein P., Goodale C., Heiman M., Houghton R.A., Melillo J.M., Moore III B., Murdiyarso D., Noble I., Pacala S.W., Prentice I.C., Raupach M.R., Rayner P.J., Scholes R.J., Steffen W.L. and Wirth C. (2001). Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature* 414: 169-172.
- Shaver G.R., Canadell J., Chapin F.S. III, Gurevitch J., Harte J., Henry G., Ineson I., Jonasson S., Melillo J., Pitelka L. and Rustad L.E. (2000). Global warming and terrestrial ecosystem: a conceptual framework for analysis. *Bioscience* 50: 871-882.
- Søe A.R. and Buchmann N. (2005). Spatial and temporal variations in soil respiration in relation to stand structure and soil parameters in an unmanaged beech forest. *Tree Physiology* 25: 1427-1436.
- Søe A. R. B., Giesemann A., Anderson T. H., Weigel H. J. and Buchmann N. (2004). Soil respiration under elevated CO₂ and its partitioning into recently assimilated and older carbon sources. *Plant and Soil* 262: 85-94.
-

Stoyan H., De-Polli H., Böhm S., Robertson G.P. and Paul E.A. (2000). Spatial heterogeneity of soil respiration and related properties at the plant scale. *Plant and Soil* 222: 203-214.

Subke J.A., Hahn V., Battipaglia G., Linder S., Buchmann N. and Cotrufo M.F. (2004). Feedback interactions between needle litter decomposition and rhizosphere activity. *Oecologia* 139: 551-559.

Subke J.A., Reichstein M. and Tenhunen J.D. (2003). Explaining temporal variation in soil CO₂ efflux in a mature spruce forest in Southern Germany. *Soil Biology Biochemistry* 35: 1467-1483.

Swift M.J., Heal O.W. and Anderson J.M. (1979). *Decomposition in terrestrial ecosystems*, Blackwell Science.

Tang J., Baldocchi D. and Xu L. (2005). Tree photosynthesis modulates soil respiration on a diurnal time scale. *Global Change Biology* 11: 1298-1304.

Tang J., Misson L., Gerhenson A., Cheng W. and Goldstein A.H. (2005). Continuous measurements of soil respiration with and without roots in a ponderosa pine plantation in the Sierra Nevada Mountains. *Agricultural and Forest Meteorology*. *In press*.

Tang J., Qi Y., Misson L. and Goldstein A.H. (2005). Forest thinning and soil respiration in a ponderosa pine plantation in the Sierra Nevada. *Tree Physiology* 25: 57-66.

Thierron V. and Laudelout H. (1996). Contribution of root respiration to total CO₂ efflux from the soil of a deciduous forest. *Canadian Journal of Forest Research* 26: 1142-1148.

Thompson D. and Matthews R. (1989). CO₂ in trees and timber lowers greenhouse effect. *Forestry and British timber* 19-24.

Toland D.E and Zak D.R. (1994). Seasonal patterns of soil respiration in intact and clear-cut northern hardwood forests. *Canadian Journal of Forest Research* 24: 1711-1716.

Valentini R., Matteucci G., Dolman A. J., Schulze E. D. and Jarvis P. G. (2003). The carbon sink strength of forests in Europe: a synthesis of results. In: *Fluxes of carbon, water and energy of European forests*. Valentini R. (Ed.) Ecological studies. 163 Berlin, 270p.

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., Guomundsson J., Thorgeirsson H., Ibrom A., Morgenstern K., Clement R., Moncrieff J.B., Montagnani L., Minerbi S. and Jarvis P.G. (2000). Respiration as the main determinant of carbon balance in European forests. *Nature* 404: 861-864.

Wang C. K., Bond-Lamberty B. and Gower S. T. (2002). Environmental controls on carbon dioxide flux from black spruce coarse woody debris. *Oecologia* 132: 374-381.

Wang, W. J., R. C. Dalal, P. W. Moody and C. J. Smith (2003). Relationships of soil respiration to microbial biomass, substrate availability and clay content. *Soil Biology and Biochemistry* 35: 273-284.

Wang K. Y., Kellomaki S., Zha T. S. and Peltola H. (2004). Component carbon fluxes and their contribution to ecosystem carbon exchange in a pine forest: an assessment based on eddy covariance measurements and an integrated model. *Tree Physiology* 24: 19-34.

Wang W.J., Zu Y.G., Wang H.M., Hirano T., Takagi K., Sasa K. and Koike T. (2005). Effect of collar insertion on soil respiration in a larch forest measured with a LI-6400 soil CO₂ flux system. *Journal Forest Research* 10: 57-60.

Yanai R. D., Currie W. S. and Goodale C. L. (2003). Soil carbon dynamics after forest harvest: An ecosystem paradigm reconsidered. *Ecosystems* 6: 197-212.

Yuste J. C., Janssens I. A., Carrara A. and Ceulemans R. (2004). Annual Q_{10} of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Global Change Biology* 10: 161-169.

Yuste J. C., Janssens I. A., Carrara A., Meiresonne L. and Ceulemans R. (2003). Interactive effects of temperature and precipitation on soil respiration in a temperate maritime pine forest. *Tree Physiology* 23: 1263-1270.

Zha T., Kellomaki S., Wang K. Y. and Rouvinen I. (2004). Carbon sequestration and ecosystem respiration for 4 years in a Scots pine forest. *Global Change Biology* 10: 1492-1503.

ARTICLES

SOMMAIRE

Article 1 : Ngao J., Longdoz B., Perrin D., Vincent G., Epron D., Le Dantec V., Soudani K., Aubinet M., Willm F., Granier A. Cross-calibration functions for soil CO₂ efflux measurement systems. *Annals of Forest Science*, *in press*.

Article 2 : Ngao J., Epron D., Brechet C., Granier A. (2005). Estimating the contribution of leaf litter decomposition to soil CO₂ efflux in a beech forest using ¹³C depleted litter. *Global Change Biology*, 11: 1768-1776.

Article 3 : Ngao J., Yernaux M., Le Goff N., Longdoz L., Nys C., Aubinet M., Granier A. Decomposition and CO₂ release of woody residues from a young thinned beech (*Fagus sylvatica* L.) stand. *In prep*.

Article 4 : Ngao J., Longdoz B., Granier A., Epron D. Separating autotrophic and heterotrophic respiration in two young beech stands: Impact of corrections for root decomposition in trenched plots. *In prep*.

Article 5 : Ngao J., Longdoz B., Epron D., Breda N., Granier A. Spatial variation of soil CO₂ efflux in a beech forest in relation with soil and stand characteristics. *In prep*.

ARTICLE 1: Cross-calibration functions for soil CO₂ efflux measurement systems

**Jérôme Ngao^a, Bernard Longdoz^{a*}, Dominique Perrin^b, Gaëlle Vincent^c, Daniel Epron^d,
Valérie Le Dantec^e, Kamel Soudani^f, Marc Aubinet^g, François Willm^a, André Granier^a**

^aUMR Ecologie et Ecophysiologie Forestières, Centre INRA Nancy, 54280 Champenoux, France

^b Unité de Biologie Végétale, Faculté Universitaire des Sciences Agronomiques, B 5030 Gembloux, Belgium^c
Laboratoire Biologie et Ecophysiologie, Université de Franche-Comté, 25030 Besançon Cedex, France

^d UMR Ecologie et Ecophysiologie Forestière, Université Henri Poincaré Nancy 1, 54506 Vandoeuvre-lès-Nancy Cedex, France

^e UMR CESBIO, Equipe Modélisation du Fonctionnement des Ecosystèmes, BPI 2801, 31401 Toulouse Cedex 9, France

^f Laboratoire Ecologie Systématique Evolution, Département Ecophysiologie Végétale, Université Paris-Sud XI, 91405 Orsay Cedex, France

^g Unité de Physique des Biosystèmes, Faculté Universitaire des Sciences Agronomiques, B 5030 Gembloux, Belgium

***Corresponding author:**

Bernard Longdoz (longdoz@nancy.inra.fr)

Telephone: +33 3 83 39 40 41

Fax: +33 3 83 39 42 40

Short title: Cross-calibration of soil respiration systems

Accepté dans Annals of Forest Science

Abstract

Different soil CO₂ efflux measurement systems and methodologies were used to estimate the annual soil respiration of different forest sites. To allow comparison between these annual values, this study aimed to cross-calibrate five soil CO₂ efflux (S_R) closed dynamic chamber systems, and compare the *in situ* measurement methodologies. We assessed first the impact of the measurement methodology on S_R through 3 parameters: record duration, time-lag before starting to record and the mode of chamber-soil contact (use of collar or insertion of chamber in the soil). Secondly, we compared directly systems with identical methodology through field measurements in three forest sites. We have found a significant influence of the chamber-soil contact mode (no impact of the record duration and duration before starting to record). Measurements obtained by insertion led to significantly higher estimates of S_R than those obtained using collars (up to 28%). Our inter-comparison showed that deviations existing between *in situ* measurements performed with the different systems are partly systematic and could be corrected using simple linear equations. Measurements of pressure difference between the inside and the outside of soil chambers allowed explaining a part of observed deviations between systems. Finally, we assessed the influence of the cross-calibration equations on annual respiration of 2 beech forest soils.

Keywords: cross calibration / forest ecosystem / measurement system / pressure effect / soil CO₂ efflux

Fonctions d'inter-calibration pour des systèmes de mesure du flux de CO₂ du sol

Résumé

Différents systèmes et protocoles ont été utilisés pour estimer la respiration annuelle du sol de plusieurs sites forestiers. Afin de comparer ces valeurs annuelles, cette étude avait pour but d'inter-calibrer cinq systèmes de mesure du flux de CO₂ du sol (S_R) à chambre fermée dynamique, et de comparer les méthodes de mesure *in situ*. Nous avons évalué dans un premier temps l'impact la méthodologie de mesure sur S_R à travers 3 paramètres: la durée de mesure, le délai avant de commencer la mesure et le mode de contact chambre-sol (utilisation de colliers ou insertion de la chambre). Dans un second temps, nous avons comparé directement les systèmes au cours de 3 campagnes de mesures sur le terrain dans 3 sites forestiers. Nous avons trouvé une influence significative du mode de contact chambre-sol, mais pas d'impact des paramètres de mesure. Les mesures obtenues par insertion de la chambre donnent des estimations plus importantes de S_R que celles obtenues par utilisation de colliers (jusqu'à 28%). Notre inter-comparaison a montré que des écarts entre des mesures faites avec les différents systèmes sont partiellement systématiques, et pourraient être corrigés par des équations linéaires simples. Les mesures de différences de pressions entre l'intérieur et l'extérieur de la chambre ont permis d'expliquer en partie les écarts observés. Finalement, l'influence des équations d'intercomparaison sur la respiration annuelle du sol de deux hêtraies est présentée.

Mots-clefs: écosystème forestier / effet de pression / flux de CO₂ du sol / inter-calibration / système de mesure

Introduction

After photosynthesis, soil CO₂ efflux (S_R) is the second CO₂ forest flux of importance [20] and soil constitutes the major carbon reserve in terrestrial ecosystems [4]. Even small S_R response to global climatic change can induce important variation in CO₂ atmospheric concentration ([CO₂]) [26]. Accurate measurements are required for improving the understanding of the soil respiration process and its modeling.

Different methods have been used for S_R measurements, such as static chamber systems (alkali solution, soda lime [1]), closed or open dynamic chamber connected to an infrared gas analyzers (IRGA) [18] [21], eddy covariance below the canopy [12] and soil CO₂ concentration ([CO₂]) gradient [22]. The choice of the measurement system mostly depends on the specific spatial and temporal resolution requested, as underlined for chamber techniques by Savage & Davidson [24].

This study only includes closed dynamic chamber systems (CDC). Indeed, these systems are easy portable allowing a high number of measurement repetitions and therefore are able to integrate the intra-plot spatial variability. When frequent measurement campaigns are performed within a stand (every week or every two weeks), these systems are also able to capture the S_R seasonal evolution [22] [5]. They are the most appropriate to estimate the annual soil respiration of plots and then to achieve our objective of comparison between annual respiration values from different forest sites.

Five different CDC systems are usually employed to measure the S_R on the different sites taking part in our plot comparison project. The S_R data recorded with these systems cannot be directly compared since the inter-plot variability can be masked by significant systematic deviations already observed among the different closed dynamic systems in number of studies [9] [13], mainly due to differences in air circulation and pressure conditions in the chamber headspace. It had also been shown that (i) most of these deviations were linear and (ii) correction coefficients could be applied for more accurate comparisons of soil CO₂ efflux values, revealing the necessity of cross-calibrations [10] [11] [19]. Unfortunately, each of these studies have been realized on one single site or using a calibration device in standardized conditions. Then the influence of site characteristics as soil moisture, soil type or texture has not yet been taken into account on deviations between systems [14] [19].

Adding to the soil chamber type, the soil-chamber contact mode (i.e. inserted into soil or laid on a pre-inserted collar) is another methodological point that has been well discussed [11] [17]. Both of these methods present advantages and drawbacks. The direct insertion of a chamber into the soil potentially disturbs the litter-soil layer at a short-term (within 24 hours) and does not allow multiple measurements in the same location, but it allows a large number of measurements. The use of collars is suspected to cut the litter and superficial soil fine root networks and thus to suppress a significant part of the root respiration [11] [25] while it avoids the short-term soil disturbance as the collar is inserted several days before measurements. Despite these considerations, both methods are still used.

In this study we aimed to compare five CDC systems and three measurement methodology parameters. The objective was to establish cross-calibration functions between the different systems and methodologies usually used by the team involved in this paper. We first tested the impact of measurement methodology on S_R measured, and focused on the soil-chamber contact mode. In a second step, we cross-calibrated these systems on 3 sites that mainly differ in their soil and humus type and tree-species compositions. Comparing systems and methodologies under different site conditions provided calibration functions, which can be used to correct the systematic divergences among the tested systems, also taking into account the influence of the site characteristics. In the final stage, annual soil respiration values of studied forest were compared after the use of cross-calibration functions to erase

the experimental set up impact.

Materials and methods

1. Sites

Our study was conducted in 3 forests sites. The Vielsalm forest (Belgium, 50°18'N, 6°00'E) and the Hesse forest (France, 48°40'N, 7°05'E) were described in Aubinet *et al.* [2] and in Granier *et al.* [6], respectively. Soil type in Vielsalm is classified as drystic cambisol (FAO classification) covered by a moder humus type. Soil type in Hesse is a stagnic luvisol covered by an oligo-mull humus type. The third site located in the Chaux forest (France, 47°07'N, 05°42'E) in a mixed deciduous stratified stand; the dominant species are oaks (*Quercus robur* L., *Quercus petraea* ((Mattuschka) Liebl.)) and several other deciduous species as *Carpinus betulus* L., *Fagus sylvatica* L., *Populus Tremula* L. and *Betula verrucosa* Ehrh. are mainly in coppice. Mean annual temperature and precipitations averages 10.3°C and 950 mm respectively. The soil is a gleyic luvisol with a meso-mull humus type.

2. Presentation of tested systems

There were five CDC systems involved in our cross-calibration experiment. The principle of the closed dynamic system is to calculate the soil CO₂ efflux from the rate of increase of the [CO₂] in a chamber that is hermetically in contact with a small area of soil [11]. The five systems are classified in two groups. The first group is constituted by three systems based on the Licor company products (Licor, Lincoln, USA):

- the "Li-Gx" system (Faculté Universitaire des Sciences Agronomiques, Gembloux), described by Longdoz *et al.* [16] consists of a Li-6252 (Licor, Lincoln, USA) IRGA connected to a homemade respiration chamber (185 mm height x 80 mm diameter) built following Norman *et al.* [18],

- the "Li-He" and "Li62" systems (Unité Ecologie et Ecophysiologie Forestières, Nancy) both consists of a Li-6252 IRGA connected with a Li 6000-9 chamber (Licor, Lincoln, USA).

For these 3 systems, air circulation inside the chamber is provided by the pump of the Li-6252 (flow rate 1.5 l.min⁻¹) and driving the air inside the chamber through a drilled ring that allows air mixture and homogenization. The second group is consisted of two systems based on the PP-systems company products (PP-Systems, Hutchin, UK):

- the "PP-Ch" system (Université de Franche-Comté, Besançon) consists of a upgraded EGM-4 IRGA connected with a modified version of the SRC-1 chamber including a metal mesh in the lower part of the chamber,

- the "PP-Or" system (Université Paris-Sud XII, Orsay) consists of a upgraded CIRAS-1 IRGA connected to the first version of the SRC-1 chamber that is not equipped with the metal mesh.

In these two last chambers, a vertical fan provided air mixture and homogenization inside the chamber. The flux data provided by all systems were compared to those from the "Li62" that has been arbitrarily chosen as the common comparative system at each site.

3. Methodology parameters tested during the intercomparison

The methodology measurement usually used by each operator for S_R survey of their forest plots (therefore called "particular protocol") differs by (a) the time-lag between the placement of the chamber and the beginning of the record of the CO₂ increase (defined as the

“waiting time”), (b) the duration of this record and (c) the chamber-soil contact mode. These three modalities are set up by the operators and are not imposed by the system itself.

4. *In situ comparisons*

Four campaigns of soil respiration measurements took place at the Vielsalm (May 2003), Chaux (June 2004) and Hesse (mid and end of September 2003) forest sites. These campaigns, aiming at comparison of methodologies and systems, were divided in two steps. The first step concerned the impact of the different measurement methodologies on S_R values, in relation with the system characteristics and the operators. The second step concerned the system comparisons and cross-calibrations.

4.1 *Step 1: Methodology comparisons*

Table 1 shows the different tested parameters for each system. The “waiting time” varies from 10 to 15 s or the record starts when CO_2 concentration in the chamber is 15 ppm below the ambient value by using a soda lime scrub for Licor systems.

The rate of increase of CO_2 concentration is recorded during a constant time that ranges from 60 s to 120 s or during an increase of 30 ppm or 50 ppm of the CO_2 concentration in the chamber [11] (Table 1). The impact of the “waiting time” and the record duration was tested at Vielsalm forest campaign for all systems except for the “PP-Or” system. For this purpose, measurements performed with the different particular protocols were compared to measurements obtained with a common protocol (Table 1) employed by all systems. For this comparison, S_R were measured on 24 PVC collars (60 mm height, 119 mm diameter) inserted into soil (15 mm depth) 2 weeks before measurements in order to avoid S_R measurements perturbations.

Two chamber-soil contact modes were used. The chamber can be either directly inserted in the soil or laid on collars pre-inserted in the soil. The chamber-soil contact mode was only assessed for both “PP-Ch” and “Li-He” because the three other systems were never used with the insertion mode (Table 1). We compared two successive flux measurements, the first one performed with the chamber laid on larger PVC collar (60 mm height, 119 mm diameter, a foam gasket ring provided an airtight seal between chambers and the collar), and the second one with the chamber inserted in the soil (15 mm depth) inside the collar. This test was realized in all sites, on 7 to 8 collars per site. The collars were inserted into soil 2 weeks before measurements in order to avoid S_R measurement perturbations.

4.2 *Step 2: Cross calibration*

The four campaigns of system comparison and cross-calibration were performed in the Vielsalm (May 2003) forest with “Li62”, “Li-He”, “Li-Gx” and “PP-Ch”, on 12 PVC collars. We performed campaigns in the Hesse forest with “Li62” and “Li-He” on 23 PVC collars (mid-September 2003), and with “Li62”, “Li-He”, “Li-Gx” and “PP-Ch” on 23 collars (end of September 2003). The fourth campaign was performed in the Chaux forest (June 2004) with “Li62”, “Li-He”, “PP-Ch” and “PP-Or” on 29 PVC collars. The collars were inserted in the forest soil 2 weeks before measurements. A foam gasket ring provided an airtight seal between chambers and the collar. For each system, a S_R value corresponded to the mean of three measurements on the same collar, the measurements on a same collar being alternated with those made on other collars.

Before the Vielsalm and Chaux campaigns, the pressure difference between the chamber headspace and the atmosphere (PDC) was verified for each system with a FCO42 (Furness Controls Ltd, Bexhill, UK). Each PDC measurement was performed with chambers laid on a collar that was hermetically sealed with a PVC disc. A PDC, induced by a leak in the air

circulation circuit, is known to cause important measurement error on S_R by pressure pumping or blocking [3] [16]. PDC was not checked before the Hesse campaign. Because no significant variation have been observed between the values obtained at Vielsalm and Chaux, the PDC impact can be considered as constant for all the campaign (see results).

5. Impact of cross-calibration on annual soil CO_2 efflux

S_R was monitored within the Hesse forest in 2003 and 2004 in three plots every 2-3 weeks on 36 collars in each plots with "Li-He". Soil temperature at -10 cm (T_S) and volumetric soil water content of the 0-6 cm layer (θ_{Vsurf}) were measured simultaneously with S_R by using homemade copper-constantan thermocouple (Faculty of Agronomy of Gembloux, Belgium) and a capacitive ML2x ThetaProbe (Delta-T Device, Cambridge, UK), respectively. In Vielsalm forest, S_R was monitored between August 1997 and August 1998 with "Li-Gx" in 29 collars inserted within a dominated beech patch (see [16] for more details). For Hesse data, an empirical model was fitted to either measured or corrected S_R values:

$$S_R = S_{R10} Q_{10}^{(T_S-10)/10} e^{-e^{(a-b*\theta_{Surf})}} \quad (1)$$

Where S_{R10} is the soil CO_2 efflux at $10^\circ C$, Q_{10} the temperature sensitivity of soil respiration, a and b are the parameters for the Gompertz function [9]. For Vielsalm data, an Arrhenius-type function was fitted to data:

$$S_R = S_{R10} e^{\left\{ \frac{E_a (T_S - 283.2)}{283.2 R T_S} \right\}} \quad (2)$$

with $E_a = \frac{E_{a0} 10^3 T_S}{T_S - T_0}$

where S_{R10} is the soil CO_2 efflux at $10^\circ C$, R is the universal gas constant ($8.314 \text{ J mol}^{-1} \text{ K}^{-1}$), T_S is the soil temperature (K), T_0 is a reference temperature and E_{a0} a reference activation energy (J mol^{-1}). Following Lloyd & Taylor [15], the parameters T_0 and E_{a0} were fixed to 227.13K and 12970 J mol^{-1} , respectively [16]. The influence of soil water content was not taken into account, as it had not been observed. Annual soil CO_2 efflux (S_{RA}) in Hesse were computed for 2003 and 2004 separately by applying equation (1) with continuous measurements of T_S and θ_{Vsurf} , while S_{RA} in Vielsalm was computed by applying equation (2) with T_S data. Relationships deduced from cross-calibrations among systems were used to assess the impact of systems on S_{RA} (see Results). For Hesse dataset, we converted each values measured by the "Li-He" system into a corrected value that represented S_R as it would be if measurements were performed by either the "Li62", "Li-Gx" or "PP-Ch" systems. For Vielsalm dataset, we converted each values measured by the "Li-Gx" system into a corrected value that represented S_R as it would be if measurements were performed by either the "Li62", "Li-He" or "PP-Ch" systems. Depending on the site and the measuring system, the corrected values were either fitted to equation (1) or (2), and corrected annual soil respiration (cS_{RA}) were obtained following the same procedures as presented above.

6. Statistical analysis

Linear regressions (Statview 5.0, SAS Institut Inc., N.C., USA) were used to cross-compare data from each system to the "Li-62" system used as the comparative system. Comparisons tests of the mean between the systems, measurement methodologies and campaign were performed by two-way ANOVA tests and post-hoc Fisher's Protected Least Significant Difference tests. Least square non-linear regression analyses were performed to fit empirical models to S_R data (Statgraphics Plus 4.1).

Results

1. Pressure difference between the chamber headspace and the atmosphere (PDC)

Measurements of PDC in the center of the chambers gave values lower than 0.05 ± 0.01 Pa (mean \pm standard deviation) in the "Li62", "Li-Gx" and "Li-He" systems. PDC values reached 0.01 ± 0.001 Pa in "PP-Ch" and 0.92 ± 0.35 Pa in "PP-Or".

2. Impact of the different measurement methodologies (Step 1)

Measurements obtained with the methodologies usually used by the different teams (particular protocol) did not differ significantly (PLSD, $p > 0.05$) from those obtained with the common measurement methodology (common protocol, *Table I*). Thus during the system comparison (step 2), each system measured S_R measurements with its particular protocol without introducing methodological divergences.

A significant impact of the chamber-soil contact mode (use of "collar" or "insertion" in the soil) has been found for the two tested systems ("Li-He" and "PP-Ch"). *Figure 1a* shows a significant linear relationship between "collar" and "insertion" values for "Li-He", when the data from the different campaigns were regrouped. The "insertion" values gave fluxes 28% higher than "collar" values. A similar result is observed for "PP-Ch" with an increase due to insertion going from 2% to 13% (*figure 1b*) when "collar" values ranged from $1 \mu\text{mol}_{\text{CO}_2} \text{m}^{-2} \text{s}^{-1}$ to $6 \mu\text{mol}_{\text{CO}_2} \text{m}^{-2} \text{s}^{-1}$ (range usually measured, data not shown). However when considering the campaign separately, the "PP-Ch" system showed a decrease of about -11% when passing from "collar" to "insertion" during the Chaux campaign. This decrease has been verified for this site during other campaigns (data not shown).

3. System cross calibration (Step 2)

Table II summarizes the mean S_R values measured by the different systems for each campaign. At the Vielsalm site, mean S_R values did not differ among systems. At the Hesse site, the "PP-Ch" system measured significantly higher mean S_R values ($p < 0.05$) than the other systems. At the Chaux site, a significant difference of mean S_R values was found ($p < 0.05$) among the systems, but the "Li62" and "Li-He" systems recorded no significant different mean S_R values. When considering the variability among sites, the "Li-Gx" and "PP-Ch" systems recorded mean S_R values that significantly differed among the three sites (Fisher's PLSD, $p < 0.05$) when both "Li62" and "Li-He" systems recorded a significantly higher mean S_R value ($p < 0.0001$) at Chaux than at the other sites. Significant differences among mean values of S_R calculated with all the systems were also observed among sites ($p < 0.0001$).

Figure 2 shows the linear relationship between the S_R values of different systems and those of "Li62". The values of slopes (*Table III*) revealed very low deviations for "Li-He" and "Li-Gx". However the relationship between "Li62" and "Li-Gx" measurements presented a larger variability than with "Li-He", in addition with a significant intercept from the regression analysis found for "Li-Gx". Considering the same system characteristics, values given by "Li-He" were very close to those of the "Li62" one. *Figure 2* shows a higher deviation for "PP-Ch" and "PP-Or". For "PP-Ch", a constant discrepancy of about 20% was found. According to the higher mean S_R value recorded by "PP-Or" at the Chaux site, the slope revealed a high deviation from "Li62" (*Table III*).

5. Annual soil CO₂ efflux

Actual annual estimates of S_R calculated directly from measurements (S_{RA}) exhibited pronounced spatial variability among plots and sites (*Table IV*), even if S_{RA} values were not established for the same time periods in both sites. Annual estimates of S_R from corrected values (cS_{RALi62}) were very close to annual estimates from S_R values measured in BO, Bre and BOR plots. Deviations for a given "X" system were calculated as: Deviation "X" = $(A_X - cS_{RALi62})/A_X * 100$, with A the actual or corrected annual soil respiration of the "X" system, cS_{RALi62} referring to the corrected annual soil respiration for the "Li62" system. Deviations for the "Li-He" were very low (between -0.6% and -0.15%, *Table IV*) despite the different site characteristics. Deviations for the "Li-Gx" were higher (between +8.2% and +21%). Deviations for the "PP-Ch" were relatively constant (around +19%) but higher than for the "Li-He".

Discussion

1. PDC

Preliminary PDC measurements showed there were no major pressure differences of pressure in the tested systems except for the "PP-Or" system. The higher PDC value obtained for "PP-Or" (overpressure of 0.92 ± 0.351 Pa) was due to the effect of air mixing by the fan action inside the chamber which is prevented in "PP-Ch" by the addition of the metal mesh at the bottom of the chamber. Following the work of Longdoz *et al.* [16], the impact of PDC on "PP-Or" overpressure for the Vielsalm forest soil lead to a S_R underestimation of 69%. Our results confirmed that addition of a metal mesh in the SRC-1 chamber was a benefit. "PP-Ch" and Licor-based systems did not induce any pressure pumping or blocking effect, and gave a good confidence in the air tightness of these systems. In consequence, the comparisons of measurement methodologies and systems were realized for these four systems without any bias coming from a pressure problem. The higher S_R values measured with "PP-Or" compared to those of "Li62" are not consistent with the overpressure recorded in the center of the "PP-Or". Indeed, the overpressure leads to a blockage of the flux. This discrepancy could be attributed to presence of a possible negative PDC measuring between the atmosphere and the points located near the chamber inner walls. Another explanation is excessive turbulence within the SRC-1 chamber due to the fan in the absence of the metal mesh [7]. Indeed, if closed dynamic chamber techniques are unable to reproduce wind conditions prevailing in the forest floor and boundary layer conditions inside the chamber [17], it seems that the unmodified SRC-1 configuration implies artificial conditions. In previous tests, measurements of mean wind speed inside the chamber gave 0.9 m s^{-1} [13] and 0.13 m s^{-1} (unpublished data) for the unmodified and modified version of the SRC-1, respectively. This large difference in wind speed and the PDC could explain the S_R values divergence between "PP-Or" and the other systems. Such deviations between systems using the first version of SRC-1 and Li 6000-9 chambers have already been reported [10] [13] [18].

2. Chamber-soil contact mode

The chamber-soil contact mode has a significant impact on the S_R measurements. Three hypotheses could explain the general higher S_R values obtained for the "insertion" mode. First, a transient change of diffusion conditions of the CO₂ in the litter and the upper mineral soil layers would occur when inserting the chamber. For the soil types met in this study, the insertion would have perturbed the soil aggregates and leaf litter structure increasing the

vertical diffusivity coefficient, inducing a rapid release of upper soil CO₂. Second, the collar placement could affect S_R measurements at long-term because of the cutting of fine roots [8] [11]. Wang *et al.* [24] showed that a reduction in S_R values for a larch forest occurs when measurements were performed at least 12 hours after collar installation. Third, the distance between the soil and the drilled ring ("Li-He") or the fan ("PP-Ch") insuring air mixing inside the chambers, differs between the "insertion" and "collar" cases. This distance being lower without collars, a thinner boundary layer would be induced for "insertion" measurements, leading to higher S_R values. This argumentation shows also that both chamber-soil contact modes have advantages and disadvantages and each one could not be considered as a reference method.

In opposition to all other observations, the "PP-Ch" system during the Chaux campaign (*figure 1b*) was the only situation giving lower values for "collar" than for "insertion". This has been confirmed by other campaigns at the same site (data not shown). A possible cause is that the "insertion" of the SRC-1 chamber would not have trenched the broadleaf litter layer at Chaux, but would only have compressed it. Then airtightness between the chamber's edge and the soil-litter interface may not be sufficient, leading to consequent CO₂ leaks and an underestimation of the fluxes.

The highly significant linear relationships between "collar" and "insertion" S_R values (*figure 1a & 1b*) suggest that scaling coefficients could be used when "collar" and "insertion" data have to be compared. The difference in the relationship parameters between the two systems tested shows that the scaling coefficient is dependent on the system. More experiments are needed to recommend coefficients adapted to each site (soil type).

3. Cross-calibration

The S_R values measured during the cross-calibration experiments were in good agreement with the range observed during a seasonal evolution survey performed on each site (data not shown). Differences in mean S_R values among sites could be partially explained by the influence of soil temperature variation among sites and campaigns, especially for the high S_R during the Chaux campaign where the soil was exceptionally warm (*Table II*).

The linear regression presented in the *figure 2* shows that systematic deviations existed between *in situ* measurements performed by different systems. However these deviations could be corrected with a linear equation, even if the accuracy of corrections would be depend on the similarity of measurements performed by the different systems, and vary according to the R² values.

Logically, when the same system materials are considered ("Li62" and "Li-He") S_R values are very close in all of the campaigns. The lower R² of the relationship between measurements of "Li62" and "Li-Gx" may be due to a higher variability in measurements due difference in to the foam gaskets assuring the airtight seal of the chambers of these two systems. This may induce a imperfection in the air tight of one of both systems when the chambers are laid on a not perfectly horizontal collar's edge. Consequently an over or underestimation could be induced, depending on the importance of the small PDC or/and potential CO₂ leak.

The higher S_R values given by "PP-Ch" compared to those of "Li62" could be explained by a thicker boundary layer resistance in the Li 6000-9 chamber than in the SRC-1 modified chamber. In spite of a higher wind speed in the Li 6000-9 (0.4 m s⁻¹ [12]) and the presence of a grid mesh in the SRC-1, the position of the drilled ring in the Li 6000-9 chamber would allow airflow more parallel to the soil surface that the airflow induced by the fan placed to produce vertical air movement in SRC-1. Therefore a thicker boundary layer would be more easily induced in the Li 6000-9 chamber. This hypothesis, while explaining the cause of the

divergence, does not allow a conclusion on which system presents measuring conditions closer to the natural situation. The slope of the linear regression for the comparison between "PP-Ch" and "Li62" (1.21, *figure 2c, Table III*) is in the range of the results presented by Pumpanen *et al.* [19] for equivalent systems and performed on a calibration tank (slopes ranged from 1.16 for coarse sand to 1.33 for wet fine sand). Finally, as explained in the first section of this discussion, the PDC problem could explain the large deviation between S_R measurements of "Li62" and those of "PP-Or" (*figure 2d, Table III*).

4. Impact of corrections on annual S_{RA}

Annual S_{RA} calculated directly from measurements exhibited pronounced spatial variability among plots and sites, even when data were cross-calibrated to obtain corrected flux (cS_{RALi62} , *Table IV*). However the impact of this cross-calibration on the spatial variability was important. For example, the Vielsalm actual annual soil respiration value (S_{RA}) became one of the lowest after correction (cS_{RALi62}). Beyond this spatial variability, these results showed that, logically, the two identical systems ("Li62" and "Li-He") gave very close annual soil respiration on all plots. The values obtained from the "Li-Gx" system were slightly higher, because of the particularities of this system (air circulation, foam gasket). Comparing to the "Li62" is able to partly mask the natural inter-plot variability, especially when considering Vielsalm forest. Finally, the comparison "PP-Ch" with "Li62" showed clearly that the discrepancies between two different materials do not allow inter-plot comparison without cross-calibration functions.

Conclusion

Our study showed that systematic deviations exist among *in situ* measurements performed with different systems, however these deviations are in the range of the already published results. Deviations were coherent with possible causes and could be corrected with simple linear equations. Thus, S_R values provided by different systems for different study sites can be used to compare soil respiration effluxes. We confirmed that the unmodified SRC-1 chamber induced consequent deviations, but confidence in the measured values was improved by including a grid mesh in the chamber ("PP-Ch" system) as proposed by the manufacture. The discussion on the possible causes of differences among systems and the choice of soil contact mode revealed that properties such as soil texture, soil-litter interface porosity and chamber design influenced S_R values, with a strong dependence on the study site. The influence of the measuring system on the estimation of the annual soil respiration is able to mask partly (when the compared systems were built on the same model) or completely (when the compared systems came from different manufactories) the inter-plot variability.

Acknowledgments

We gratefully thank M. Michel Yernaux for his technical knowledge on the soil respiration systems, and M. Laurent Vanbostal for helping us to make measurements at the Chaux forest. This work was supported by the European programme CarboEurope IP ("Assessment of European Ecosystem Carbon balance") and the Belgian-French TOURNESOL Programme Grant (n° 06718WG: "Etude des flux nocturnes de CO_2 dans les écosystèmes forestiers"). This study is a part of the GERS (Group Studying the Soil Respiration) activities. We greatly thank the two anonymous reviewers for their constructive suggestions for improving this paper.

Reference

- [1] Anderson J.M., Carbon dioxide evolution from two temperate deciduous woodland soils, *J. Appl. Ecol.* 10 (1973) 361-378.
- [2] Aubinet M., Chermanne B., Vandenhoute M., Longdoz B., Yernaux M., Laitat E., Long term carbon dioxide exchange above a mixed forest in the Belgian Ardennes, *Agri. For. Meteorol.* 108 (2001) 298-315.
- [3] Davidson E.A., Savage K., Verchot L.V. and Navarro R., Minimizing artifacts and biases in chamber-based measurements of soil respiration, *Agri. For. Meteo.* 113 (2002) 21-37.
- [4] Dixon R.K., Brown S., Houghton R.A., Solomon A.M., Trexler M.C., Wisniewski J., Carbon pools and flux of global forest ecosystems, *Science* 263 (1994) 185-190.
- [5] Epron D., Ngao J., Granier A., Interannual variation of soil respiration in a beech forest ecosystem over a six-year study, *Ann. For. Sci.* 61 (2004) 499-505.
- [6] Granier A., Ceschia E., Damesin C., Dufrene E., Epron D., Gross P., Lebaude S., Le Dantec V., Le Goff N., Lemoine L., Lucot E., Ottorini J.M., Pontailler J.Y., Saugier B., The carbon balance of a young Beech forest, *Funct. Ecol.* 14 (2000) 312-325.
- [7] Hanson P.J., Wullschlegel S.D., Bohlman S.A., Todd D.E., Seasonal and topographic patterns of forest floor CO₂ efflux from an upland oak forest, *Tree Physiol.* 13 (1993) 1-15.
- [8] Hanson P.J., Edwards N.T., Garten C.T., Andrews J.A., Separating root and soil microbial contribution to soil respiration: A review of methods and observations, *Biogeochem.* 48 (2000) 115-146.
- [9] Janssens I.A., Kowalski A.S., Ceulemans R., Forest floor CO₂ fluxes estimated by eddy covariance and chamber-based model, *Agri. For. Meteo.* 106 (2001) 61-69.
- [10] Janssens I.A., Kowalski A.S., Longdoz B., Ceulemans R., Assessing forest soil CO₂ efflux: an *in situ* comparison of four techniques, *Tree Physiol.* 20 (2000) 23-32.
- [11] Lankreijer L.A., Janssens I.A., Buchmann N., Longdoz B., Epron D. and Dore S., Measurement of soil respiration, in: Valentini R. (Ed.), *Fluxes of carbon, water and energy of European forests*, Springer, Berlin, 2003, pp.37-54.
- [12] Law B.E., Baldocchi D.D., Anthoni P.M., Below-canopy and soil CO₂ efflux in ponderosa pine forest, *Agri. For. Meteorol.* 94 (1999), 171-188.
- [13] Le Dantec V., Epron D., Dufrene E., Soil CO₂ efflux in a beech forest: comparison of two closed dynamic systems, *Plant Soil* 214 (1999) 125-132.
- [14] Liang N., Nakadai T., Hirano T., Qu L., Koike T., Fujinuma Y., Inoue G., *In situ* comparison of four approaches to estimating soil CO₂ efflux in a northern larch (*Larix kaempferi* Sarg.) forest, *Agri. For. Meteorol.* 123 (2004) 97-117.
- [15] Lloyd J., Taylor J.A. On the temperature dependence of soil respiration, *Ecol.*, 8 (1994) 315-323.
- [16] Longdoz B., Yernaux M., Aubinet M., Soil CO₂ efflux measurements in a mixed forest: impact of chamber disturbances, spatial variability and seasonal evolution, *Global Change Biol.* 6 (2000) 907-917.
- [17] Nay S.M., Mattson K.G., Bormann B.T. Biases of chamber methods for measuring soil CO₂ efflux demonstrated with a laboratory apparatus, *Ecol.* 75 (1994) 2460-2463.
- [18] Norman J.M., Garcia R., Verma S.B., Soil surface CO₂ fluxes and the carbon budget of grassland, *J. Geophys. Res.* 97 (1992) 18845-18853.

-
- [19] Pumpanen J., Kolari P., Ilvesniemi H., Minkkinen K., Vesala T., Niinistö S., Lohila A., Larmola T., Morero M., Pihlatie M., Janssens I., Yuste J.C., Grünzweig J.M., Reth S., Subke J.A., Savage K., Kutsch W., Østreng G., Ziegler W., Anthoni P., Lindroth A., Hari P., Comparison of different chamber techniques for measuring soil CO₂ efflux, *Agri. For. Meteorol.* 123 (2004) 159-176.
- [20] Raich J.W., Schlesinger W.H., The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate, *Tellus* 44 (1992) 81-99.
- [21] Rayment M.B., Jarvis P.G., An improved open chamber system for measuring soil CO₂ effluxes in the field, *J. Geophys. Res.* 102 (1997) 28779-28784.
- [22] Reichstein M., Rey A., Freibauer A., Tenhunen J., Valentini R., Banza J., Casals P., Cheng Y., Grünzweig J.M., Irvine I., Joffre R., Law B.E., Loustau D., Miglietta F., Oechel W., Ourcival J.M., Pereira J.S., Peressotti A., Ponti F., Qi Y., Rambal S., Rayment M., Romanya J., Rossi F., Tedeschi V., Tirone G., Xu M., Yakir D., Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices, *Global Biogeochem. Cycles*, 17 (2003), 1104-1119.
- [23] Russell C.A., Voroney R.P., Black T.A., Blanken P.D., Yang P.C., Carbon dioxide efflux from the floor of a boreal aspen forest. II. Evaluation of methods - Verification by infrared analysis of a dynamic closed chamber, *Can. J. Soil Sci.* 78 (1998) 311-316.
- [24] Savage K. E. and Davidson E.A., A comparison of manual and automated systems for soil CO₂ flux measurements: trade-offs between spatial and temporal resolution, *J. Exp. Bot.* 54 (2003) 891-899.
- [25] Wang W.J., Zu Y.G., Wang H.M., Hirano T., Takagi K., Sasa K., Koike T., Effect of collar insertion on soil respiration in a larch forest measured with a LI-6400 soil CO₂ flux system, *J. For. Res.* 10 (2005) 57-60.
- [26] Watson R.T., Nonle I.R., Bolin B., Ravindranath N.H., Verardo D.J., Dokken D.J., Land use, land-use change, and forestry, Special Report of the IPCC. Cambridge University Press, New York, 2001.

Tables

	Particular protocols					Common Protocol
	"Li62"	"Li-Gx"	"Li-He"	"PP-Ch"	"PP-Or"	
"Waiting time"	15 s / 15 ppm	10 s / 15 ppm	15 s	10 s	10 s	15 s
Recording	60 s	90 s / 30 ppm	60 s	76 s	76 s	76 s
Soil-Chamber contact	Collar	Collar	Inserted / Collar	Inserted / Collar	Collar	Collar

Table I. Description of the modalities used during the methodology comparison. Particular protocols corresponded to the protocols usually used by the teams for their studies of the temporal variations of soil respiration. For the soil-chamber contact mode, the chamber can be directly inserted in the soil ("Inserted") or laid on collars ("Collar").

Site	SR "Li62"	SR "Li-Gx"	SR "Li-He"	SR "PP-Ch"	SR "PP-Or"	SR Mean	Ts
Vielsalm	1.54 (0.18)	1.50 (0.17)	1.59 (0.17)	1.55 (0.15)	-	1.53 (0.08)	7.7 (0.07)
Hesse	1.82 (0.08)	2.17 (0.15)	1.80 (0.09)	2.37 (0.13)	-	1.98 (0.06)	11.8 (0.20)
Chaux	3.93 (0.18)	-	3.87 (0.17)	4.68 (0.27)	5.21 (0.40)	4.42 (0.14)	16.0 (0.07)

Table II. Description of the modalities used during the methodology comparison. Particular protocols corresponded to the protocols usually used by the teams for their studies of the temporal variations of soil respiration. For the soil-chamber contact mode, the chamber can be directly inserted in the soil ("Inserted") or laid on collars ("Collar").

Parameters	"Li-Gx"	"Li-He"	"PP-Ch"	"PP-Or"
A	1.03	0.96	1.21	1.84
B	0.15	NS	NS	-2.05
R ²	0.58	0.94	0.92	0.69
n	53	110	83	29

Table III. Linear regression parameters between S_R values of the relationship: $S_{R_{\text{Syst}}} = A \cdot S_{R_{\text{Li62}}} + B$, where $S_{R_{\text{Syst}}}$ and $S_{R_{\text{Li62}}}$ are the S_R value of the tested system and the S_R value given by "Li62", respectively. The regression analysis was performed on the pooled data from the three campaigns. Each point represents the mean of the 3 replicates made on each collar. For "Li-He", additional data from 23 other collars were added. Each parameter was significant for $p=0.05$ level (NS indicates non significant parameter in the regression analysis).

	BO		Bre		BOR		Vielsalm 1997-1998
	2003	2004	2003	2004	2003	2004	
$S_{RA} (g_C m^{-2})$	599	544	696	627	808	737	867
$cS_{RALi62} (g_C m^{-2})$	608	552	700	631	813	742	685
$cS_{RALiHe} (g_C m^{-2})$	-	-	-	-	-	-	683
$cS_{RALiGx} (g_C m^{-2})$	687	638	774	714	885	823	-
$cS_{RAPCh} (g_C m^{-2})$	747	683	862	782	996	913	828
Deviation "Li-He" (%)	-1.5	-1.4	-0.6	-0.6	-0.6	-0.6	-0.2
Deviation "Li-Gx" (%)	11.4	13.5	9.5	11.7	8.2	9.8	21.1
Deviation "PP-Ch" (%)	18.6	19.2	18.8	19.3	18.4	18.8	17.3

Table IV. Mean annual soil CO₂ efflux ($g_C m^{-2}$) calculated from measured values (S_{RA}) or corrected values (cS_{RA}) in Hesse (BO, Bre and BOR stands) and Vielsalm sites. In Hesse and Vielsalm sites, S_{RA} was calculated from measurements performed with the "Li-He" and "Li-Gx" systems, respectively. For cS_{RA} values, subscripts referred to systems for which the corrections were applied to measured values using equations of Table III. Deviations (lower panel) were calculated as: Deviation "X" = $(A_X - cS_{RALi62})/A_X \cdot 100$, with A_X the actual or corrected annual soil respiration of the "X" system, cS_{RALi62} referring to the corrected annual soil respiration for the "Li62" system.

Figures

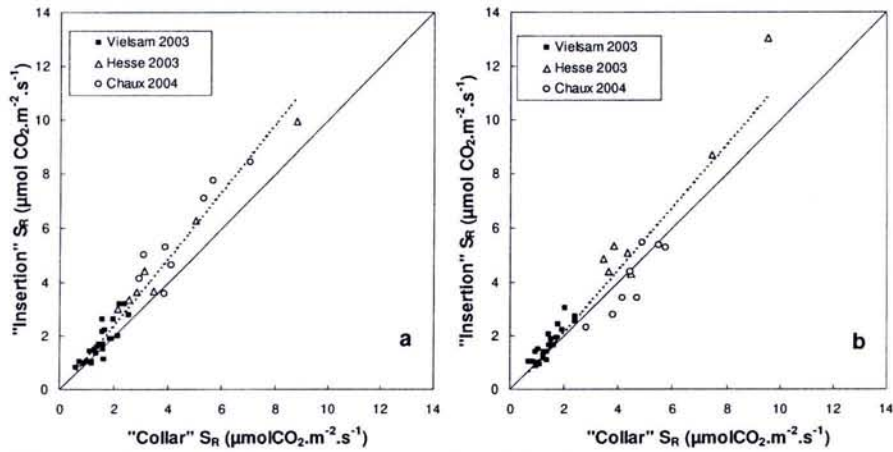


Figure 1. Comparison between S_R measured with the chamber laid on collars ("Collar" S_R) and S_R measured with the chamber inserted in the soil (Inserted S_R) for "Li-He" (a) and "PP-Ch" (b). The solid line is the 1:1 and the dashed line showed the general linear regression on all values. Regression equations are (a) ["Insertion" S_R] = $1.28 \times$ ["Collar" S_R] ($R^2 = 0.95$; $n = 39$); (b) ["Insertion" S_R] = $1.15 \times$ ["Collar" S_R] - 0.13 ($R^2 = 0.91$; $n = 39$).

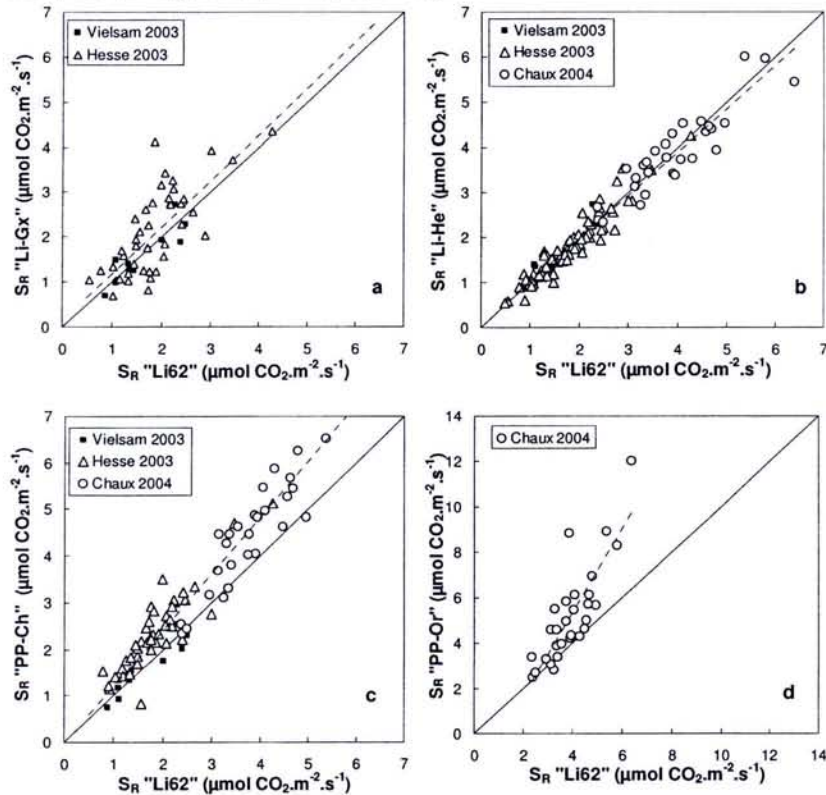


Figure 2. Comparison of S_R efflux "Li-Gx" (a), "Li-He" (b), "PP-Ch" (c) and "PP-Or" (d) with "Li62". The dashed line represents the linear regression from the overall data set. Equations and main parameters of the regressions are also presented. For analysis conveniences, for "Li-He", we gathered together data from the two campaigns performed at Hesse (see Materials and Methods section).

ARTICLE 2: Estimating the contribution of leaf litter decomposition to soil CO₂ efflux in a beech forest using ¹³C depleted litter

Jérôme NGAO^a, Daniel EPRON^b, Claude BRECHET^a, André GRANIER^a

^aUMR Ecologie et Ecophysiologie Forestière, Centre INRA de Nancy, 54280 Champenoux, France

^bUMR Ecologie et Ecophysiologie Forestière, Université Henri Poincaré Nancy 1, 54506 Vandoeuvre les Nancy cedex, France

Global Change Biology, 11: 1768-1776.

Corresponding author:

Daniel EPRON, UMR INRA-UHP Ecologie et Ecophysiologie Forestière, Université Henri Poincaré, 54506 Vandoeuvre les Nancy cedex, France

Fax: +33 3 83 68 42 40

E-mail: daniel.epron@sbiol.uhp-nancy.fr

Running title: Litter contribution to soil respiration

Abstract

The contribution of leaf litter decomposition to total soil CO₂ efflux (F_L/F) was evaluated in a beech (*Fagus sylvatica* L.) forest in eastern France. The Keeling-plot approach was applied to estimate the isotopic composition of respired soil CO₂ from soil covered with either control (-30.32‰) or ¹³C depleted leaf litter (-49.96‰). The δ¹³C of respired soil CO₂ ranged from -25.50‰ to -22.60‰ and from -24.95‰ to -20.77‰ respectively with depleted or control litter above the soil. The F_L/F ratio is calculated by a single isotope linear mixing model based on mass conservation equations. It showed seasonal variations, increasing from 2.8% in early spring to about 11.4% in mid summer, and decreasing to 4.2% just after leaf fall. Between December 2001 and December 2002, cumulated F and F_L reached 0.98 kg_C m⁻² and 0.08 kg_C m⁻² respectively. On an annual basis, decomposition of fresh leaf litter accounted for 8% of soil respiration and 80% of total C loss from fresh leaf litter. The other fraction of carbon loss during leaf litter decomposition that has entered in SOM pools, i.e. 20%, represents only 0.02 kg_C m⁻².

Keywords: Beech, *Fagus sylvatica*, Temperate Forest, Soil Respiration, Litter Decomposition, δ¹³C, Stable Isotope, Keeling plot.

Introduction

The understanding of terrestrial ecosystem functioning is a necessary step to predict their responses to the rise of global temperature and atmospheric CO₂ concentration, and to a change in the precipitation regime. In particular, the carbon balance of forest ecosystems is a result of different fluxes between the atmosphere and ecosystem compartments, i.e. aboveground living and decaying biomass and soil, which includes roots and their rhizosphere, litters and organic matter. In temperate ecosystems, the soil compartment is considered as the main contributor to ecosystem CO₂ efflux (Granier *et al.*, 2000; Janssens *et al.*, 2001). In these ecosystems, seasonal variations of soil respiration are mainly controlled by soil temperature and soil water content (Hanson *et al.* 1993; Davidson *et al.*, 1998; Epron *et al.*, 1999a). Soil CO₂ efflux includes both autotrophic (root and rhizospheric microbial communities) and heterotrophic (litter and soil organic matter decomposition) components (Cheng, 1996; Epron *et al.*, 1999b; Rochette *et al.*, 1999; Buchmann, 2000; Epron *et al.*, 2001). All components are thought to be controlled by climatic conditions and site characteristics in different ways (Lavigne *et al.* 2004). Thus, separated estimations of these components are required to analyze and model soil carbon efflux and its response to climate or perturbation, and to provide a better knowledge of carbon budgets of forest ecosystems. Previous studies have highlighted the important contribution of roots and their rhizosphere to soil respiration that often account for about 50% to 60% of total soil CO₂ efflux (Nakane *et al.*, 1983, Epron *et al.*, 1999b, Hanson *et al.*, 2000; Epron *et al.*, 2001). Litter and soil organic matter (SOM) decomposition is a key process in the carbon cycle. Leaf litter is known to have a higher decay constant than woody debris or SOM, but the contribution of its decomposition to soil respiration has been less investigated. The dynamic of litter decomposition is regulated by several factors such as seasonal soil temperature and moisture patterns, and litter quality including lignin, nitrogen or phenol contents (Swift *et al.*, 1979; Aerts, 1997; Berg, 2000; Norby *et al.*, 2001). Through the decomposition process, C can be stored in the microbial biomass or in more or less recalcitrant pools of SOM, or it can be mineralized and released as CO₂, thus participating to total soil CO₂ efflux.

Numerous studies investigated litter decomposition but only few of them were dedicated to quantify fresh-litter derived CO₂ flux (Bowden *et al.*, 1993) that contributes to the spatial variation of soil CO₂ efflux (Fang *et al.*, 1998; Longdoz *et al.*, 2000; Epron *et al.*, 2004a). A new approach is proposed in this study by using ¹³C depleted beech litter, taking advantage that flux partitioning between two sources of CO₂ differing in their ¹³C composition could be quantified by a mass balance approach (Rochette *et al.*, 1999; Hanson *et al.*, 2000). As far as the isotopic composition of the depleted litter differs from those of other soil compartments, the isotopic composition of the CO₂ produced by litter decomposition can be distinguished from the isotopic composition of the CO₂ produced by other soil processes (root and rhizosphere respiration, SOM mineralization).

Our objectives were to evaluate the contribution of fresh leaf litter decomposition to total soil CO₂ efflux (F_1/F) in a beech (*Fagus sylvatica L.*) forest using ¹³C depleted litter. We applied the Keeling-plot method adapted to soil for estimating the isotopic composition of respired soil CO₂ from plots covered with either natural or ¹³C depleted leaf litter. We estimated the fraction of carbon loss as CO₂ during litter decomposition by comparing the litter mass loss to the amount of carbon released as CO₂.

Materials and methods

Site

The experiment was set up in the Hesse state forest (48°40'N, 7°05'E, altitude 305m) in a 0.6ha experimental plot (Epron *et al.*, 1999a; Granier *et al.*, 2000). This site belongs to the European flux monitoring network (CarboEuroflux) and to the French network of forest ecosystem (ORE "fonctionnement des écosystèmes forestiers"). The site is located in the middle of a homogenous 65 ha area of 35-year-old European beeches (*Fagus sylvatica* L.). In 2002, the annual mean temperature and total precipitation were 10.5°C and 1150 mm, respectively; the mean soil temperature at -10 cm was 9.9°C. This was a rather wet year with a rainy summer, in comparison with mean annual rainfall of 820 mm usually reported (Granier *et al.*, 2000). Maximum LAI averaged 7.5. The soil type is classified as stagnic luvisol (FAO classification) covered by oligo-mull humus type (almost no O_F and no O_H layers below the O_L layer) highlighting a high biological activity. It is an acidic soil (pH_{H2O} and pH_{KCl} reaching 4.5 and 3.8 for the 0-10 cm layer respectively) that does not contain carbonate (Quentin *et al.*, 2001).

Experimental design

The general principle of our approach is based on the partitioning of leaf litter-CO₂ flux from the total soil CO₂ efflux (that includes root respiration and SOM decomposition) by an isotopic-labeling method which strongly increases the difference in ¹³C composition between leaf litter-derived CO₂ and other soil CO₂ sources. We compared the isotopic composition of CO₂ (δ¹³C) evolving from soil covered by control litter or by depleted litter. The initial δ¹³C of these litters was -30.32‰ and -49.96‰, respectively. Depleted litter was collected on 2-year-old beech seedlings grown in a greenhouse with an elevated CO₂ concentration ([CO₂]) atmosphere for two years (700 ppm with fuel combustion CO₂). Both litter types have been deposited in December 2001 directly on the forest floor. We gently removed leaf litter (mainly fresh litter fallen 4-6 weeks ago), until we reached the mineral soil from 4 plots (0.5 m x 1 m), leaving the soil undisturbed; then we put 0.35 kg_{DM} m⁻² of depleted litter on the topsoil, in agreement with the average natural litter amounts, mimicking annual litter fall. Four other plots received the control litter. Plots were distributed between 2 locations 10 m apart from each other (2 depleted and 2 control litter plots in each location). We put a large mesh size net on deposited litters in order to prevent wind dispersion and mixing with additional litterfall.

Respired CO₂ samples

CO₂ evolved from soil was sampled in a 10ml Exetainer glass-vial (fig.1) using a self-made sampling device consisted in a customized Plexiglas body connected to the output of a portable infrared gas analyzer (LiCor Li-6250, USA). When the accumulation chamber is inserted in the soil, air is conducted into the sampling device with a by-pass connection, flowing through a dessicant tube (Mg(ClO₄)₂) and the vial. The rise of [CO₂] in the closed system is due to the soil CO₂ efflux. After a certain lap of time, the air samples contain a mixture of soil-respired CO₂ and atmospheric CO₂ that was initially in the chamber. The dilution of soil CO₂ by atmospheric CO₂ can be modulated by the duration of air homogenization inside the sampling device. We defined from preliminary tests a minimum homogenization time of 2 minutes. CO₂ concentration in the

vials typically ranged between 400 and 1500 $\mu\text{mol mol}^{-1}$. Preliminary experiments have shown that the $[\text{CO}_2]$ rose linearly with time within this concentration range, suggesting that CO_2 diffusion was not inhibited and that this range of concentration would not be affected the isotope ratio of respired CO_2 . Using such large range of CO_2 concentrations gave more precise estimates of the isotopic composition of respired CO_2 (see below). We sampled 3 to 4 gas flasks at each plot (4 plots per treatments), leading to 12 to 16 samples per treatment. We sampled CO_2 evolved from soil 6 times, from day of year (DOY) 85 to DOY 316 in 2002.

Laboratory analysis

The $\delta^{13}\text{C}$ of CO_2 in the glass-vials were measured on a mass spectrometer (Delta S, ThermoFinnigan, Bremen, Germany) coupled to a gas purification device (GasBench II, ThermoFinnigan, Bremen, Germany). Analyses were performed within 48 hours after each sampling campaign. Isotopic composition values are expressed relative to the international PDB standard.

Additional analyses were performed on ground litter, roots and soil. Litter was first sample in May 2002. We sampled 5 leaves (representing about 0.3 g_{DM}) from each corner of each plot and pooled by plots ($n=4$ per treatment) in order to get enough material for $\delta^{13}\text{C}$, C and N analysis. Leaf litter was also sampled in October and November in order to determine $\delta^{13}\text{C}$ at the end of the experiment. Five soil cores were collected in May 2002 (0-15cm depth) in the vicinity of the control plots and were dried at 65°C and sieved at 2 mm mesh size. Fine roots (diameter $< 1\text{mm}$) were separated from the bulk soil of cores. Ground litter, root and soil samples were analyzed for carbon and nitrogen concentration, and $\delta^{13}\text{C}$ using a C and N analyzer (CE, Italy) coupled to the mass spectrometer.

Litter mass loss

Litter mass loss was determined by retrieving manually the remaining depleted leaf litter materials at the end of the experiment. Control litters were unfortunately lost. In order to have a more accurate estimate of the remaining litter, the superficial layer (0-1 cm) of 5 soil cores sampled within each plot was dispersed in distilled water and floating leaf fragments were manually retrieved. Because of the high rate of decomposition related with the oligo-mull humus type, only one-year-old leaf fragments were retrieved using this technique.

Calculations

The litter contribution to total soil CO_2 efflux (F_L/F) is calculated by a single isotope linear mixing model based on mass conservation equations (Balesdent, 1991; Cheng, 1996; Rochette *et al.*, 1999; Hanson *et al.*, 2000):

$$F = F_L + F_{\text{BG}} \quad [1]$$

$$F \cdot \delta = F_L \delta_L + F_{\text{BG}} \delta_{\text{BG}} \quad [2]$$

$$F_L/F = (\delta - \delta_{\text{BG}})/(\delta_L - \delta_{\text{BG}}) \quad [3]$$

where F is the total soil CO_2 flux and δ the isotopic composition of soil respired CO_2 estimated from keeling plots (see below). The two end-members of the mixing model are δ_L , the isotopic composition of litter respired CO_2 , and δ_{BG} , the isotopic composition of CO_2 produced belowground (including CO_2 produced by root and SOM decomposition). F_L and F_{BG} are their

respective associated fluxes. We used litter isotopic composition for δ_L values, assuming no discrimination during the first steps of litter decomposition (see below). δ_{BG} can be estimated by applying Eq. [3] for both treatments (subscripts **C** for control and **D** for depleted litter) and assuming that there are no differences of F_L/F ratio between both treatments:

$$F_L/F = (\delta_D - \delta_{BGD})/(\delta_{LD} - \delta_{BGD}) = (\delta_C - \delta_{BGC})/(\delta_{LC} - \delta_{BGC}) \quad [4]$$

We solved Eq. [5] by assuming that belowground CO_2 evolved from other processes than litter decomposition has the same isotopic composition in both treatments, i.e. $\delta_{BGC} = \delta_{BGD} = \delta_{BG}$:

$$\delta_{BG} = (\delta_C \delta_{LD} - \delta_D \delta_{LC}) / (\delta_C + \delta_{LD} - \delta_D - \delta_{LC}) \quad [5]$$

The isotopic composition of respired CO_2 (δ_C and δ_D in Eq. [4]) were estimated as the intercept of Keeling-plot relationships (Keeling, 1958; fig. 2) under the classical form: $\delta^{13}C_{\text{sample}} = \delta + a*(1/[CO_2]_{\text{sample}})$, the coefficient δ being the intercept and representing the isotopic composition of respired- CO_2 in Eq. [3]. Keeling plots were constructed by pooling all data for a given treatment and a given date ($n=12$ to 16). Due to uncertainties of $\delta^{13}C$ and $[CO_2]$ measurements ($\pm 0.1\%$ and 1 ppm respectively, Miller & Tans, 2003), we assessed the δ_D and δ_C terms and their uncertainties by performing a geometric mean regression leading to intercepts and their associated standard deviation (SD). The F_L/F ratio is calculated according to Eq. [3] with the measured and calculated values. Uncertainties of δ_{BG} and F_L/F ratio calculations were assessed by applying 10000 runs that were done with randomly chosen values for different terms of Eq. [4] and Eq. [5] assuming a normal distribution centered on their respective means and their standard errors (SE) for each date. The 95% of confidence interval (CI) for F_L/F ratio and δ_{BG} is calculated from the mean of these 10000 runs.

Litter decomposition contribution to total soil CO_2 efflux

Soil CO_2 efflux data (F) was not available in 2002 for technical reasons, then F was simulated using an empirical model fitted on data collected in 2001 in the Hesse forest (Epron *et al.*, 2004b, $F=1.81*\theta_v*e^{0.156T_s}$), where θ_v is the soil water content (-10 cm) and T_s the soil temperature (-10 cm). Daily F values were simulated with daily θ_v and T_s values measured continuously in 2002. We calculated a daily F_L value by multiplying the interpolated F_L/F ratio (between each air sampling dates) with the corresponding F value, and we finally summed all daily F and F_L values between December 2001 and December 2002, leading to cumulated F and F_L values. In order to complete the missing period from the litter deposition (in December 2001) to first air sampling (DOY 85), we assumed that the F_L/F ratio in December 2001 was similar to the F_L/F ratio at DOY 316 in 2002.

Statistics

One-way or two-way analysis of variance (ANOVA) was performed on $\delta^{13}C$, C and N contents values with the two treatments and sampling dates as independent variables (Statview 5, SAS Institute Inc., USA). Significant seasonal evolutions have been tested using a protected least significant difference (PLSD) test of Fisher. Geometric mean regressions were performed on Keeling plots data. Intercepts and slope with their respective CI are given.

Results

Isotopic and chemical composition of soil and litter

Isotopic and chemical composition of soil and litters are summarized in Table 1. $\delta^{13}\text{C}$ of soil organic matter in the 15cm-depth soil cores was less negative (-26.42‰) than those of control litter (-29.92‰) or fine roots (-28.66‰). Depleted litter had a higher N level than did the control litter while the C content is similar for both control and depleted litter. Isotopic composition of depleted litter was lower than those of control litter during the whole experiment time (Table 1 and Fig. 3). The $\delta^{13}\text{C}$ values of depleted litter increased significantly (+4.22‰, $p=0.03$, Fig. 3) while the slight increase of $\delta^{13}\text{C}$ of the control litter was not significant (+0.59‰) during the first year of decay.

Keeling plots, isotopic signature of respired CO_2 and contribution of litter to soil respiration

The $\delta^{13}\text{C}$ of respired CO_2 (i.e. δ_{D} and δ_{C} terms in Eq. [4]), as estimated from geometric mean regressions are presented in Table 2 with their CI. For each date, the intercepts values of depleted litter were more negative than those of control litter. The calculated belowground CO_2 isotopic composition (δ_{BG}) varied between -24.80‰ in March (DOY 85) and -19.54‰ in July (DOY 225, Table 2), being less negative than the $\delta^{13}\text{C}$ of roots and SOM components. Leaf litter contribution to total soil respiration (F_{L}/F) calculated from Eq. [4] showed a seasonal evolution (Fig. 4). It increased from 2.8% in early spring to about 11.4% in mid summer, and decreased to 4.2% at the end of experiment. Between December 2001 and December 2002, cumulated F and F_{L} reached 0.98 $\text{kg}_\text{C} \text{ m}^{-2}$ and 0.08 $\text{kg}_\text{C} \text{ m}^{-2}$ respectively, leading to an annual F_{L}/F ratio of 8%.

Uncertainties and sensitivity analyses

Errors of spectrometer measurements are $\pm 0.1\%$ but the intercepts of the keeling plots had confidence intervals that reached 2.91‰. The limits of 95% confidence interval of computed δ_{BG} ranged between $\pm 0.29\%$ (DOY 85) and $\pm 0.75\%$ (DOY 162, Table 2). The limits of confidence interval of the F_{L}/F ratio varied from $\pm 2.36\%$ (DOY 225) to $\pm 5.24\%$ (DOY 162, Fig. 4).

It was assumed in Eq. [5] that no fractionation occurs during litter decomposition. A sensitivity analysis was performed to assess whether positive or negative fractionation ranging from -10‰ to +10‰ for both treatments would affect the computed F_{L}/F ratio. The F_{L}/F ratio was almost insensitive to the tested range of isotopic fractionation occurring during litter decomposition (Fig. 5a) assuming that the fractionation was similar for control and depleted litters. Since we did not measure litter mass loss for control litter and assumed that the F_{L}/F ratio were similar for both litter (Eq. [4]), we calculated the potential error that we would have made by considering an identical ratio while it was not. In the other hand, assuming a lower F_{L}/F ratio (up to 30%) in plots covered with control litter than in plots covered with depleted litter (because of a higher C/N) only marginally decreased δ_{BG} (0.2‰ more negative) but it led to lower F_{L}/F ratios (Fig. 5b).

Carbon loss during litter decomposition

Leaf litter mass loss averaged 62% of initial litter dry mass during the experiment for depleted

litter. By considering a carbon content of 46% corresponding to the C content of the depleted litter (Table 1) and the initial amount of $0.35 \text{ kg}_{\text{DM}} \text{ m}^{-2}$, the total leaf litter C loss reached $0.10 \text{ kg}_{\text{C}} \text{ m}^{-2}$.

Discussion

Isotopic composition of respired CO₂

On the control plot, the Keeling plot intercepts represent the mixture of both autotrophic and heterotrophic respiration. Our values of $\delta^{13}\text{C}$ for respired soil CO₂ (-24.95‰ to -20.79‰ under control treatment) were in a similar range of values than those reported for other forest ecosystems. Buchmann *et al.* (1998) reported an average $\delta^{13}\text{C}$ value for soil respired CO₂ of -24.55‰ for three *A. amabilis* stands that remained almost constant during the growing season. Similar values at the lower limit of our range were also observed in a Scots pine stand (ranged from -25.81‰ to -24.58‰, Ekblad & Högberg, 2000) and in a *Picea marianna* stand (-24.45‰ in summer and -23.56‰ in autumn, Flanagan *et al.*, 1999). However, wider ranges of $\delta^{13}\text{C}$ value for soil respired CO₂ were also reported for temperate coniferous forest in Western America (-27‰ to -20‰, Fessenden & Ehleringer, 2003) or in a boreal Scots pine stand in Sweden (-27‰ to -22‰, Ekblad & Högberg, 2001). In these two latter studies, $\delta^{13}\text{C}$ value for soil respired CO₂ values were higher than expected when considering bulk tissue $\delta^{13}\text{C}$ or SOM $\delta^{13}\text{C}$. When comparing with isotopic composition of roots (-28.66‰), litter (-30.32‰) or soil carbon (-26.42‰), soil respired CO₂ also exhibited rather high values of $\delta^{13}\text{C}$ in our study, in good agreement with results reported above. Keeling plots made at the ecosystem scale were performed from air sampling at different heights between 0.2 m and 22 m at the Hesse forest during the summer 2001 and 2002. The results suggest that ecosystem respiration was less depleted than soil respiration, ranging from -30.5‰ to -25.9‰ (Granier & Hemming, unpublished data). Similar difference between ecosystem and soil respiration have already been reported (Buchmann *et al.*, 1998; Bowling *et al.*, 2003; Fessenden & Ehleringer, 2003; Still *et al.*, 2003).

Assuming a similar F_L/F ratio between both control and depleted litter despite their differences in composition, $\delta^{13}\text{C}$ of belowground CO₂ (δ_{BG}), which includes CO₂ produced by root and SOM decomposition, can be estimated. It ranged between -24.80‰ and -19.54‰ and once again, it is 2‰ to 9‰ higher than root and SOM $\delta^{13}\text{C}$, violating the mass conservation postulate. As suggested by Bowling *et al.* (2003) the high $\delta^{13}\text{C}$ of respired CO₂ might be an artifact even if fractionation during respiration or heterogeneity in plant and SOM composition cannot be excluded (Duranceau *et al.*, 1999; Andrews *et al.*, 2000; Ghashghaie *et al.*, 2001; Damesin & Lelarge, 2003). Whatever the cause, it highlighted the potential bias in source partitioning that could occur when using $\delta^{13}\text{C}$ of root and SOM as end member of mixing models rather than the $\delta^{13}\text{C}$ of belowground CO₂ evolved from these sources. In addition, using a single end-member ($\delta^{13}\text{C}$ of belowground CO₂) rather than two (^{13}C of root and SOM) discards the delicate problem of averaging the isotopic signature of roots and SOM as sources, and allows to account for the seasonal variation of isotopic signature of respiration (see below).

Seasonal variations of $\delta^{13}\text{C}$ of litter and belowground CO_2 and of litter contribution to soil respiration

Seasonal increase in $\delta^{13}\text{C}$ of litter is much more pronounced for depleted than for control litter. A seasonal increase is expected if microbial reactions preferentially used lighter carbon substrates (Ehleringer *et al.* 2000), but this should have led to a similar effect on both control and depleted litter. A strong increase in $\delta^{13}\text{C}$ of depleted litter and a slight increase in $\delta^{13}\text{C}$ of control litter may highlight the mixing of litter carbon with bacterial or fungal carbon as soon as leaf litter is decomposing. Such drifts in $\delta^{13}\text{C}$ of depleted and control litters would be expected if the microbial source was 3-4‰ heavier than the control litter, i.e. if the microbial source has an isotopic composition of about -26‰. Indeed, both bacterial and fungi are thought to be enriched in ^{13}C values relative to their substrate (Gleixner *et al.*, 1993; Ehleringer *et al.* 2000), and a similarly high $\delta^{13}\text{C}$ values (-26‰) has been recorded for fungal mycelium in this beech stand (F. Le Tacon, INRA Nancy, pers. comm.).

Seasonal variation of $\delta^{13}\text{C}$ of below ground CO_2 (δ_{BG} , $\pm 5\text{‰}$) should reflect changes in the relative contribution of the different sources (i.e. root and microbial respiration). In the case of roots, it was well established that autotrophic respiration is directly linked to photosynthesis rate (Craine *et al.*, 1999; Högberg *et al.*, 2001; Kuzyakov & Cheng, 2001; Cardon *et al.*, 2002). The increase in δ_{BG} during summer when the contribution of root respiration to soil CO_2 efflux is the highest (Epron *et al.* 2001) suggest that root respiration produced heavier CO_2 than microbial respiration. In addition, short-term variations of ecosystems or soil respiration $\delta^{13}\text{C}$ could be attributed to a change of discrimination in recent photosynthetical products (Ekblad & Högberg, 2001; Bowling *et al.*, 2002; Fessenden & Ehleringer, 2003; Scartazza *et al.*, 2004). Decreased stomatal conductance during summer would increase $\delta^{13}\text{C}$ of photosynthetate and it could account for the observed seasonal change in δ_{BG} (Ekblad & Högberg, 2001; Bowling *et al.*, 2002). Our suggestion that root-evolved CO_2 is heavier than SOM-evolved CO_2 seems in contradiction with lighter carbon in root than in SOM (Table 1). However, heavier carbon in respired CO_2 compared to bulk tissue has already been reported for beech stem and it was thought to reflect difference in isotopic signature between respired substrates and bulk tissue. (Damesin & Lelarge, 2003). Seasonal changes of $\delta^{13}\text{C}$ of SOM-derived CO_2 should also account for seasonal variation in δ_{BG} , especially if the microbial community composition changes with soil temperature (Andrews *et al.* 2000). Once again, our results highlighted the potential bias in source partitioning that could occur when using $\delta^{13}\text{C}$ of root and SOM as end member of mixing models rather than the $\delta^{13}\text{C}$ of belowground CO_2 evolved from these sources.

It has previously been shown that root contribution to total soil respiration reached maximum values in summer (Boone *et al.* 1998 Epron *et al.* 2001). Our results suggest a similar pattern for litter contribution to soil respiration. High rates of litter decomposition are thought to occur following rain events after drying cycles during summer (Hanson *et al.*, 2003) and it would lead to peaks in microbial respiration in the litter layer. With our design we were not able to measure this fine scale temporal variability and this could have resulted in underestimation of the mean litter contribution to soil respiration. However summer 2002 was rather wet and peaks of respiration following the rewetting of dry litter were therefore probably limited.

Leaf litter contribution to total soil CO_2 efflux

Few studies have been dedicated to litter respiration and its contribution to total soil CO_2

efflux. The contribution of litter and humus layer to soil respiration, as estimated from decomposition data, ranged between 10% and 20% on an annual basis in a *Pinus elliotti* plantation (Ewel *et al.*, 1987). In other experiment, litter manipulation was used to estimate the contribution of litter to soil respiration: 37% of total soil CO₂ efflux derived from the litter layer, but only 10% was from annual litter in a mixed deciduous forest (Massachusetts, USA, Bowden *et al.*, 1993). Using the same approach, Maier & Kress (2000) estimated that 10% of CO₂ produced by soil was generated by leaf litter decomposition in a *Pinus taeda* plantation. Upscaling litter specific respiration rates from *ex situ* incubations, Hanson *et al.* (2003) calculated a contribution of litter and forest organic horizons that averaged 23% of soil CO₂ efflux in an oak forest while Edwards & Harris (1977) reported a lower contribution (i.e. 10%) in a *Liriodendron* forest. Quantitative comparisons between studies are difficult because the organic layer can be very different, with an O_H and O_F layer more or less developed. O_F and O_H layers are insignificant in our site and there is only the O_L layer that is mainly composed of fresh leaf litter. Therefore, the contribution of fresh leaf litter decomposition to soil respiration accounted for most of the contribution of the organic layer in Hesse. It ranged from 2.8% to 11.4% with an annual value of 8%. This rather low contribution of fresh litter decomposition to soil respiration is consistent with a major contribution of root respiration to soil CO₂ efflux in this beech forest (Epron *et al.* 1999b).

The annual soil CO₂ efflux estimated from the seasonal variation of soil temperature and soil water content using model parameters derived from the 2001 data set (Epron *et al.*, 2004b) was 0.98 kg_C m⁻² y⁻¹. The contribution of fresh litter decomposition to soil respiration (8%) accounted for 0.08 kg_C m⁻² y⁻¹, i.e. about 80% of total C loss from fresh litter. This ratio is higher than the one assumed for carbon flow from plant residues in the CENTURY model (Parton *et al.* 1987), but similar to the one used in the Rothamsted turnover model (Jenkinson, 1990). The other fraction of carbon loss during leaf litter decomposition that is assumed to have entered the SOM pool, i.e. 20%, represents only 0.02 kg_C m⁻².

By scaling up litter and soil layer laboratory incubation, it was recently calculated that fresh litter accounted for about 20-30% of heterotrophic soil respiration in European beech forests covered by mull type humus (T. Persson, Univ. of Uppsala, per. comm.). Here, assuming a 60:40 partitioning between autotrophic and heterotrophic components (Epron *et al.*, 1999b), fresh litter decomposition accounts for about 8% of annual soil respiration and 20% of the heterotrophic components of soil respiration.

Conclusions

The contribution of leaf litter decomposition to total soil CO₂ efflux can be evaluated using ¹³C depleted litter despite some uncertainties with the isotopic signature of evolved CO₂. Our results suggest a seasonal variation in litter contribution to soil CO₂ efflux. On an annual basis, this contribution remains small when compared with the one of root respiration in a young beech forest exhibiting mull type humus. Our results also suggest that most of the carbon lost during leaf litter decomposition is lost as CO₂. On an annual basis, only 20% of carbon lost during leaf litter decomposition will be retained in soil organic matter.

Acknowledgment

We thank M. F. Willm and B. Clerc for their friendly help in field measurements and technical assistance. We are grateful to M. B. Zeller for helpful discussions concerning soils, litter dynamics and sample preparations. This work was supported by the European project CarboEuroflux (EVK2-CT-1999-00032). D. Hemming (Met Office, UK), F. Le Tacon and T. Persson are warmly thanked for their data concerning ecosystem $\delta^{13}\text{C}$ values, fungi $\delta^{13}\text{C}$ values and the contribution of litter to microbial soil respiration, respectively. We also thank the two anonymous reviewers for their helpful comments on a first submission.

References

- Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos*, 79, 439-449.
- Andrews JA, Matamala R, Westrover KM, Schlesinger WH (2000) Temperature effects on the diversity of soil heterotrophs and the $\delta^{13}\text{C}$ of soil respired CO_2 . *Soil Biology and Biochemistry*, 32, 699-706.
- Balesdent J (1991) Estimation du renouvellement du carbone des sols par mesure isotopique ^{13}C . Précision, risque de biais. *Cahiers ORSTOM, série Pédologique*, XXVI, 315-326.
- Berg B (2000) Litter decomposition and organic matter turnover in northern forest soils. *Forest Ecology and Management*, 133, 13-22.
- Boone RD, Nadelhoffer KJ, Canary JD, Kaye JP (1998) Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature*, 396, 570-572.
- Bowden RD, Nadelhoffer KJ, Boone RD, Melillo JM, Garrison JB (1993) Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. *Canadian Journal of Forestry Research*, 23, 1402-1407.
- Bowling DR, McDowell NG, Bond BJ, Law BE, Ehleringer JR (2002) ^{13}C content of ecosystem respiration is linked to precipitation and vapour pressure deficit. *Oecologia*, 131, 113-124.
- Bowling DR, Pataki DE, Ehleringer JR (2003) Critical evaluation of micrometeorological methods for measuring ecosystem-atmosphere isotopic exchange of CO_2 . *Agricultural and Forest Meteorology*, 116, 159-179.
- Buchmann N (2000) Biotic and abiotic factors controlling soil respiration rates in *Picea abies* stands. *Soil Biology and Biochemistry*, 32, 1625-1635.
- Buchmann N, Hinckley TM, Ehleringer JM (1998) Carbon isotope dynamics in *Abies amabilis* stands in the Cascades. *Canadian Journal of Forest Research* 28, 808-819.
- Cardon ZG, Czaja AD, Funk JL, Vitt PL (2002) Periodic carbon flushing to roots of *Quercus rubra* saplings affects soil respiration and rhizosphere microbial biomass. *Oecologia* (2002), 133, 215-223.
- Cheng W (1996) Measurement of rhizosphere respiration and organic matter decomposition using natural ^{13}C . *Plant and Soil*, 183, 263-268.
- Craine JM, Wedin DA, Chapin III FS (1999) Predominance of ecophysiological controls on soil CO_2 flux in a Minnesota grassland. *Plant and Soil*, 207, 77-86.
- Damesin C, Lelarge L (2003) Carbon isotope composition of current-year shoots from *Fagus sylvatica* in relation to growth, respiration and use of reserves. *Plant, Cell and Environment*, 26, 207-219.

-
- Davidson EA, Belk E, Boone RD (1998) Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biology*, 4, 217-227.
- Duranceau M, Ghashghaie J, Badeck F, Deléens E, Cornic G (1999) $\delta^{13}\text{C}$ of CO_2 respired in the dark in relation to $\delta^{13}\text{C}$ of leaf carbohydrates in *Phaseolus vulgaris* L. under progressive drought. *Plant, Cell and Environment*, 22, 515-523.
- Edwards NT, Harris WF (1977) Carbon cycling in a mixed deciduous forest floor. *Ecology*, 58, 431-437.
- Ehleringer JR, Buchmann N, Flanagan LB (2000) Carbon isotope ratios in belowground carbon cycle processes. *Ecological Applications*, 10, 412-422.
- Ekblad A, Högberg P (2000) Analysis of ^{13}C of CO_2 distinguishes between microbial respiration of added C_4 -sucrose and other soil respiration in a C_3 -ecosystem. *Plant and Soil*, 219, 197-209.
- Ekblad A, Högberg P (2001) Natural abundance of ^{13}C in CO_2 respired from forest soils reveals speed of link between tree photosynthesis and root respiration. *Oecologia*, 127, 305-308.
- Epron D, Farque L, Lucot E, Badot PM (1999a) Soil CO_2 efflux in a beech forest: dependence on soil temperature and soil water content. *Annals of Forest Sciences*, 56, 221-226.
- Epron D, Farque L, Lucot E, Badot PM (1999b) Soil CO_2 efflux in a beech forest: the contribution of root respiration. *Annals of Forest Sciences*, 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 Physiology*, 21, 145-152.
- Epron D, Nouvellon Y, Roupsard O et al. (2004a) Spatial and temporal variations of soil respiration in a Eucalyptus plantation in Congo. *Forest Ecology and Management*, 202, 149-160.
- Epron D, Ngao J, Granier A. (2004b) Interannual variation of soil respiration in a beech forest ecosystem over a six-year study. *Annals of Forest Sciences*, 61, 499-505.
- Ewel KC, Cropper WP, Gholz HL (1987) Soil CO_2 evolution in Florida slash pine plantations. I. Changes through time. *Canadian Journal of Forest Research*, 17, 325-329.
- Fang C, Moncrieff JB, Gholz HL, Clark KL (1998) Soil CO_2 efflux and its spatial variation in a Florida slash pine plantation. *Plant and Soil*, 205, 135-146.
- Fessenden JE, Ehleringer JR (2003) Temporal variation in $\delta^{13}\text{C}$ of ecosystem respiration in the Pacific Northwest: links to moisture stress. *Oecologia*, 136, 129-136.
- Flanagan LB, Kubien DS, Ehleringer JR (1999) Spatial and temporal variation in the carbon and oxygen stable isotope ratio of respired CO_2 in a boreal forest ecosystem. *Tellus*, 51B, 367-384.
- Ghashghaie J, Duranceau M, Badeck F, Cornic G, Adeline MT, Deléens E (2001) $\delta^{13}\text{C}$ of CO_2 respired in the dark in relation to $\delta^{13}\text{C}$ of leaf metabolites: comparison between *Nicotiana sylvestris* and *Helianthus annuus* under drought. *Plant, Cell and Environment*, 24, 505-515.
- Gleixner G, Danier HJ, Werner RA, Schmidt HL (1993) Correlations between the C-^{13} content of primary and secondary plant-products in different cell compartments and that in decomposing basidiomycetes. *Plant Physiology*, 102, 1287-1290.
- Granier A, Ceschia E, Damesin C et al. (2000) The carbon balance of a young Beech forest. *Functional Ecology*, 14, 312-325.

Hanson PJ, O'Neill EG, Chambers MLS, Riggs JS, Joslin JD, Wolfe MH (2003) 10. Soil respiration and litter decomposition. In: North America temperate deciduous forest responses to changing precipitation regimes (eds Hanson PJ, Wullschleger SD), pp. 472. Springer, New York.

Hanson PJ, Edwards NT, Garten CT, Andrews JA (2000) Separating root and soil microbial contribution to soil respiration: A review of methods and observations. *Biogeochemistry*, 48, 115-146.

Hanson PJ, Wullschleger SD, Bohlman SA, Todd DE (1993) Seasonal and topographic patterns of forest floor CO₂ efflux from an upland oak forest. *Tree Physiology*, 13, 1-15.

Högberg P, Nordgren A, Buchmann N et al. (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature*, 411, 789-792.

Janssens IA, Kowalski AS, Ceulemans R (2001) Forest floor CO₂ fluxes estimated by eddy covariance and chamber-based model. *Agricultural and Forest Meteorology*, 106, 61-69.

Jenkinson DS (1990) The turnover of organic carbon and nitrogen in soil. *Phil Trans. R. Soc Philosophical Transaction of the. Royal. Society of London: Biological Sciences*, 329, 361-368.

Keeling CD (1958) The concentration and isotopic abundances of atmospheric carbon dioxide in rural areas. *Geochimica and Cosmochimica Acta*, 13, 322-334.

Kuzyakov Y, Cheng W (2001) Photosynthesis controls of rhizosphere respiration and organic matter decomposition. *Soil Biology and Biochemistry*, 33, 1915-1925.

Lavigne MB, Foster RJ, Goodine G (2004) Seasonal and annual changes in soil respiration in relation to soil temperature, water potential and trenching. *Tree Physiology*, 24, 415-424.

Longdoz B, Yernaux M, Aubinet M (2000) Soil CO₂ efflux measurements in a mixed forest: impact of chamber disturbances, spatial variability and seasonal evolution. *Global Change Biology*, 6, 907-917.

Maier CA, Kress LW (2000) Soil CO₂ evolution and root respiration in 11 year-old loblolly pine (*Pinus taeda*) plantations as affected by moisture and nutrient availability. *Canadian Journal of Forest Research*, 30, 347-359.

Miller JB, Tans PP (2003) Calculating isotopic fractionation from atmospheric measurements at various scales. *Tellus*, 55B, 207-214.

Nakane K, Yamamoto M, Tsubota H (1983) Estimation of root respiration rate in a mature forest ecosystem. *Japanese Journal of Ecology*, 33, 397-408.

Norby RJ, Cotrufo MF, Ineson P, O'Neill EG, Canadell JG (2001) Elevated CO₂, litter chemistry and decomposition: a synthesis. *Oecologia*, 127, 153-165.

Parton WJ, Schimel DS, Cole CV, Ojima DS (1987) Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal*, 51, 1173-1179.

Quentin C, Bigorre F, Bréda N, Granier A, Tessier D (2001) Etude des sols de la forêt de Hesse (Lorraine). Contribution à l'étude du bilan hydrique. *Etude et Gestion des sols*, 8(4), 215-229.

Rochette P, Flanagan LB, Gregorich EG (1999) Separating soil respiration into plant and soil components using analyses of the natural abundance of carbon-13. *Soil Science Society of America Journal*, 63, 1207-1213.

Scartazza A, Mata C, Matteucci G, Yakir D, Moscatello S, Brugnoli E (2004) Comparison of $\delta^{13}\text{C}$ of photosynthetic products and ecosystem respiratory CO₂ and their responses to seasonal climate variability. *Oecologia*, 140, 340-351.

Still CJ, Berry JA, Ribas-Carbo M, Helliker BR (2003) The contribution of C3 and C4 plants to the carbon cycle of a tallgrass prairie: an isotopic approach. *Oecologia*, 136, 347-359.

Swift MJ, Heal OW, Anderson JM (1979) *Decomposition in terrestrial ecosystems. Studies in ecology 5*, Blackwell Sciences Publishing, 372pp.

Material	$\delta^{13}\text{C}$ (‰)	C (%)	N (%)
Depleted litter	-46.40 (0.95)	46.02 (0.16)	1.53 (0.09)
Control litter	-29.92 (0.20)	46.22 (0.12)	1.17 (0.02)
Fine roots (< 1 mm)	-28.66 (0.15)	37.88 (0.68)	0.73 (0.03)
Sieved soil (0-15 cm)	-26.42 (0.12)	2.02 (0.15)	0.15 (0.01)

Table 1. Mean $\delta^{13}\text{C}$, C and N contents of litters (n=4), fine roots (n=5) and bulk soil (n=5) in May 2002. Standard errors are under brackets.

Day of Year	Depleted			Control			δ_{BG} \pm CI	
	δ_{D}	\pm CI	R^2	δ_{C}	\pm CI	R^2		
85	-25.50	1.81	0.88	-24.95	0.77	0.97	-24.80	0.29
137	-23.80	1.52	0.93	-22.74	0.99	0.89	-22.20	0.46
162	-24.70	2.91	0.71	-23.03	1.43	0.80	-22.18	0.75
225	-22.60	1.15	0.88	-20.77	2.45	0.91	-19.54	0.44
291	-22.74	0.97	0.95	-22.74	1.09	0.94	-22.32	0.44
316	-23.13	1.26	0.91	-22.49	1.28	0.91	-22.15	0.52

Table 2. The isotopic composition of respired CO_2 by soil covered with depleted litter (δ_{D}) or control litter (δ_{C}) was estimated as the Keeling plot intercept under the classical form: $\delta^{13}\text{C}_{\text{sample}} = \delta + a \cdot (1/[\text{CO}_2]_{\text{sample}})$ where the subscript "sample" refers to $\delta^{13}\text{C}$ and $[\text{CO}_2]$ of air samples respectively (n=12 to 16). 95% confidence intervals (\pm CI) of estimates and determination coefficient (R^2) were calculated from geometric mean regressions. $\delta^{13}\text{C}$ of belowground respired CO_2 (δ_{BG}) was calculated with Eq. [6]. For δ_{BG} , the CI values were calculated on the mean of 10000 values of δ_{BG} with randomly chosen values for each term of Eq.[6] assuming a normal distribution centered on their respective mean with their standard error.

Figures legends

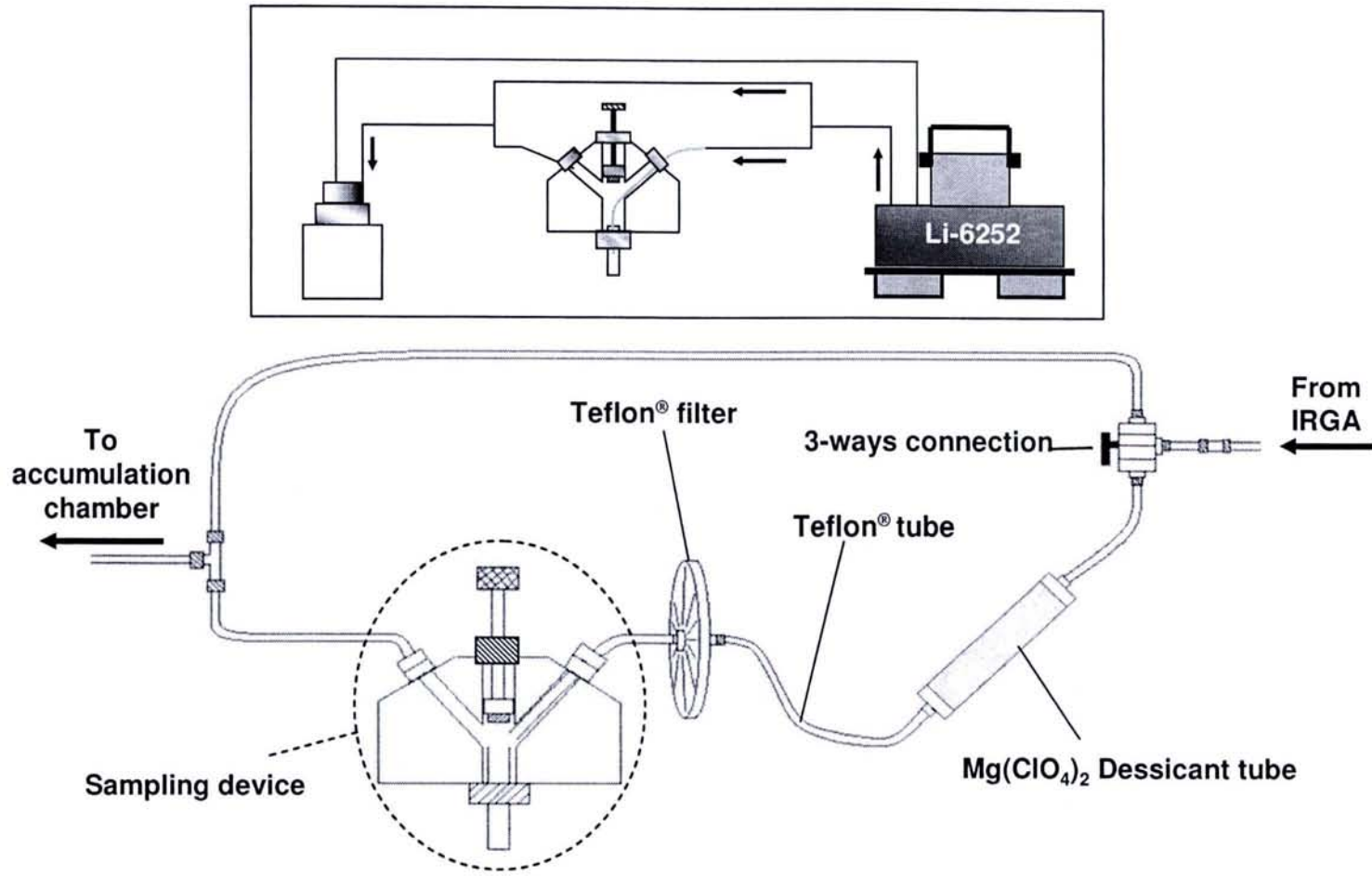
Fig. 1 Soil CO₂ sampling device. The Plexiglas body allows sampling air coming from the accumulation chamber inside a 10ml Exetainer glass-vial. Arrows indicate the flow direction through the whole system.

Fig. 2 A typical example of Keeling plot constructed by pooling all data from the control treatment in March 2002 (DOY 85). Regression equation is $\delta^{13}\text{C} = -24.95 + 0.0062 \cdot 1/[\text{CO}_2]$ ($R^2 = 0.97$, $p < 0.0001$, $n=15$).

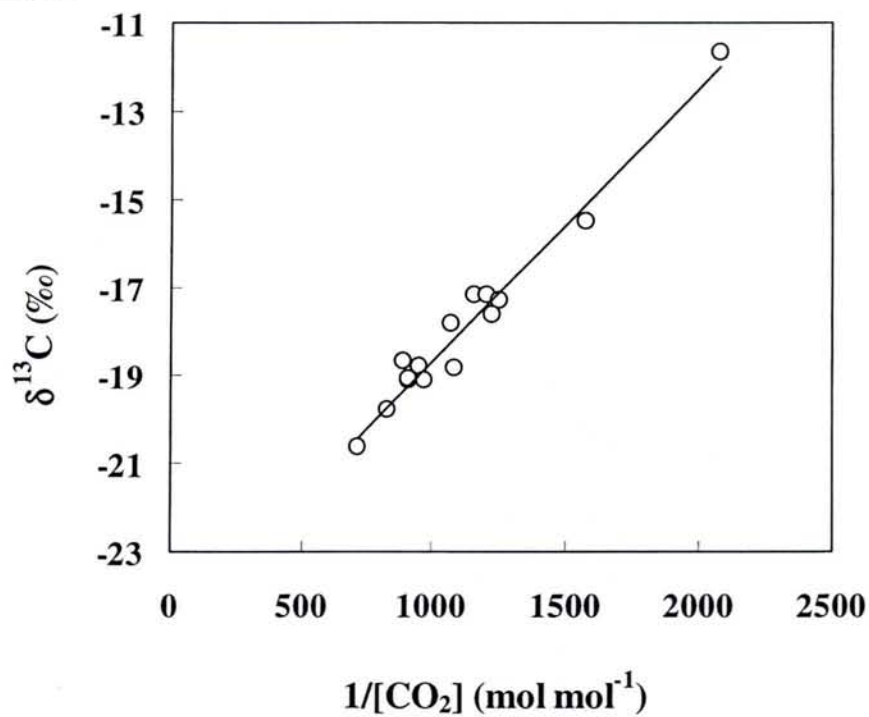
Fig. 3 Seasonal evolutions of the $\delta^{13}\text{C}$ of depleted (open circles) or control (closed circles) litter. Vertical bars represent standard errors ($n=4$). Values for day 0 indicated the initial state of litters.

Fig. 4 Seasonal evolution of leaf litter contribution to total soil CO₂ efflux (F_L/F ratio). Closed circles are the computed ratio from keeling plot intercepts. Open circles are the upper limits of the range that content 95% of 10000 F_L/F ratio values computed with randomly chosen values for δ_D and δ_C (Eq. [4]) assuming a normal distribution centered on their respective mean with their standard error.

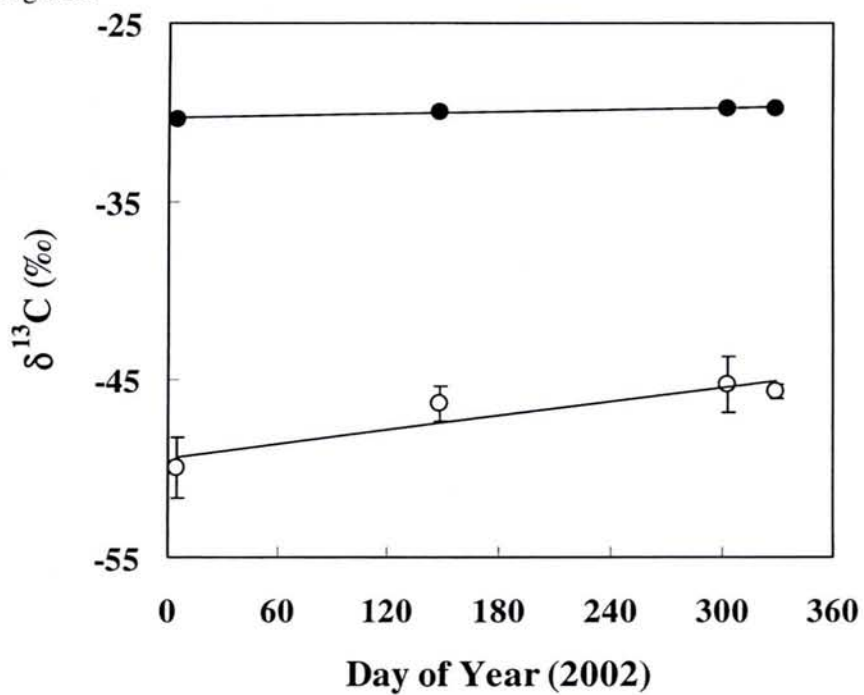
Fig. 5 Sensitivity tests on error in F_L/F ratio calculations. (a) a $\pm 10\text{‰}$ fractionation was introduced for litter decomposition. (b) A 0 to 30% lower F_L/F ratio for control litter than for depleted litter were introduced for accounting the difference in litter composition (lower C/N in control litter than in depleted litter).



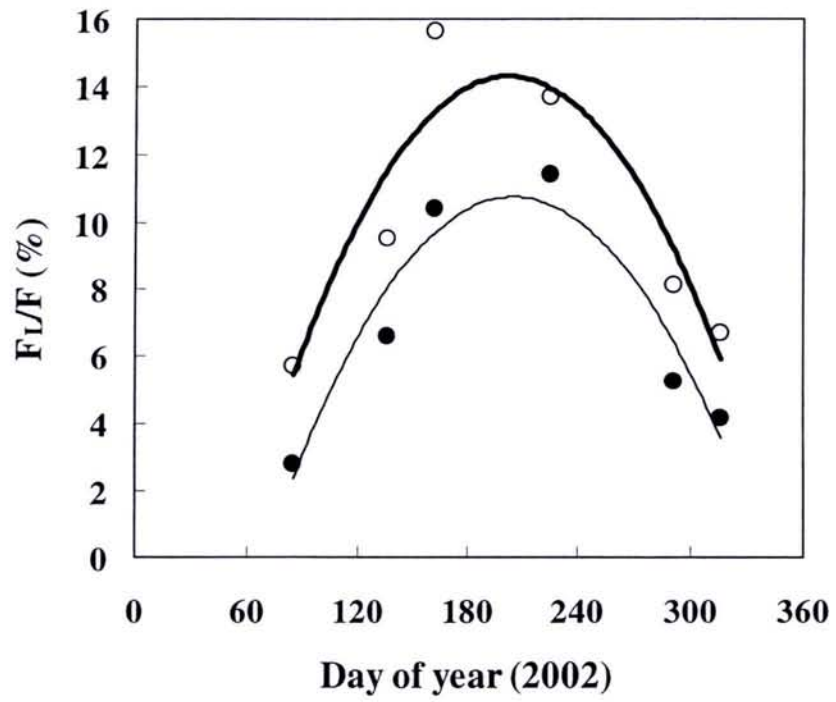
Ngao *et al.* Figure 2



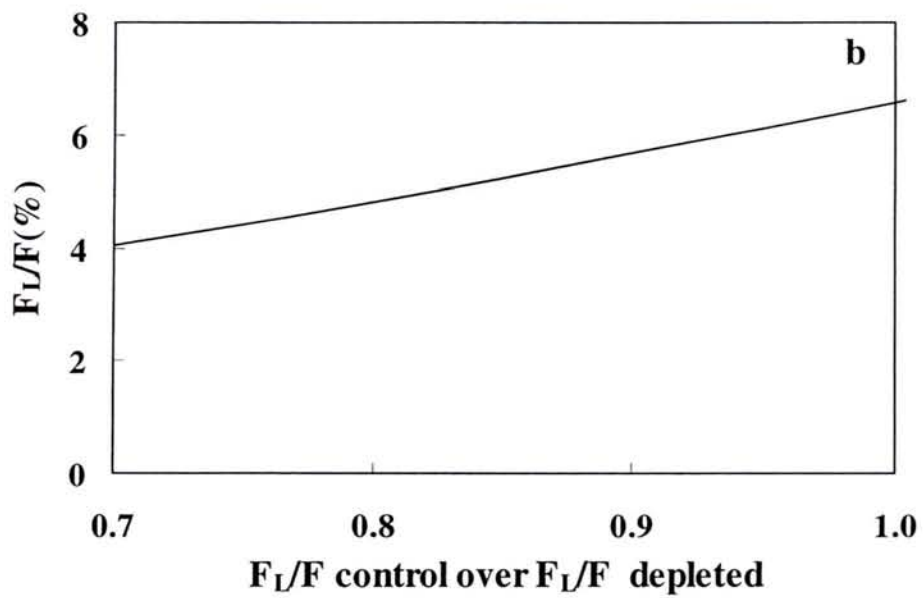
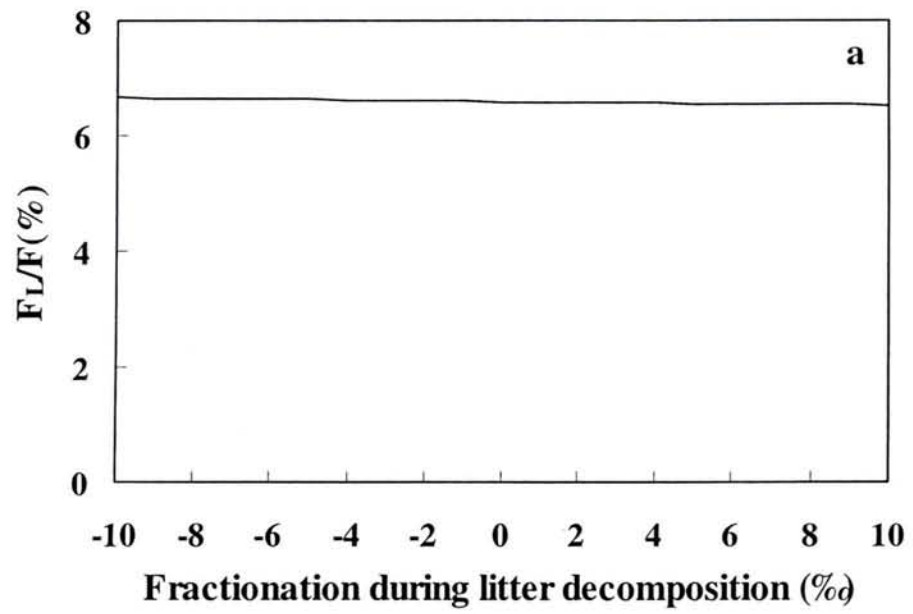
Ngao *et al.* Figure 3



Ngao *et al.* Figure 4



Ngao *et al.* Figure 5



**ARTICLE 3: Decomposition and CO₂ release of woody residues
from a young thinned beech (*Fagus sylvatica* L.) stand**

J. Ngao¹, M. Yernaux³, N. Le Goff², B. Longdoz¹, C. Nys⁴, M. Aubinet³, A. Granier^{1*}

¹ UMR Ecologie et Ecophysiologie Forestière, Centre INRA de Nancy, 54280 Champenoux, France

² UMR INRA-ENGREF LERFOB, Equipe Croissance et Production, Centre INRA de Nancy 54280 Champenoux, France

³ Unité de Physique des Biosystèmes, Faculté Universitaire des Sciences Agronomiques, B 5030 Gembloux, Belgium

⁴ Unité INRA Biogéochimie des Ecosystèmes Forestiers, Centre INRA de Nancy 54280 Champenoux, France

* Corresponding author:

André Granier (agranier@nancy.inra.fr)

Fax: (+33) 383 394 069

Phone: (+33) 383 394 038

Running Title: Decomposition and respiration of woody debris

Abstract

Woody debris (WD) is often neglected in ecosystem carbon balance studies. We aimed at establishing the dynamics of small WD decay in a 35-year old European beech stand in Hesse Forest. We measured the mass and density variation during a 2-year decomposition field experiment. Total mass loss after 2 years averaged 30%, and decay evolution fitted well with the negative exponential model. Decay constant k was determined more accurately with mass loss data ($k = 0.21 \text{ y}^{-1}$) than with density data. During a classical thinning, an allometric relationship was established in order to relate total woody debris mass with diameter at breast height. Relationship was applied to total thinned trees and total woody debris at the stand level has been determined. We applied results of the decomposition experiment to thinning woody debris for estimating total C loss ($0.7 \text{ Mg}_C \text{ ha}^{-1} \text{ y}^{-1}$) and annual CO_2 efflux ($0.6 \text{ Mg}_C \text{ ha}^{-1} \text{ y}^{-1}$) that represented 8% of total ecosystem respiration. We assessed the response of decomposing WD CO_2 efflux (WD_R) to temperature. We addressed the opportunity of scaling up temperature response of WD_R from short-term incubations to field decomposition. Annual CO_2 efflux estimated from WD CO_2 efflux measurements averaged $1.6 \text{ Mg}_C \text{ ha}^{-1} \text{ y}^{-1}$. These results allowed quantifying a significant component of total ecosystem respiration. The discrepancy between the CO_2 effluxes estimated by the decomposition experiment and the direct CO_2 measurements highlighted the necessary of improving field CO_2 efflux measurement methods in order to improve carbon budget in managed ecosystems.

Introduction

Plant residues decomposition is a key process participating to nutrient cycling, which influence soil fertility and forest productivity (Swift *et al.*, 1979; Berg, 2000), and to carbon (C) cycle. Indeed C can be stored in the microbial biomass or in more or less recalcitrant pools of soil organic matter (SOM), or it can be mineralized and released as CO₂. Thus the contribution of organic matter decomposition to total soil CO₂ efflux (also called heterotrophic respiration) is recently investigated for improving ecosystem C budgets and for modeling responses of ecosystems to global changes (Epron *et al.*, 1999; Hanson *et al.*, 2000; Bond-Lamberty *et al.*, 2004; Lavigne *et al.*, 2004). But large uncertainties still exist to predict the long-term evolution of forest ecosystem C balance and pools, especially when considering the hypothetical increase of ecosystem respiration with global temperature increase (Grace and Rayment, 2000).

Leaf litter decomposition has been widely investigated since decades. Aboveground woody debris (WD) is an important, but often neglected, compartment of the terrestrial ecosystems, by influencing nutrient cycling, soil carbon (C) dynamic and providing habitat for a large number of species communities (Harmon *et al.*, 1986; Jabin *et al.*, 2004). Decomposition of small WD was poorly investigated (Scheu and Schauermaun, 1994; McColl and Powers, 2003) while decomposition of coarse WD was more investigated in relation to substrate quality (Idol *et al.*, 2001) and nutrient release (Foster and Lang, 1982; Torres, 1994; Brown *et al.*, 1995; Ganjegunte *et al.*, 2004). However, in managed forest, small WD originating from thinning or clear-cut may account for a large C input (Sollins, 1982) as compared with leaf litterfall. Such amount of assumed slow-decomposing material would represent a potential C source, but a better understanding of decomposition dynamic is required in order to improve ecosystem C budgets at medium term time step (Paul *et al.*, 2003). Especially, estimating CO₂ production of decomposing WD is important for quantifying the C lost as CO₂ during decay or it can be also used as indicator of actual microbial activity (Mackensen and Bauhus, 2003); but studies still remain limited (Boddy, 1983; Chen *et al.*, 2000; Chambers *et al.*, 2001; Wang *et al.*, 2002, Bond-Lamberty *et al.*, 2003), in particular in temperate forests.

Dynamics of WD decomposition is driven by several factors such as seasonal soil temperature and moisture patterns, and substrate quality, including lignin, nitrogen or phenol contents (Swift *et al.*, 1979; Aerts, 1997; Berg, 2000; Norby *et al.*, 2001). WD density is often measured and provides a direct estimation of the decay rate. Density would furthermore influence O₂ diffusivity (Hicks and Harmon, 2002), which is an important regulator of physiological processes involved in decomposition and CO₂ production. WD CO₂ efflux (WD_R) is largely controlled by environmental factors as temperature and moisture conditions (Chen *et al.*, 2000; Wang *et al.* 2002). Currently, laboratory measurements constitute the most appropriate approach for measuring accurately WD_R; static methods of CO₂ efflux measurement as alkali traps were shown to underestimate the actual CO₂ efflux (Prongacic *et al.*, 1997; Janssens *et al.*, 2000). Only few studies focused on temperature dependence of WD respiration (either air, soil or wood temperature), which have been shown to be frequently expressed as a Q₁₀-type function and to vary with soil water content (Boddy, 1983; Chen *et al.*, 2000; Wang *et al.*, 2002). But under temperate climate, temperature and water content would be consider as confounded factors (Davidson *et al.*, 1998), while seasonal variations of WD volumetric water content would not be as pronounced in field conditions than for soil or leaf litter (Fraver *et al.*, 2002).

In the Hesse forest (Northeastern of France), which is included in the CarboEurope IP flux-monitoring network (Granier *et al.*, 2000), European beech (*Fagus sylvatica* L.) leaf

litterfall averaged $1.6 \text{ Mg}_C \text{ ha}^{-1} \text{ y}^{-1}$ (Ngao *et al.*, 2005). A previous study determined that branch production (which is a large proportion of WD) in a young thinned stand accounted for about $10 \text{ Mg}_C \text{ ha}^{-1} \text{ y}^{-1}$ (Bouriaud, unpublished data), which is a significant C pool. In this study we aimed at establishing the dynamics of small WD decay in a 35-year old beech stand in Hesse Forest. We measured the mass and density variation during a 2-year decomposition field experiment. We assessed the response of decomposing WD CO_2 efflux to temperature and applied a temperature-based empirical model in order to estimate the fraction loss as CO_2 during the WD decomposition. Thus we addressed the opportunity of scaling up temperature response of WD_R from short-term incubations to field decomposition.

Material and Methods

Site description

The study was conducted in the CarboEurope site of Hesse (Northeast of France, $48^\circ 40' 27'' \text{N}$, $7^\circ 03' 53'' \text{E}$, 305 m elevation). The site is located in the middle of a homogenous 65 ha sapling of 35-year-old European beeches (90% of *Fagus sylvatica* L.). Understory vegetation is sparse. Table I gives main characteristics for 2002, 2003 and 2004. In 2003 a severe drought occurred with exceptionally high midsummer temperature. Soil type is classified as stagnic luvisol (FAO classification) covered by an oligo-mull humus type (almost no O_F and no O_H layers below the O_L layer), highlighting a high biological activity. It is an acidic soil ($\text{pH}_{\text{H}_2\text{O}}$ and pH_{KCl} reaching 4.5 and 3.8 for the 0-10 cm layer, respectively) that does not contain carbonate (Quentin *et al.*, 2001). Air temperature above the stand (T_{Air}), as other meteorological variables is continuously monitored since 1996 with platinum (Pt100) probes (Granier *et al.*, 2000). Data were acquired every 10 s and 30-min averages were stored (Model CR7 datalogger, Campbell Scientific, Courtaboeuf, France). Regular thinning occurred every 5 years, removing ca. 25% of stand basal area. The last one occurred during winter 1999-2000.

Experimental thinning and WD decomposition experiment

Decomposition experiment was conducted using faggots that were assumed to constitute and to simulate the remaining WD after a classical thinning (woody material including trunks, branches and twigs, all diameters < 7 cm). Such material has usually not commercial value and left on the ground in large piles. For this purpose, 70 beech trees were randomly chosen in the close surrounding (similar soil, litter and LAI environment) of the study plot and cut in February 2003. The diameter at breast height (DBH) of chosen trees were ranging between 3.1 cm and 7.9 cm. Branches, twigs and trunks were separated and cut into 75 cm-long segments (Brown and *al.*, 1996). Sections of trunks that had a diameter higher than 7 cm were excluded. Faggots (40 cm diameter x 75 cm length) were constructed by pooling several fresh logs of ca. 6 kg. Each faggot was weighted for initial fresh mass determination and numbered. During the faggot production process, 24 faggots were randomly chosen and dried at 65°C until constant weight for initial dry mass determination, as resumed by:

$$\text{DM} = 0.54 \text{ FM} + 226 \quad (1)$$

with DM and FM the dry and fresh mass of faggots, respectively ($p < 0.0001$; $R^2 = 0.97$). Then, 153 faggots were randomly placed on the ground within a 200 m^2 -area (homogenous in soil properties, LAI, local topography, microclimate, species composition) inside the study plot and were safe from wildlife and perturbations. All former WD and woody litter on forest floor were preliminary removed before. For avoiding interactions with log position and log

surface in contact with soil, each log was carefully set the most horizontally as possible in contact with soil-litter surface. From February 2003 to December 2004, a destructive sampling was performed. Every 1-2 month, 7 randomly chosen faggots were sampled, fresh weighted for gravimetric water content determination, and dried until constant weight. Volumetric water content (VWC) was calculated by multiplying gravimetric water content by density (see below). Remaining mass was determined by reporting current dry mass to initial dry mass calculated with equation (1). Decomposition constant rate (k) was calculated following a negative exponential model (Olsen, 1963) fitted on data:

$$M_t = M_0 e^{-kt} \quad (2)$$

where M_0 and M_t are the mean initial dry mass (kg_{DM}) and the mean remaining mass at a given time, t (year), respectively.

Laboratory analyses

For chemical analyses, we separated fine branches and twigs from larger logs. C and N contents were determined with a NCS2500 elemental analyzer (CE Instrument ThermoQuest, Italy) on disks (5 cm thick) taken in the middle of each log. Assuming that each log decomposed similarly, we pooled all disks of a same faggot into a composite sample for C and N analysis.

Density of individual log was determined from sections of logs (10 cm length) by measuring their volume with an Archimedes's principle-based method. A specific scale that allows measurements by suspension was tarred with a dry sample attached with a heavy mass (HM). The sample and HM were totally immersed in water and weighted, the HM insuring stability of measurement. The weight of immersed sample corresponded to water weight moved by immersion, and converted to volume assuming the volumic mass of water (1 kg dm^{-3}). Density was calculated by reporting the section's volume by his dry mass (kg dm^{-3}) and by the volumic mass of water. For density, C and N contents determination, bark was not removed. For assessing the reliability of the method, we compared measurements of volume of wood cylinders either by the immersion method or by direct geometric measurements for volume with an electronic calliper rule (precision $\pm 0.1\text{mm}$), respectively..

Woody debris CO₂ efflux measurements

WD_R measurements were performed on WD samples of 3 decay classes (DC): WD after one month of decomposition (DC I), WD after 23 months of decomposition (DC II), and WD after 3 years of decomposition (DC III). DC I and DC II samples came from faggots of the decomposition experiment, while DC III sample were from the previous thinning. All samples were 10 cm length and were stored at 4°C at field water content. WD_R was measured with a dynamic closed system that consists of a chamber connected with an infrared gas analyzer (IRGA, BINOS 100, Leybold S.A.). A water vapor trap connected to air circuit prevents interferences between CO₂ and H₂O inside the measurement cell of the IRGA. Airflow inside the system is activated by a pump (flow rate of 1.5 l min^{-1}) and can be bypassed through a perchlorate dessicant scrub in order to decrease the CO₂ concentration ($[\text{CO}_2]$). The chamber is made up of a cylindrical steel bowl (20.7 cm diameter, 2.36 l volume) that is thermo-regulated by 6 Peltier elements. A perforated manifold insures sufficient $[\text{CO}_2]$ mixing and homogenization within the chamber. A small aperture (2 mm diameter) is connected to a tube, thus allowing pressure equilibrium between the inside and the outside. The WD_R values were calculated from the slope of the increase of the $[\text{CO}_2]$ inside the chamber during 90 s and expressed per dry mass (in $\mu\text{mol}_{\text{CO}_2} \text{ kg}_{\text{DM}}^{-1} \text{ s}^{-1}$). When

[CO₂] was over 450 ppm, airflow was automatically driven through perchlorate scrub for decreasing [CO₂] until 370 ppm, afterwards airflow was by-passed through main circuit. The WD_R values were selected for [CO₂] above 370 ppm and a 95% confidence interval lower than 10% of the slope value. Three copper-constantan thermocouples inside the chamber measured the temperature of the chamber surface (T_{REF}), air (T_{Air}) and at 0.5 cm depth inside WD sample (T_W). Temperature regulation, temperature measurements and by-pass activation were automated, and all data (time, temperatures, [CO₂]) were recorded every second.

We investigated the effect of temperature by incubating WD samples at field moisture. WD_R was measured continuously during 120 minutes for each WD sample while T_{REF} increased from 4°C to 34°C automatically. Nine replicates by DC were incubated. For each sample we fitted the WD_R and T_{Air} values to the following Q₁₀ function:

$$WD_R = R_{10} Q_{10}^{(T_{Air}-10)/10} \quad (3)$$

where the fitted parameters R₁₀ and Q₁₀ are the basal CO₂ efflux at 10°C and the temperature sensitivity of WD_R, respectively. WD_R was therefore expressed either per dry matter (g_{DM}⁻¹), surface (m⁻²) or volume (m⁻³). Previous tests revealed that fitting was slightly better when using T_W; but, as T_W was not routinely measured at Hesse, daily WD_R were estimated using T_{Air} in equation (3). After incubations, all samples were dried at 65°C until constant weight for VWC determination.

Thinning of the stand

Within the site, inventory of all trees in DBH was performed in 2004 before thinning operations, which were conducted in February 2005. DBH of all thinned trees were measured. Mass of WD left after thinning were assessed from a 15-trees subsample selected in all diameter classes. Twigs, branches and trunks of diameter < 7 cm were weighted in field, while subsamples were taken back to laboratory and dried at 65°C until constant weight for water content correction of field weight values. Several models (exponential, power, polynomial) were fitted to DBH and dry mass of WD data.

Statistics

Least square non-linear regression analyses were performed for k, R₁₀ and Q₁₀ determination (SAS 8.1, SAS Institute, N.C., USA), as well as for DBH and WD mass relationship, for which valid model criteria were high R² and minimum root mean square error (RMSE). Standard errors and 95% confidence intervals of fitted parameters were calculated. Linear regression was used for comparing remaining mass and density evolution, and to compare cylinder volumes measured by the two methods above. ANCOVA and post-hoc Fisher's Protected Least Significant Difference tests was used for comparing mean mass loss. ANCOVA test was used for comparing WD_R measured in a range of T_{Air} comprised between 10°C and 12°C among DCs with diameter and water content as covariable (p=0.05 level).

Results

WD decomposition experiment

The mass of faggots decreased significantly (p<0.0001) during the measurement period (Figure 1). Indeed, as revealed by PLSD test, mass decrease was significant from day of year (DOY) 42 to 387, followed by no significantly different remaining masses from DOY 274 to

458. Afterward, remaining mass decreased significantly until the end of experiment. Remaining mass after 23 months in field averaged 70% of the initial dry mass. As expected, density of faggots decreased during the same period, evolving from $0.68 \pm 0.03 \text{ kg dm}^{-3}$ (mean \pm confidence interval) to $0.47 \pm 0.04 \text{ kg dm}^{-3}$ ($p < 0.0001$, Figure 1). These density values were reliable insofar as cylinders volumes determined by immersion were very close to volumes measured directly (slope = 1.02; $R^2 > 0.99$, $p < 0.0001$). At DOY 458, the significant increase in density could not be explained. C content was rather constant during the experiment time, averaging 48%, while N content increased from 0.13% to 0.15% (DOY 211) and thereafter averaged 0.10%. Gravimetric water content evolved seasonally from $0.31 \text{ kg}_{\text{H}_2\text{O}} \text{ dm}^{-3}$ to $0.64 \text{ kg}_{\text{H}_2\text{O}} \text{ dm}^{-3}$, that corresponded to VWC of WD ranging from $0.16 \text{ m}_{\text{H}_2\text{O}}^3 \text{ m}^{-3}$ to $0.39 \text{ m}_{\text{H}_2\text{O}}^3 \text{ m}^{-3}$ (Figure 2). Decay constant k was determined more accurately with mass loss data ($k = 0.21 \text{ y}^{-1}$; $R^2 = 0.95$; RMSE = 0.02; $p < 0.0001$) than with density data ($k = 0.21 \text{ y}^{-1}$; $R^2 = 0.8$; RMSE = 0.04; $p < 0.0001$).

WD CO₂ efflux

WD CO₂ efflux (WD_R) measured within a temperature range of 10°C-12°C and expressed per dry matter ($\mu\text{mol}_{\text{CO}_2} \text{ kg}_{\text{DM}}^{-1} \text{ s}^{-1}$) differed significantly among DCs, as revealed by ANCOVA analysis with DC as independent variable and VWC as covariable ($p = 0.01$, Table 2). Significantly higher WD_R values were measured for DCIII samples, while no significant differences were found between DCI and DCII. However, samples from DC I exhibited higher VWC than DC II, while no significant influences of VWC or interaction with DC were found. When expressing WD_R per volume ($\mu\text{mol}_{\text{CO}_2} \text{ m}^{-3} \text{ s}^{-1}$), ANCOVA analysis also revealed significant higher WD_R values measured for DCIII samples ($p = 0.0008$), but with a significant interaction with VWC ($p = 0.0028$), while no significant differences were found between DCI and DCII. WD_R expressed per surface ($\mu\text{mol}_{\text{CO}_2} \text{ m}^{-2} \text{ s}^{-1}$) was lower for DCII samples ($p = 0.0187$), with also a significant interaction with VWC ($p = 0.02$).

Incubations with full range of temperature lead to typical exponential-type response of WD_R to T_{Air} (Figure 3). From the overall dataset, fluxes ranging between $0.23 \mu\text{mol}_{\text{CO}_2} \text{ kg}_{\text{DM}}^{-1} \text{ s}^{-1}$ and $5.4 \mu\text{mol}_{\text{CO}_2} \text{ kg}_{\text{DM}}^{-1} \text{ s}^{-1}$. Fitting equation (4) on each WD_R Vs T_{Air} relationship resulted in different values of R_{10} ($0.25 - 2.98 \mu\text{mol}_{\text{CO}_2} \text{ kg}_{\text{DM}}^{-1} \text{ s}^{-1}$) and Q_{10} ($1.21 - 2.40$) parameters (R^2 ranged between 0.81 and 0.98), revealing a large variability among samples. Q_{10} value did not differ while fitting equation (4) with WD_R in different units. ANCOVA test, realized on R_{10} or Q_{10} as dependant variable, DC as independent variable and Q_{10} or R_{10} as covariable, revealed no significant effect of DC on R_{10} or Q_{10} parameters. R_{10} and Q_{10} determined with WD_R values expressed by unit of area did not differ significantly among DCs while introducing diameter of samples as covariable. Moreover, no significant relationship between R_{10} and VWC was found. Thus, when equation (4) was fitted to overall WD_R and T_{Air} dataset, R_{10} and Q_{10} were $0.51 \pm 0.03 \mu\text{mol}_{\text{CO}_2} \text{ kg}_{\text{DM}}^{-1} \text{ s}^{-1}$ and 1.57 ± 0.07 , respectively ($R^2 = 0.39$). In order to estimate the annual WD_R, daily WD_R values were calculated by applying equation (4) with T_{Air} values measured in the field, summed. Thus, in 2003 and 2004 annual WD_R were $0.22 \text{ kg}_C \text{ kg}_{\text{DM}}^{-1}$ and $0.20 \text{ kg}_C \text{ kg}_{\text{DM}}^{-1}$, respectively.

Annual C loss

During commercial thinning, $6.7 \text{ m}^2 \text{ ha}^{-1}$ in basal area was removed, corresponding to a decrease of 28% of 2004 value. Relationship between DBH and total WD dry mass was best predicted with a 2nd order polynomial function (Figure 4). Thus, from thinning DBH

inventory, WD dry mass left after thinning averaged $4.1 \text{ Mg}_C \text{ ha}^{-1}$. Estimated total C loss using a k constant of 0.21 y^{-1} determined above was $1.4 \text{ Mg}_C \text{ ha}^{-1}$ for the 2003-2004 period, i.e. $0.7 \text{ Mg}_C \text{ ha}^{-1} \text{ y}^{-1}$. On the other hand, total CO_2 loss from WD of commercial thinning (following annual WD_R) averaged $3.2 \text{ Mg}_C \text{ ha}^{-1}$, i.e. $1.6 \text{ Mg}_C \text{ ha}^{-1} \text{ y}^{-1}$

Discussion

Decomposition of beech WD

Determination of remaining mass and decomposition rate constant were based in estimating precise initial dry mass. Calibration equation (1) revealed that initial dry mass could be determined accurately within the considered mass (fresh and dry) range. Plus, regression analysis determined a classical exponential-type decay evolution in dry mass. It also showed a rapid decrease of woody debris mass after 2 years of field decomposition comparable to mass loss and decay rates already published (Table 3). Our k constant is close to decomposition rate of lignin-like compounds than cellulose (0.22, Model Yaso, Liski *et al.*, 2005), but higher than those of stem-branches in GRC3 model (0.1-0.15; Paul *et al.*, 2003).

Several reviews of decomposition constant rate are available (Harmon *et al.*, 1986; Chambers *et al.*, 2000; Todd and Hanson, 2003), but few dealt with woody material decomposition of temperate species. Extending the decomposition time of our model over 3 years (instead of 2 years) would lead to a mass loss of -47% of initial mass. That is lower but consistent with Scheu and Schauerermann (1994) who measured a more rapid decay of beech twigs averaging -67% of initial mass after 3 years of field decomposition. Moreover, extending the decomposition time of our model over the interval between 2 successive thinning (5 years) would lead to a wood density averaging 0.24 kg dm^{-3} . But as far our experiment did not exceed 2 years, fragmentation process would not or poorly have started (Harmon *et al.*, 1986), thus we only considered C loss by either microbial respiration or soluble leaching (Brown *et al.*, 1996). That matches with wood density of DCIII samples (0.25 kg dm^{-3} , Table 2), which were from the thinning occurred during winter 1999-2000. In addition, Ngao *et al.* (2005) showed that mass loss of beech litter in the same site averaged 61.5% after a one-year field decomposition using $\delta^{13}\text{CO}_2$, corresponding to a k constant of 0.78. Such high values of k highlighted the very important biological activity within the site, especially with regard with oligo-mull humus type.

Surprisingly, WD water content showed rather limited range in gravimetric, in comparison with values tested in laboratory experiment (Boddy, 1983; Harmon *et al.*, 1986; Wang *et al.*, 2002). Few studies followed the time evolution of WD water content. In this study, range of wood density over 2 years may not allowed higher GWC, while in more decomposed WD, GWC could represent a consistent water reserve (Fraver *et al.*, 2002).

WD CO_2 efflux

Simple exponential decay model assumes a constant substrate quality, i.e. decay rate is a constant fraction of the amount of mass remaining. Analyses revealed that WD samples incubated at air temperature range of $10\text{-}12^\circ\text{C}$ did not differed significantly between DCI and DCII, which corresponded to the WD taken from the decomposition experiment. No significantly different respiration rate across the different decomposition class confirmed the suitability of single exponential decay model (Mackensen and Bauhus, 2003). Otherwise, effect of DC on WD_R (Table 2) would resulted from a trade-offs among both limited O_2

diffusivity and low water content related to high wood density in DCI and DCII, saprotroph biota colonization pattern, and substrate quality limitation in DCIII (Progar *et al.*, 2000; Hicks and Harmon, 2002; Wang *et al.*, 2002; Hicks *et al.*, 2003).

Modeling WD_R with air temperature

Fitted Q_{10} of WD values were low in comparison with most Q_{10} commonly reported for soil respiration (Janssens *et al.*, 2003). In our study, the main process involved in WM_R would probably be due to decomposer activities, while soil respiration integrates more processes (i.e. root and rhizosphere respiration, soil organic matter decomposition, priming effect, soil fauna activity) that also interact each other (Kuzyakov and Cheng, 2001; Subke *et al.*, 2004), leading to higher Q_{10} values. It is known that Q_{10} varies with temperature range (Lloyd and Taylor, 1994; Chen *et al.*, 2000; Janssens *et al.*, 2003; Wang *et al.*, 2002; Yuste *et al.*, 2003), but also with moisture level (Lankreijer *et al.*, 2003). In our study, no significant relationships were found between Q_{10} and VWC of WD samples, even by either expressing WD_R per dry mass or volume discarding the possible influence of wood density on WD_R . In spite of no significant differences of fitted parameters among DCs, rather large variability of WD_R response to T_{Air} among samples exists. A first hypothesis could involve VWC of WD . Working on WD samples at field moisture rather than artificially water-saturated may allow a more realistic estimation annual WD_R (Boddy, 1983, Chen *et al.*, 2000; Bond-Lamberty *et al.*, 2003). Field VWC would indeed allow at measuring the actual a metabolic level, but be not sufficient to determine the potential microbial activity in response to temperature increase. As compared with soil respiration processes, several authors determined that below a soil moisture threshold, soil respiration responded poorly to soil temperature variation. Under these conditions, soil respiration was rather controlled by soil water content, improving empirical models in explaining the seasonal variance of soil respiration (Davidson *et al.*, 1998; Epron *et al.*, 1999; Yuste *et al.*, 2004; Reth *et al.*, 2005). A second hypothesis would therefore be in relation variability in saprotroph colonization extend and microbial biomass and/or activity among and within DC (Hicks *et al.*, 2003). Whatever the hypothesis, our study is still unable to discard them, but it gave a relative precise overview of WD_R response to temperature.

Annual C loss

Annual C loss as CO_2 by respiration has been estimated to 1.6 MgC ha^{-1} , while annual C loss determined by field decomposition was estimated to 0.7 MgC ha^{-1} . Considering a fraction lost as CO_2 during decomposition of 0.8 (Dewar, 1991), annual C loss as CO_2 averaged 0.6 MgC ha^{-1} , the remaining fraction entering SOM. Despite very few studies integrating annual CO_2 flux from WD in forest C budgets, both estimates of C loss were consistent with published results (Chambers *et al.*, 2000; Wang *et al.*, 2002; Bond-Lamberty *et al.*, 2003). However, Chen *et al.* (2000) and Wang *et al.* (2002) pointed out cautions about long-term mass loss extrapolation based on short-term measurement, mainly due to several uncertainties in scaling-up WD respiration. In our study, temperature-based model of WD_R did not integrate a large part of variability among samples ($R^2 = 0.39$). But as our temperature incubations were ranged above 4°C , the model also did not reproduce a possible limitation of by low temperature occurring at Hesse during winter that was hardly simulated by the system.

Although uncertainties, annual WD_R (i.e. 0.6 MgC ha^{-1} , calculated from decomposition experiment) would account for 7% and 8% of total ecosystem respiration (R_{ECO}) in 2003 and

2004 ($R_{ECO} = 8.8$ and 7.7 MgC ha^{-1} , respectively) and would represent a.c. 10% of annual soil respiration (R_S) in 2003 and 2004 ($R_S = 6.0 \text{ MgC ha}^{-1}$, respectively; unpublished data). Using closed dynamic chamber for measuring R_S generally did not take into account the WD, thus WD_R represent a significant part of R_{ECO} . In comparison, Hesse forest, annual CO_2 efflux from litter decomposition was estimated to 8% of annual R_S (Ngao *et al.*, 2005), i.e. 0.5 MgC ha^{-1} . Using modeling approach, Song *et al.* (2003) showed that evolving with stand age, decomposing harvest and thinning residues would much more participate to heterotrophic respiration until old-growth stands can be a source or sink of C. These results emphasize the important role of WD debris in managed forest C budgets.

Conclusion

The decomposition of beech woody debris showed a rapid decrease after 2 years of decomposition experiment. Density losses were consistent with respiration rate at 10°C - 12°C range, while woody debris CO_2 efflux was poorly sensitive to air temperature. Water content status, decay class or diameter class seemed to not influence samples. However, samples were representative of rather early decomposition stage. Annual C loss estimations differed following the method, but remained in consistent range of published results. This discrepancy would lie in uncertainties in modeling woody debris respiration, and to scaling up short-term measurements. Finally, our results showed that decomposition of thinning residues accounts for a significant part of Hesse C balance. Improving and scaling these results at the ecosystem level, and combining them with silvicultural models would be useful to predict the respiratory balance of forest ecosystems following forest activities.

Acknowledgments

M. F. Willm and B. Clerc are warmly thanked for their technical skills and friendship in field and laboratory operations. Prof. D. Epron is greatly thanked for helpful discussion concerning temperature response of CO_2 efflux. This work was supported by (1) the European project CarboEurope IP, (2) the ESF Grants of the Programme: "Role of Soils in the Terrestrial Carbon Balance", and (3) the French National Forest Office (ONF)

References

- Aerts R. (1997). Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79:439-449.
- Berg B. (2000). Litter decomposition and organic matter turnover in northern forest soils. *Forest Ecology and Management* 133: 13-22.
- Boddy, L. (1983). Carbon dioxide release from decomposing wood: effect of water content and temperature. *Soil Biology and Biochemistry* 15: 501-510.
- Bond-Lamberty, B., C. K. Wang and S. T. Gower (2004). A global relationship between the heterotrophic and autotrophic components of soil respiration? *Global Change Biology* 10: 1756-1766.
- Bond-Lamberty B., Wang C. and Gower S.T. (2003). Annual carbon flux from woody debris for a boreal black spruce fire chronosequence. *Journal of Geophysical Research* 108: 9.
- Brown S., Mo J., McPherson J.K. and Bell D.T. (1995). Decomposition of woody debris in Western Australian forests. *Canadian Journal of Forest Research* 26: 954-966.

-
- Chambers J.Q., Higuchi N., Schimel J.P., Ferreira L.V. and Melack J.M. (2000). Decomposition and carbon cycling of dead trees in tropical forests of central Amazon. *Oecologia* 122: 380-388.
- Chen, H., M.E. Harmon, R.P. Griffiths and W. Hicks (2000). Effects of temperature and moisture on carbon respired from decomposing woody roots. *Forest Ecology and Management* 138: 51-64.
- Davidson E.A., Belk E. and 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 Biology* 4: 217-227.
- Epron D., Farque L., Lucot E. and Badot P.M. (1999). Soil CO₂ efflux in a beech forest: dependence on soil temperature and soil water content. *Annals of Forest Science* 56: 221-226.
- Foster J.R. and Lang G.E. (1982). Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. *Canadian Journal of Forest Research* 12: 617-626.
- Ganjegunte G.K., Condon L.M., Clinton P.W., Davis M.R. and Mahieu N. (2004). Decomposition and nutrient release from radiata pine (*Pinus radiata*) coarse woody debris. *Forest Ecology and Management* 187: 197-211.
- Granier A., Ceschia E., Damesin C., Dufrene E., Epron D., Gross P., Lebaude S., Le Dantec V., Le Goff N., Lemoine L., Lucot E., Ottorini J.M., Pontailler J.Y. and Saugier B. (2000). The carbon balance of a young Beech forest. *Functional Ecology* 14: 312-325.
- Hanson P.J., Edwards N.T., Garten C.T. and Andrews J.A. (2000). Separating root and soil microbial contribution to soil respiration: A review of methods and observations. *Biogeochemistry* 48: 115-146.
- Harmon M.E., Franklin J.F., Swanson F.J., Sollins P., Gregory S.U., Lattin J.D., Anderson N.H., Cline S.P., Aumen N.G., Sedell J.R., Lienkaemper G.W., Cromack K. and Cummins K.W. (1986). Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15: 133-302.
- Hicks W.T. and Harmon M.E. (2002). Diffusion and seasonal dynamics of O₂ in woody debris from the Pacific Northwest, USA. *Plant Soil* 243: 67-79.
- Hicks, W. T., M. E. Harmon and D. D. Myrold (2003). Substrate controls on nitrogen fixation and respiration in woody debris from the Pacific Northwest, USA. *Forest Ecology and Management* 176: 25-35.
- Idol T.W., Figler R.A., Pope P.E. and Ponder Jr F. (2001). Characterization of coarse woody debris across a 100 year chronosequence of upland oak-hickory forests. *Forest Ecology and Management* 149: 153-161.
- Janssens I.A., Kowalski A.S., Longdoz B. and Ceulemans R. (2000). Assessing forest soil CO₂ efflux : an in situ comparison of four technique. *Tree Physiology* 20: 23-32.
- Janssens, I. A. and K. Pilegaard (2003). Large seasonal changes in Q(10) of soil respiration in a beech forest. *Global Change Biology* 9: 911-918.
- Lankreijer, H., I. A. Janssens, N. Buchmann, B. Longdoz, D. Epron and S. Dore (2003). Measurement of soil respiration. *Fluxes of Carbon, Water and Energy of European Forests*. Berlin, Springer-Verlag Berlin. 163: 37-54.
- Lavigne, M. B., R. J. Foster and G. Goodine (2004). Seasonal and annual changes in soil respiration in relation to soil temperature, water potential and trenching. *Tree Physiology* 24: 415-424.
- Liski J., Palosuo T., Peltoniemi M. and Sievänen R. (2005). Carbon and decomposition model Yasso for forest soils. *Ecological Modelling*. *In press*.
- Lloyd J. and Taylor J.A. (1994). On the temperature dependence of soil respiration. *Functional Ecology* 8: 315-323.

-
- Mackensen, J. and J. Bauhus (2003). Density loss and respiration rates in coarse woody debris of *Pinus radiata*, *Eucalyptus regnans* and *Eucalyptus maculata*. *Soil Biology & Biochemistry* 35: 177-186.
- McCull J.G. and Powers R.F. (2003). Decomposition of small woody debris of California red fir: mass loss and elemental content over 17 years. *Soil Science Society of America Journal* 67: 1227-1233.
- Ngao J., Epron D., Brechet C. and Granier A. (2005). Estimating the contribution of leaf litter decomposition to soil CO₂ efflux in a beech forest using ¹³C-depleted litter. *Global Change Biology* 11: 1-9.
- Norby R.J., Cotrufo M.F., Inesson P., O'Neill E.G. and Canadell J.G. (2001). Elevated CO₂, litter chemistry and decomposition : a synthesis. *Oecologia* 127: 153-165.
- Paul, K. I., P. J. Polglase and G. P. Richards (2003). Sensitivity analysis of predicted change in soil carbon following afforestation. *Ecological Modelling* 164: 137-152.
- Pongracic S., Kirschbaum M.U.F. and Raison R.J. (1997). Comparison of soda lime and infrared gas analysis techniques for in situ measurement of forest soil respiration. *Canadian Journal Forest Research* 27: 1890-1895.
- Reth S., Reichstein M. and Falge E. (2005). The effect of soil water content, soil temperature, soil pH-value and the root mass on soil CO₂ efflux - A modified model. *Plant and Soil* 268: 21-33.
- Subke J.A., Hahn V., Battipaglia G., Linder S., Buchmann N. and Cotrufo M.F. (2004). Feedback interactions between needle litter decomposition and rhizosphere activity. *Oecologia* 139: 551-559.
- Swift M.J., Heal O.W. and Anderson J.M. (1979). *Decomposition in terrestrial ecosystems*, Blackwell Science. 279 pp.
- Wang, C., B. Bond-Lamberty and S. T. Gower (2002). Environmental controls on carbon dioxide flux from black spruce coarse woody debris. *Oecologia* 132: 374-381.
- Yuste, J. C., I. A. Janssens, A. Carrara and R. Ceulemans (2004). Annual Q(10) of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Global Change Biology* 10: 161-169.
- Yuste, J. C., I. A. Janssens, A. Carrara, L. Meiresonne and R. Ceulemans (2003). Interactive effects of temperature and precipitation on soil respiration in a temperate maritime pine forest. *Tree Physiology* 23: 1263-1270.

Tables

Year	T _{Air} (°C)	P (mm)	LAI (m ² m ⁻²)	G (m ² ha ⁻¹)	Litterfall (gC m ⁻²)
2002	10.5	1150	7.7	24.1	161
2003	10.8	660	7.7	25.2	180
2004	9.7	913	8.1	26.2	171

Table 1. Mean characteristics of the experimental plot. Mean air temperature (*T*_{Air}), total precipitations (*P*), leaf area index (*LAI*), basal area (*G*) and total leaf litterfall are given for three successive years.

	n	Mean	VWC	Density
DC1	16	0.54 (0.18)	0.44 (0.02)	0.65 (0.02)
DC2	18	0.72 (0.17)	0.24 (0.02)	0.44 (0.02)
DC3	31	1.22 (0.15)	0.42 (0.08)	0.25 (0.02)

Table 2. Mean WD CO₂ efflux (WD_R, μmolCO₂ kg_{DM}⁻¹ s⁻¹) from n measurements within range of air temperature comprised between 10°C and 12°C for each decomposition class (DC). Mean volumetric water content (VWC, m³ m⁻³) and wood density (kg dm⁻³) were also given by DC. Values in brackets are standard errors

Study	Species	<i>k</i>	mass loss (year)
Sollins, 1981	<i>Pseudotsuga menziesii</i> (Mirb.) Franco	0.028	
Mattson <i>et al.</i> , 1987	Various temperate species	0.185	
Harmon <i>et al.</i> 1995	Various tropical species	0.008-1.019	
Brown <i>et al.</i> , 1995	<i>Eucalyptus Calophylla</i> R.Br.	0.22	
Brown <i>et al.</i> , 1995	<i>Eucalyptus marginata</i>	0.05	
Brown <i>et al.</i> , 1995	<i>Pinus pinaster</i>	0.07	
O'Lear <i>et al.</i> , 1996	<i>Gonystylus bancannus</i>	0.27	
Frangi <i>et al.</i> , 1997	<i>Nothofagus sp</i>	0.17-0.47	
Stone <i>et al.</i> , 1998	<i>Pseudotsuga menziesii</i> (Mirb.) Franco	0.067	
Bond-Lamberty <i>et al.</i> , 2003	<i>Picea mariana</i> (Mill.) BSP	0.016-0.045	
Mackensen and Bauhus, 2003	<i>Eucalyptus regnans</i> F. Muell.	0.041	
Mackensen and Bauhus, 2003	<i>Eucalyptus maculata</i> Hook	0.049	
Mackensen and Bauhus, 2003	<i>Pinus radiata</i> D. Don	0.127	
Ganjegunte <i>et al.</i> , 2004	<i>Pinus radiata</i> D. Don	0.074	
McColl and Powers, 2003	<i>Abies magnifica</i> A. Murr.		-37% (17)
Scheu and Scauermann, 1994	<i>Fagus sylvatica</i> L.		-67% (3)
Ngao <i>et al.</i> , (this study)	<i>Fagus sylvatica</i> L.	0.21	-30% (2)

Table 3. List of published decay rate constants in various ecosystems. When the decay rate constant (*k*, y⁻¹) was not available, total mass loss (in percent of initial mass) was given (under brackets the time in year of decomposition).

Figures

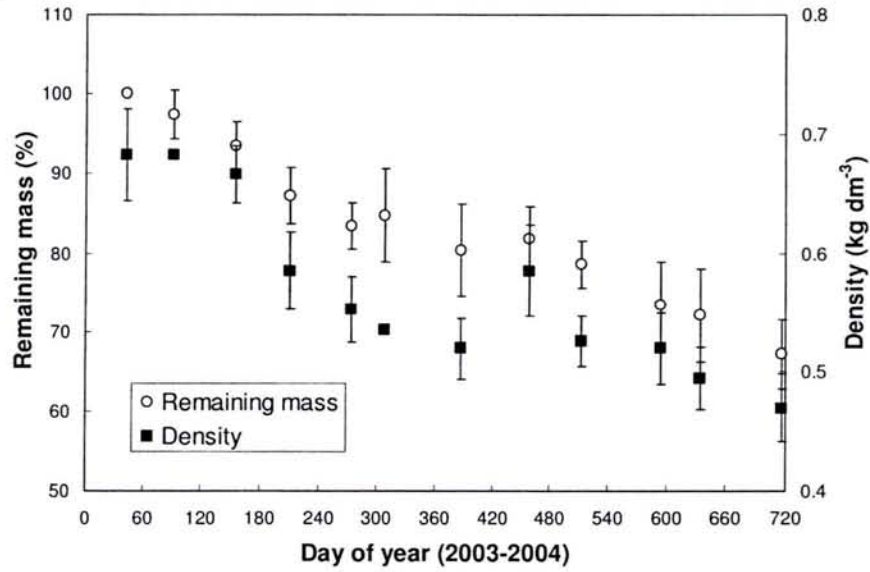


Figure 1. Seasonal evolution of remaining mass (in percent of initial mass, open circles), and wood density (filled squares) of faggots. Vertical bars are 95% confidence intervals.

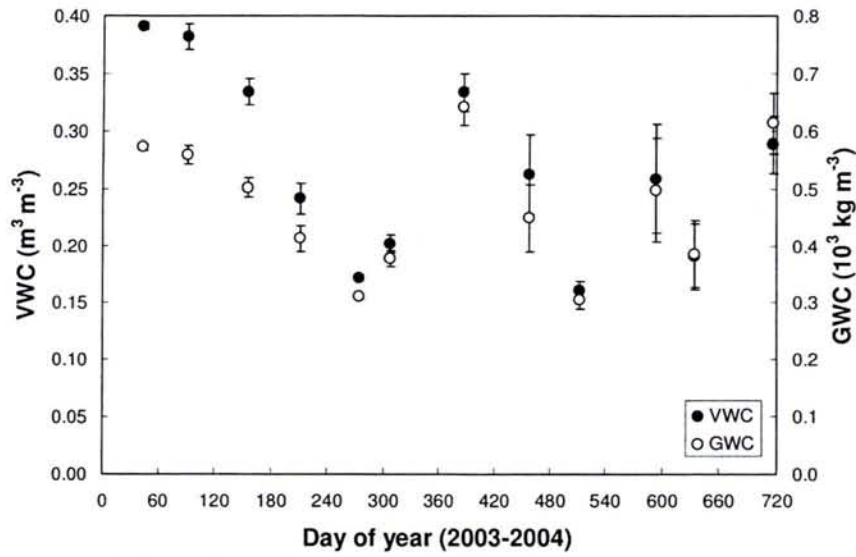


Figure 2. Seasonal evolution of volumetric (filled circles) and gravimetric (open circles) water content of faggots. Vertical bars are 95% confidence intervals.

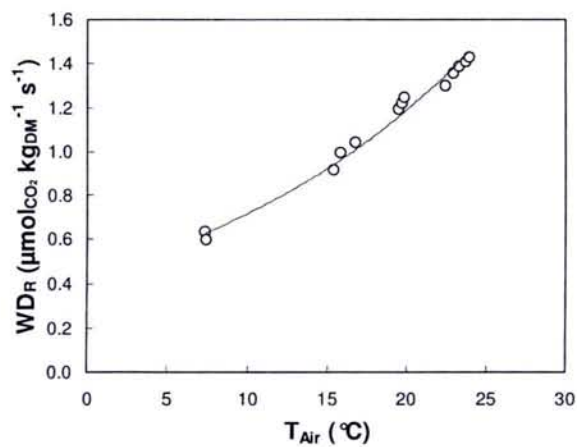


Figure 3. Typical exponential fit curves between woody debris respiration (WD_R) and air temperature (T_{Air}). Exponential model fitted on data was: $WD_R : R_{10} * Q_{10}^{(T_{Air}-10)/10}$ ($R^2 = 0.96$, $p < 0.0001$).

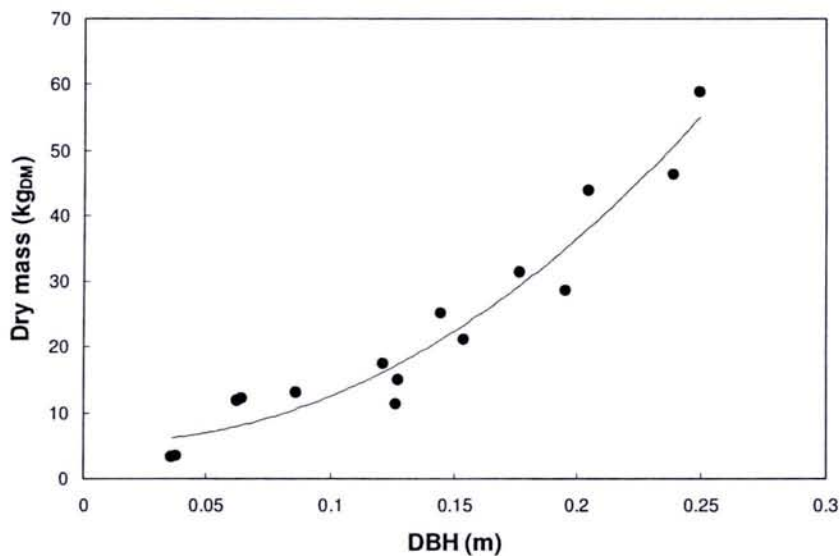


Figure 4. Relationship between woody debris dry mass and diameter at breast height (DBH) determined on a 15-tree sample in the thinned stand. Equation of the curve was: $Dry\ mass = 865.19\ DBH^2 - 19.156\ DBH + 5.8209$ ($R^2 = 0.94$; $p < 0.0001$).

ARTICLE 4: Separating autotrophic and heterotrophic respiration in two young beech stands: Impact of corrections for root decomposition in trenched plots

J. Ngao¹, B. Longdoz¹, A. Granier¹, D. Epron^{2*}

¹UMR Ecologie et Ecophysiologie Forestière, Centre INRA de Nancy, 54280 Champenoux, France

²UMR Ecologie et Ecophysiologie Forestière, Université Henri Poincaré Nancy 1, 54506 Vandoeuvre-les-Nancy Cedex, France

*Corresponding author:

Daniel Epron (Daniel.Epron@scbiol.uhp-nancy.fr)

Fax: (+33) 383 394 069

Phone: (+33) 383 394 038

Running title: Separating autotrophic and heterotrophic respiration

Abstract

In this study, we aimed to quantify the relative contribution of soil autotrophic (R_{Auto}) and heterotrophic (R_{Hetero}) respiration components in two different stands (H1 and H2) by measuring soil CO_2 efflux from control plot and trenched plots in a young beech forest. The effects of trenching on trenched root decomposition and soil microbial biomass were also assessed to obtain corrected fluxes. Deduced from seasonal survey of R_{S} , uncorrected relative contribution of R_{Auto} to total soil respiration reached 36% and 25% in H1 and H2, respectively. When applying corrections for additional root decomposition, relative contribution of R_{Auto} averaged 72% and 59% of total annual soil respiration in H1 and H2, respectively. With regards with these relative important corrections, error analyses highlighted a high sensitivity of calculations to initial root biomass determination. While errors on both decomposition rate constant and fraction of C loss as CO_2 during root decomposition induced less variations on R_{Auto} . Root biomass did not explain difference in autotrophic contribution between sites would. Alternatively, heterotrophic contribution would rather be explained by higher fine root productivity and variation microbial activity.

Keywords: autotrophic respiration, heterotrophic component, microbial activity, root decomposition, sensitivity analysis, soil respiration,

Introduction

Net carbon (C) exchange between forest ecosystems and the atmosphere (net ecosystems exchange, NEE) results from the difference between gross primary production (GPP) and respiration (R_{ECO}) fluxes. Any small variations of these fluxes can lead to switching the role of ecosystems between sink and source of CO_2 (Janssens *et al.*, 2001). On average, range of estimates of European forests C sink (varying between 70 and 160 $\text{g}_\text{C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) is rather large because of uncertainties in forest soil C sequestration (Janssens *et al.*, 2003) while R_{ECO} would be considered as the main determinant of European forest C balance (Valentini *et al.*, 2000). Moreover soil is the major carbon reserve in terrestrial ecosystems (IPCC., 2000) and total soil CO_2 efflux (R_{S}) represents the second CO_2 forest flux of importance (Raich and Schlesinger, 1992). Janssens *et al.*, 2001 reported for 18 European forest ecosystems that mean R_{S} accounted for 55% of GPP and 69% of R_{ECO} . Numerous studies provided various models of R_{S} using abiotic (soil temperature, soil water content, precipitations, various soil parameters) and biotic (root biomass, photosynthesis) factors as independent variables explaining both temporal and spatial variability of R_{S} (Lloyd and Taylor, 1994; Longdoz *et al.*, 2000; Hogberg and Ekblad, 2001; Reichstein *et al.*, 2003; Lankreijer *et al.*, 2003; Epron *et al.*, 2004; Reth *et al.*, 2005; Tang *et al.*, 2005). But they also pointed out the need to distinguish processes participating to R_{S} because of difference of C sources and regulation patterns beneath the CO_2 production.

Two main processes participating to R_{S} are commonly distinguished: (a) autotrophic respiration (R_{A}) that includes living root growth and maintenance respiration associated to the rhizospheric activity, and (b) heterotrophic respiration (R_{H}) that results from litter and soil organic matter decomposition by non-mycorrhizal fungi and microbes activities, and by soil fauna. By definition, estimating R_{A} is required for calculating net primary production, as well as R_{H} is required for calculating net ecosystem production. Plus, it had been shown that R_{S} is linked to GPP through rapid allocation of newly incorporated C to roots and rhizosphere (Janssens *et al.*, 2001; Ekblad and Hogberg, 2001; Hogberg *et al.*, 2001; Fessenden and Ehlringer, 2003), underlining the importance of separating both autotrophic and heterotrophic component of R_{S} . Several studies investigated spatial variability of R_{S} among different forest sites (Janssens *et al.* 2001; Reichstein *et al.*, 2003). Few studies aimed to investigate the spatial variability of R_{S} partitioning within a forest site from which potential driving factors such as stand age, structure, species composition, soil type, and stand productivity may vary subsequently with silvicultural stage or location and influence R_{S} (Fang *et al.*, 1998; Epron *et al.*, 2004; Gough *et al.*, 2004; Yuste *et al.*, 2005). Partitioning R_{S} in contrasted stands may improve the understanding of the main determinants of both R_{A} and R_{H} (Bond-Lamberty *et al.*, 2004, Lavigne *et al.*, 2003).

Previous studies estimated the contribution of R_{A} averaging 50-60% of R_{S} from various forest ecosystems (Russel and Voroney, 1998; Epron *et al.* 1999; Hanson *et al.*, 2000, Ohashi *et al.*, 2000). Various methods have been used for estimating R_{A} , as direct root or soil core excavation (Thierron and Laudelout, 1996; Pregitzer *et al.*, 1998), direct field measurement of root respiration (Bouma *et al.*, 1997; Kutsch *et al.*, 2001), large-scale girdling (Hogberg *et al.*, 2001; Bhupinderpal-Singh *et al.*, 2003), isotopic methods (Balesdent and Balabane, 1996; Kuzyakov, 2001; Ekblad and Hogberg 2001; Formanek and Ambus, 2004) and root exclusion by trenching. This last method could be rather easily implemented in small forest surfaces (Rochette *et al.*, 1999; Epron *et al.*, 1999; Hanson *et al.*, 2000; Lee *et al.*, 2003, Bond-Lamberty *et al.*, 2004a; Lavigne *et al.*, 2003, 2004); R_{A} is deduced by subtracting soil respiration measured either in undisturbed plots or trenched plot in which roots are killed after trenching. This method has been shown to provide reliable and consistent estimates of

R_A , even if corrections have to be done to consider the additional decomposition of trenched roots (Ewel *et al.*, 1987; Bowden *et al.*, 1993; Lavigne, *et al.*, 2003; Lee *et al.*, 2003; Bond-Lamberty *et al.*, 2004). In addition, changes in soil water content status have been poorly considered (Epron *et al.*, 1999) in spite of the possible consequence on microbial biomass/activity within trenched plots.

This study aimed to quantify the relative contribution of R_A and R_H fluxes in two different stands by measuring soil CO_2 efflux from control plot (CP) and trenched plots (TP) in a young beech (*Fagus sylvatica* L.) forest. The effects of trenching on trenched root decomposition and soil microbial biomass were also assessed to obtain corrected fluxes. From these results, hypotheses concerning the effect of stand characteristics on R_S partitioning were proposed.

Material and Methods

Sites

The study was performed in two distinct stands of the state forest of Hesse (Moselle, Northeast of France) from March 2004 to April 2005. Both sites belong to the European flux monitoring network (CarboEurope IP) and to the French network of forest ecosystem (ORE "fonctionnement des écosystèmes forestiers"). The first site H1 (48°40'27"N, 7°03'53"E, 305 m elevation) is located in the middle of a homogenous 65 ha sapling of 35-year-old European beeches (90% of *Fagus sylvatica* L.). Surroundings of the studied site were thinned in February 2004. The second site H2 (48°40'40"N, 7°04'05"E, 300 m elevation) is located in a 20-year-old beech thicket (63% of total ground surface, G) mixed with hornbeam (*Carpinus betulus* L., 26% of G), oaks (*Quercus petraea* (Matt.) Lielb. and *Q. robur* L. averaging 7% G), willow (*Salix caprea* L., 2% of G) and birch (*Betula pendula* Roth, 1% of G). The stand originated from a natural regeneration and is organized in furrows and ridges. Stand characteristics were summarized in Table 1. Both sites are distant of about less than 400 m. The soil is classified as a stagnic luvisol (FAO classification) covered by an oligo-mull humus type in both stand and understory vegetation is rather sparse in both H1 and H2.

Experimental design

Two TP were installed in both sites on November 19th 2003. Two TP of about 9 m² (3 x 3 m) were installed in H1 by digging a trench (about 1 m deep) around an area without trees. Before being filled back, each TP was lined with a specific plastic canvas cover, which allowed gravimetric water to flow laterally and thus, prevented from excessive water retention and external root regrowth inside the TP. One CP of about 35 m² (7 x 5 m) was established in the same LAI environment as the TP in order to have a maximum distance between each plot of 15 m. Two TP were installed in H2 as for those in H1 but their surface were reduced to about 3 m² (2 x 1.5 m each) because of sparse free appropriate location with regard with the higher tree density than in H1 and the stand organization. One CP was established in a dominated-beech patch, even if several oaks and willows were near but distant to more 1 m of two collars. The CP was distant of about 5 m and 30 m from the first and second TP, respectively. Herbaceous seedlings within all TP were sparse and periodically removed. Preliminary geostatistic studies conducted in both sites did not reveal clear spatial structure of S_R semivariance at a 10 m scale (unpublished data), thus we assumed that in each site, CP and TP were installed in a homogenous location.

Soil CO₂ efflux measurements were performed using a Licor 6200 system (Licor, Lincoln, USA), which consisted in an infrared gas analyzer Li-6252 connected with a closed dynamic chamber (Li 6000-9). Air circulation inside the chamber is provided by the pump of the Li-6252 (flow rate 1.5 l.min⁻¹) and drives the air inside the chamber through a drilled ring that allows air mixture and homogenization. R_S values were calculated by measuring the rate of increase of the CO₂ concentration inside the chamber during 60 s. The chamber was laid on PVC collars (110 mm diameter) to measure R_S without soil disturbance. Collars were inserted into soil (1.5 cm depth) two weeks before the first measurements, and left during the entire experiment time. A foam gasket ring provided an airtight seal between the chamber and the collar. No significant difference of pressure between the inside and the outside of the chamber was found, thus major risks of air leak were avoided (Longdoz *et al.*, 2000). Inside the TP, collars were installed at least 50 cm from the edge of the plot, in order to avoid possible disturbance following trenching. Twelve collars were installed in each CP of both sites; twelve collars were installed in each TP of H1, while 7 to 8 collars were inserted in each 2 TP of H2. We conducted measurements in all plots of both sites during the same daytime about every 2 weeks from March 2004 to April 2005, and daily means were calculated for each treatment (CP or TP).

Soil temperature at -10 cm (T_{SC}) was continuously monitored by 5 and 4 copper-constantan thermocouples in H1 and H2 sites, respectively. Data were acquired every 10 s and 30-min averages were stored (Model CR7 datalogger, Campbell Scientific, Courtaboeuf, France). Daily averages were calculated. In addition, local soil temperature at -10 cm (T_S) and soil water content for the first 0-6 cm (θ_{Surf}) were also measured in the vicinity of soil respiration chamber concurrently with R_S by using a homemade copper-constantan thermocouple (Faculty of Agronomy of Gembloux, Belgium) and a capacitive ML2x ThetaProbe (Delta-T Device, Cambridge, UK), respectively. A simple empirical model was fitted to daily R_S data:

$$R_S = R_{10} Q_{10}^{(T_S-10)/10} e^{-e^{(a-b*\theta_{Surf})}} \quad (1)$$

where R₁₀ is basal respiration at 10°C, Q₁₀ the temperature sensitivity of soil respiration, a and b the fitted parameters of the Gompertz function (Janssens *et al.*, 2001). Assuming a similar effect of θ_{Surf} on R_S in both sites, a and b were set at 0.946 and 25.4, respectively, in all fit. These values were determined from a preliminary fit performed on a larger dataset including data acquired in 2003 and 2004 in the CP of H1 site. Equation (1) was fitted to data of each treatment in each site; thus, for each site we pooled together data from the two TP (see Results). Standard errors on each parameter were given by the regression analysis.

Root and microbial biomasses

Four soil cores were sampled inside each TP in both sites in March 2004. Initial root biomass (B₀) was determined by manually disaggregating each core (0-15 cm) while roots were manually retrieved. Remaining aggregates were partly dissolved in distilled water for 24 hours and sieved (2 and 1 mm mesh size) for retrieving the remaining roots. One year after trenching (March 2005) root biomass (B) was determined from 4 soil cores (as done as previously) sampled inside TP to estimate the root mass loss (B₀ - B), but as well from soil cores sampled outside TP (B₀') to compare with initial root biomass B₀. The carbon concentration (c) in roots was determined with a CHN analyzer.

Initial microbial biomass was assumed to be similar between CP and TP. In March 2005, 4 soil cores were sampled in each treatment of both sites for microbial biomass determination. From these soil cores, a first set of 15 g of root-free sieved soil samples were fumigated following Nguyen and Guckert (2001). Soil samples were installed within a glass dessicator with ethanol-free chloroform. The vacuum was made until the chloroform boiled for 5 min. Then, the dessicator was maintained under vacuum in the dark for 24 h at 25°C. Afterwards, chloroform vapors were removed six times (-0.09 MPa) by evacuation. A second set of non fumigated soil and fumigated soils were extracted by mixing with 60 ml of K₂SO₄ (0.5 M) during 45 min and filtrated on Whatman N°42 paper disc. K₂SO₄ solutions were analyzed by a TOC-V CSH analyzer (Shimadzu Deutschland GmbH) for total organic carbon determination. Mean microbial C, mean dissolved organic carbon (DOC) and microbial nitrogen (N) contents were calculated for each treatment on each site.

Annual contribution of R_A

We simulated daily R_S values from each treatment and each site from March 15th 2004 to 15 March 2005 by applying equation (1) with continuously monitored daily T_{SC} data for this period, and cumulated daily values for estimating annual flux in each plot. Corrections for additional CO₂ efflux from trenched root decomposition (R_E) were performed following Epron *et al.* (1999) as:

$$R_E = (1-\alpha) (B_0 - B) \quad (2)$$

where α is the fraction incorporated into soil organic matter during root decomposition ($1-\alpha$ being the fraction lost as CO₂), and (B₀ - B) is the root biomass loss during the experiment time. We set α to 0.3, which represents an intermediate value between those proposed by Parton *et al.* (1987) and Jenkinson *et al.* (1990). Annual R_A was calculated as:

$$R_A = R_{SCP} - (R_{STP} - R_E) \quad (3)$$

where R_{SCP} is the annual R_S of CP, R_{STP} the annual R_S of TP and R_E additional CO₂ efflux from trenched root decomposition as calculated by equation (2).

Statistics

Least square non-linear regression analyses were performed to fit empirical model to R_S data (Statgraphics Plus 4.1). Linear regression analysis was used for comparing T_S and T_{SC} data. Two-way ANOVA and Fisher's Protected Least Significant Difference (PLSD) post-hoc tests were used for comparing daily means among plots and sites at a p=0.05 level for each date. We calculated the 95% confidence intervals (CI) of annual CO₂ efflux from CP and TP by drawing randomly 10000 couples of equation (1) parameters assuming a normal distribution centered on their respective means and their standard errors (SE) for each treatment. Each couple of parameters was used to calculate annual CO₂ efflux as described above, and CI were calculated from the mean of these 10000 runs for each treatments.

Results

Values of R_S in CP of both sites were ranged between 0.3 μmol_{CO₂} m⁻² s⁻¹ in winter and 3.7 μmol_{CO₂} m⁻² s⁻¹ in early summer, revealing pronounced seasonal variations of R_S in all plots (Figure 1). Values of R_S in TP of H1 site were ranged between 0.4 μmol_{CO₂} m⁻² s⁻¹ and 1.9 μmol_{CO₂} m⁻² s⁻¹ while they were ranged in TP of H2 between 0.2 μmol_{CO₂} m⁻² s⁻¹ and 2.6 μmol_{CO₂} m⁻² s⁻¹. In both sites, daily means of R_S did not differ significantly between the 2 TP, thus their data were pooled to calculate a daily mean per site. In H1 and H2 sites, mean

values of R_S during winter and early spring did not differ significantly between treatments while during the growing season, significant higher R_S values ($p < 0.05$) for CP than for TP were generally found. In another hand, when considering CP alone, significant differences were found between sites ($p < 0.001$) for only 2 dates (DOY 298 and 343). When considering mean R_S values from TP only, R_S from the H2 site was significantly higher for more several dates (DOY 77, 161, 222, 242, 257, 343 and 373) than from the H1 site. During the midsummer (DOY 222) mean R_S values were rather similar between treatments in H1, and R_S from TP was significantly ($p = 0.003$) higher than from CP in H2. Mean soil temperature evolved with a seasonal range comprised between 0.9°C and 18.8°C (Figure 2a). Mean daily T_S values of each plot (either CP or TP) followed a very similar pattern, and differed only on few dates. Values of θ_{surf} in CP of both sites ranged from less than $0.07 \text{ m}^3 \text{ m}^{-3}$ in midsummer to $0.37 \text{ m}^3 \text{ m}^{-3}$ and $0.40 \text{ m}^3 \text{ m}^{-3}$ in winter (H1 and H2 respectively, Figure 2b). Trenching on both sites, in spite of the canvas cover, induced a smaller range of variation of θ_{surf} than for the CP, between around $0.28 \text{ m}^3 \text{ m}^{-3}$ in late spring and above $0.40 \text{ m}^3 \text{ m}^{-3}$ in winter.

The empirical model described most of temporal variations of S_R in all plots. The fitted parameters are presented in Table 2. The R_{10} was higher in the CP than in TP, but remain rather similar between sites. Temporal distribution of residuals presented no major deviations (Figure 4), even if during mid spring (DOY 134) and mid fall (DOY 327-343) periods higher residuals than expected. Q_{10} parameter seems to be lower in the TP but difference in Q_{10} values were lower than the standard errors. Parameters were used to simulate annual R_S by applying equation (1) with the continuously acquired T_{SC} data, from March 15th 2004 to March 15th 2005. Only small deviations occurred between T_S and T_{SC} data ($T_S = 1.04 T_{SC} - 0.09$; $R^2 = 0.93$; $p < 0.0001$; $n = 48$ from both sites). The annual R_{SCP} efflux was $529 \text{ gC m}^{-2} \text{ y}^{-1}$ and $528 \text{ gC m}^{-2} \text{ y}^{-1}$ for H1 and H2, respectively. Annual R_{STP} was $337 \text{ gC m}^{-2} \text{ y}^{-1}$ and $398 \text{ gC m}^{-2} \text{ y}^{-1}$ for H1 and H2, respectively. Deduced from these estimates (uncorrected for R_E), relative contribution of R_A to total soil respiration reached 36% and 25% in H1 and H2, respectively.

Initial root biomass estimated from soil cores averaged $304 \pm 135 \text{ gC m}^{-2}$ and $390 \pm 106 \text{ gC m}^{-2}$ for H1 and H2, respectively, as C content determined from root samples averaged 39%. Assuming a correcting factor of 0.45 for depth and spatial integration (Epron *et al.*, 1999), total initial root biomass (B_0) averaged $675 \pm 299 \text{ gC m}^{-2}$ and $867 \pm 235 \text{ gC m}^{-2}$ in H1 and H2, respectively. Total root biomass determined outside the TP (B_0') averaged $581 \pm 259 \text{ gC m}^{-2}$ and $641 \pm 143 \text{ gC m}^{-2}$ for H1 and H2, respectively. ANOVA test revealed that B_0 and B_0' did not differ significantly in both sites. Thus, further calculations assumed mean root biomass calculated from soil cores sampled in both March 2004 and March 2005, i.e. $641 \pm 172 \text{ gC m}^{-2}$ and $708 \pm 128 \text{ gC m}^{-2}$ in H1 and H2, respectively. One year after trenching, total root biomass (B) averaged $371 \pm 48 \text{ gC m}^{-2}$ and $447 \pm 68 \text{ gC m}^{-2}$. Such root mass loss corresponded to an annual CO_2 efflux from decaying trenched roots (R_E , equation (2)) of $189 \text{ gC m}^{-2} \text{ y}^{-1}$ and $183 \text{ gC m}^{-2} \text{ y}^{-1}$ in H1 and H2, respectively, accounting for 56% and 46% of R_{STP} , respectively. Annual autotrophic respiration R_A (equation (3)) in H1 and H2 was estimated to $381 \text{ gC m}^{-2} \text{ y}^{-1}$ and $312 \text{ gC m}^{-2} \text{ y}^{-1}$ as a relative contribution of 72% and 59% of total annual soil respiration, respectively.

Microbial C estimated from fumigation-extraction samples in March 2005 was significantly higher in CP of H1 than in other plots (Table 3). The DOC content was significantly higher in H2 than H1 ($p = 0.006$) while microbial N content was significantly higher in CP of H1 than in other plots. No significant relationships between microbial C and DOC content were found.

Discussion

Temporal variations of soil respiration

R_S values in this study were within a similar range of values than those given by Epron *et al.*, 2004. In addition, seasonal variability of soil respiration was rather well described by the model (R^2 values varying Table 2). However, Q_{10} -based models is known to underestimate fluxes at low soil temperatures and overestimated at high temperatures (Lloyd and Taylor, 1994). Distribution of residuals did not show major biases (Figure 3) when plotted against T_S . Seasonal evolution of residuals seemed to describe a slight underestimation and overestimation of the model during low and high temperature periods, respectively. Two periods would not follow this trend; in mid summer (DOY 222) a 2-week drought period would have lowered R_S in CP only, as shown by fluxes values in Figure 2. Plus, slight overestimation of model may occur during the mid fall period, that would correspond to resorption and root activities prior leaf litter fall, which happened from DOY 298, and in addition to an enhanced microbial activity due to fresh leaf litter leaching (Ibrahima *et al.*, 1995; Subke *et al.*, 2004). Future models aiming to describe temporal evolution of S_R would have to take into account such phenological patterns (Yuste *et al.*, 2004).

Very low CI of annual fluxes suggested an accurate estimation of annual R_S in CP of H1, which could be considered significantly lower than those calculated in 1997-1998 in the same site ($663 \text{ g}_C \text{ m}^{-2} \text{ y}^{-1}$ and $713 \text{ g}_C \text{ m}^{-2} \text{ y}^{-1}$, respectively, Epron *et al.*, 1999; Janssens *et al.*, 2003). This would be due to several factors, such as the use of collar in this study, which typically gave lower R_S values in comparison with measurements taken by inserting the chamber directly into soil (unpublished data). Correcting values as if they were measured by inserting chamber would lead to an increment of $299 \text{ g}_C \text{ m}^{-2} \text{ s}^{-1}$, which is too much to explain lower annual R_S with regards with previous studies. Another possible cause would be a limitation by θ_{Surf} during a drought period in midsummer, soil moisture being below $0.12 \text{ m}_{\text{H}_2\text{O}}^3 \text{ m}^{-3}$, in spite of higher total precipitations than in 1997-1998 (Janssens *et al.*, 2003). In addition to these climatic differences, a thinning in H1 that occurred in February 2004 could have decreased the root respiration in CP of H1 (Coleman *et al.*, 2002).

Site variability of autotrophic contribution to soil CO_2 efflux

Annual autotrophic contributions to soil respiration, estimated to 72% and 59% in H1 and H2, respectively, were rather high (especially in H1) but remained within the range of published estimations (Table 4). H1 and H2 differ through beech age, soil hydromorphy and stand structure. For a quasi-similar annual R_S value ($529 \text{ g}_C \text{ m}^{-2} \text{ y}^{-1}$), higher R_A contribution to total R_S in H1 than in H2 could be explained by several hypotheses. Autotrophic component might be higher in H1, in relation with root surface or biomass with increasing stand age until adult but not mature stands (Gough *et al.*, 2004; Claus and George, 2005). Recently, a chronosequence approach in a black spruce (*Picea marianna* (Mill.) BSP) forest found a lowest R_A contribution in youngest and oldest stands (7 and 152 years old, respectively) in comparison with other stand ages, but they related those differences even more to influence of understory vegetation on root biomass than overstory age (Bond Lamberty *et al.*, 2004a). Moreover, our estimation in root biomass revealed no significant differences between sites. Another hypothesis would lead to the possible relationship between R_A and forest productivity, as supported by recent advances highlighting the importance of linkage between plant gross primary production and R_S via rapid allocation of newly assimilated C to roots (Janssens *et al.*, 2001; Höglberg *et al.*, 2001; Cardon *et al.*, 2002;

Högberg *et al.*, 2002; Ciais *et al.*, 2005; Tang *et al.*, 2005). However, total aboveground biomass increment, which could be considered as an indicator of forest productivity, calculated in 2004 for H1 ($5.0 \cdot 10^3 \text{ kg}_{\text{DM}} \text{ ha}^{-1}$) and H2 ($8.8 \cdot 10^3 \text{ kg}_{\text{DM}} \text{ ha}^{-1}$, Le Goff, INRA Nancy, France, pers. comm.), did not match the higher R_A contribution in H1 than in H2. Total belowground biomass increment, fine root turnover and nitrogen content in root biomass were shown to influence root respiration (Burton *et al.*, 1998; Pretgizer *et al.*, 1998; Widén and Majdi, 2001).

Alternatively, higher R_A contribution to total R_S could inversely be considered as lower R_H contribution, partly due to lower microbial biomass or/and activity. One year after trenching, microbial C and N in CP of H1 was higher than in other plots, while lower microbial C for lower R_H contribution would be expected. In the other hand, DOC content, which was not related significantly with microbial C, was higher in H2. Such results would then suggest a greater microbial activity in H2 but further observations are needed to confirm this hypothesis.

Temperature sensitivity of R_S seemed to not differ between sites (Table 2) while trenching affected Q_{10} values. Integrating several processes as both root and heterotrophic respirations (as in our CP) and their responses to soil temperature and moisture is known to exhibit high Q_{10} values (Davidson *et al.*, 1998; Janssens and Pilegaard, 2003). However, several authors pointed out the role of roots in the temperature sensitivity of R_S , leading to higher Q_{10} values for autotrophic respiration than for heterotrophic respiration (Boone *et al.*, 1998; Epron *et al.*, 2001, Reichstein *et al.*, 2005), as shown by our results. This difference would be attributed to a confounding effect of plant phenological variations across seasons, soil water content and temperature sensitivity itself (Epron *et al.*, 2001; Baath and Wallander, 2003; Janssens *et al.*, 2003; Lavigne *et al.*, 2003; Yuste *et al.*, 2004; Reichstein *et al.*, 2005).

Effect of trenching on root decomposition and microbial biomass

Our study assumed that trenching would suppress R_A inside TP by severing roots inside TP. One of the most important concerns is the necessary of correcting the measured flux inside TP for the additional CO_2 from decaying roots due to trenching Hanson *et al.* (2000). We estimated in H1 and H2 annual CO_2 effluxes from decaying roots (R_E) averaging $189 \text{ gC m}^{-2} \text{ y}^{-1}$ and $183 \text{ gC m}^{-2} \text{ y}^{-1}$, corresponding, respectively, to 56% and 46% of total soil CO_2 efflux from TP (R_{STP}), and 36% and 35% of total soil CO_2 efflux from CP (R_{SCP}). Corrections were rather higher but consistent with those already published studies (Table 4). However, R_E calculations were subject to several uncertainties. First, our approach was based on determination of initial root biomass (B_0) inside TP, which exhibited rather high CI in comparison with remaining root biomass estimates. We performed a sensitivity analysis to assess whether varying B_0 within his CI (see Results) would affect R_E estimations and, consequently, on contribution of R_A to total R_S . Autotrophic contribution was very sensitive to B_0 estimation (Figure 4a), ranging from 51% (H1) and 44% (H2) at the lower limit of IC to 101% (H1) and 82% (H2), partly due to intrinsic spatial variability of root biomass at a fine scale.

It was assumed a correcting factor of 0.45 for spatial and vertical correction for total root biomass from soil core (Epron *et al.*, 1999). Varying this correcting factor from 0.1 (root biomass from soil cores would represent 10% of total root biomass) to 0.7 revealed a high sensitivity of R_A contribution (Figure 4b) that ranged from 217% (H1) and 309% (H2) to 57% (H1) and 56% (H2). Despite the fact that our study was located in the same stand, such assumed value of 0.45 could overestimate total B_0 , as we would have installed TP in an area

with more superficial hydromorphic trait. Then, vertical root biomass profile would differ in a higher proportion of roots in superficial layers.

Another assumption was made when considering the fraction of C incorporated in SOM during decomposition (α) that was set at 0.3. Despite few studies available, this value was chosen as intermediate value between 0.22 (Jenkinson, 1990) and 0.4 (Parton *et al.*, 1987). Fraction of C incorporated in SOM during beech leaf litter decomposition was estimated to 0.2 (Ngao *et al.*, 2005). Sensitivity analysis on α varying between 0.2 and 0.4 lead to autotrophic contribution ranging from 77% (H1) and 64% (H2) to 67% (H1) and 54% (H2), respectively ($\pm 5\%$ in contribution), suggesting that within the tested range of α , R_A contribution was slightly sensitive to α parameter (Figure 4c).

By severing roots for suppressing R_A , trenching also canceled evapotranspiration within the TP that greatly affected θ_{Vsurf} evolution compared to CP (Figure 2b). But calculating annual CO_2 effluxes using interpolated values of θ_{Vsurf} of TP lead to only increase of 5-7% in all treatments, and to low but no negligible change in R_A contribution (71% and 56% in H1 and H2, respectively). These results suggested that θ_{Vsurf} in CP would be more limiting and controlling for R_S than T_S during only a short period in summer (Yuste *et al.*, 2003; Lavigne *et al.*, 2004). While T_S and θ_{Vsurf} often covaried in temperate forests (Davidson *et al.*, 1998; Janssens *et al.*, 2003), they were decoupled in TP as well as T_S varied in his full seasonal range in no limiting moisture conditions. Thus, similar slight increase in annual R_S mentioned above would refer to an influence of θ_{Vsurf} more on heterotrophic component than roots (Epron *et al.*, 2001) contrary to Lavigne *et al.* (2004), and adding evidence for a confounding effect between T_S and θ_{Vsurf} through high Q_{10} values in intact soil.

Acknowledgements

M. F. Willm and B. Clerc are warmly thanked for their technical supply in trenching plots. M. C. Nguyen and Patrice Marchal (ENSAIA, Vandoeuvre-Lès-Nancy, France) and Ms J. Marchand are also thanked for the microbial biomass determination, and C/N measurements, respectively. The authors also thanked Ms N. Bréda for her helpful discussion concerning field and soil water content measurement. M. Laurent Saint-André (CIRAD, Montpellier, France) is warmly thanked for helping the author in using Monte-Carlo simulations. This work was supported by the European project CarboEurope IP.

References

- Baath E. and Wallander H. (2003). Soil and rhizosphere microorganisms have the same Q_{10} for respiration in a model system. *Global Change Biology* 9: 1788-1791.
- Balesdent J. and Balabane M. (1996). Major contribution of roots to soil carbon storage inferred from maize cultivated soils. *Soil Biology Biochemistry* 28: 1261-1263.
- Bhupinderpal-Singh, Nordgren A., Löfvenius M.O., Högberg M.N., Mellander P.E. and Hogberg P. (2003). Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year. *Plant Cell Environment* 26: 1287-1296.
- Bond-Lamberty B., Wang C. K. and Gower S. T. (2004). A global relationship between the heterotrophic and autotrophic components of soil respiration? *Global Change Biology* 10: 1756-1766.
- Boone R.D., Nadelhoffer K.J., Canary J.D. and Kaye J.P. (1998). Root exert a strong influence on the temperature sensitivity of soil respiration. *Nature* 396: 570-572.

-
- Bouma T.J., Nielsen K.L., Eissenstat D.M. and Lynch J.P. (1997). Estimating respiration of roots in soil: interaction with soil CO₂, soil temperature and soil water content. *Plant soil* 195: 221-232.
- Bowden R.D., Nadelhoffer K.J., Boone R.D., Melillo J.M. and Garrison J.B. (1993). Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. *Canadian Journal Forest Research* 23: 1402-1407.
- Cardon Z.G., Czaja A.D., Funk J.L. and Vitt P.L. (2002). Periodic carbon flushing to root of *Quercus rubra* saplings affects soil respiration and rhizosphere microbial biomass. *Oecologia* 133: 215-223.
- Ciais P., Reichstein M., Granier A., Ogée J., Allard V., Aubinet M., Buchmann N., Bernhofer C., Carrara A., Chevallier F., De Noblet N., Friend A., Friedlingstein P., Gründwald T., Heinesch B., Keronen P., Knohl A., Krinner G., Lousteau D., Manca G., Matteucci G., Miglietta F., Ourcival J.M., Papale D., Pilegaard K., Rambal S., Seufert G., Soussana J.F., Sanz M.J., Schulze E.D., Vesala T. and Valentini R. (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* doi: 10.1038/nature03972.
- Ekblad A. and Hogberg P. (2001). Natural abundance of ¹³C in CO₂ respired from forest soils reveals speed of link between tree photosynthesis and root respiration. *Oecologia* 127: 305-308.
- Epron D., Farque L., Lucot E. and Badot P.M. (1999). Soil CO₂ efflux in a beech forest: dependence on soil temperature and soil water content. *Annals of Forest Science* 56: 221-226.
- Epron D., Farque L., Lucot E. and Badot P.M. (1999). Soil CO₂ efflux in a beech forest: the contribution of root respiration. *Annals of Forest Science* 56: 289-295.
- Epron D., Le Dantec V., Dufrene E. and Granier A. (2001). Seasonal dynamics of soil carbon dioxide efflux and simulated rhizosphere respiration in a beech forest. *Tree Physiology* 21: 145-152.
- Epron D., Nouvellon Y., Roupsar O., Mouvondy W., Mabiata A., Saint-Andre L., Joffre R., Jourdan C., Bonnefond J.M., Berbigier P. and Hamel O. (2004). Spatial and temporal variations of soil respiration in a Eucalyptus plantation in Congo. *Forest Ecology and Management* 204: 149-160.
- Ewel K.C., Cropper W.P. and Gholz H.L. (1987). Soil CO₂ evolution in Florida slash pine plantations. I. Changes through time. *Canadian Journal Forest Research* 17: 325-329.
- Fang C. and Moncrieff J.B. (1998). An open-top chamber for measuring soil respiration and the influence of pressure difference on CO₂ efflux measurement. *Functional Ecology* 12: 319-325.
- Fessenden J. E. and Ehleringer J. R. (2003). Temporal variation in delta C-13 of ecosystem respiration in the Pacific Northwest: links to moisture stress. *Oecologia* 136: 129-136.
- Formanek P. and Ambus P. (2004). Assessing the use of d13C natural abundance in separation of root and microbial respiration in a Danish beech (*Fagus sylvatica* L.) forest. *Rapid Communication in Mass Spectrometry* 18: 1-6.
- Gough C. M. and Seiler J. R. (2004). The influence of environmental, soil carbon, root, and stand characteristics on soil CO₂ efflux in loblolly pine (*Pinus taeda* L.) plantations located on the South Carolina Coastal Plain. *Forest Ecology and Management* 191: 353-363.
- Hanson P.J., Edwards N.T., Garten C.T. and Andrews J.A. (2000). Separating root and soil microbial contribution to soil respiration : A review of methods and observations. *Biogeochemistry* 48: 115-146.
- Högberg P., Nordgren A., Buchmann N., Taylor A.F.S, Ekblad A., Hogberg M.N., Nyberg G., Ottoson-Löfvenius M. and Read D.J. (2001). Large scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411: 789-792.
- Ibrahima A., Joffre R. and Gillon D (1995). Changes in litter during the initial leaching phase: an experiment on the leaf litter of Mediterranean species. *Soil Biology Biochemistry* 27: 931-939.

IPCC (2000). L'utilisation des terres, le changement d'affectation des terres et la foresterie. Nairobi, GIEC: 24.

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., Gudmundson J., Minerbi S., Berbigier P., Ibrom A., Moncrieff J.B., Aubinet M., Bernhofer C., Jensen N.O., Vesala T., Granier A., Schulze E.D., Lindroth A., Dolman A.J., Jarvis P.G., Ceulemans R. and Valentini R. (2001). Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology* 7: 269-278.

Janssens I. A., Dore S., Epron D., Lankreijer H., Buchmann N., Longdoz B., Brossaud J. and Montagnani L. (2003). Climatic influences on seasonal and spatial differences in soil CO₂ efflux. *Fluxes of Carbon, Water and Energy of European Forests*. Berlin, Springer-Verlag Berlin. 163: 233-253.

Janssens I. A. and Pilegaard K. (2003). Large seasonal changes in Q(10) of soil respiration in a beech forest. *Global Change Biology* 9: 911-918.

Kutsch W.L., Staack A., Wötzel J., Middelhoff U. and Kappen L. (2001). Field measurements of root respiration and total soil respiration in an alder forest. *New Phytologist* 150: 157-168.

Kuzyakov Y. and Cheng W. (2001). Photosynthesis controls of rhizosphere respiration and organic matter decomposition. *Soil Biology Biochemistry* 33: 1915-1925.

Lankreijer H., Janssens I. A., Buchmann N., Longdoz B., Epron D. and Dore S. (2003). Measurement of soil respiration. *Fluxes of Carbon, Water and Energy of European Forests*. Berlin, Springer-Verlag Berlin. 163: 37-54.

Lavigne M. B., Boutin R., Foster R. J., Goodine G., Bernier P. Y. and Robitaille G. (2003). Soil respiration responses to temperature are controlled more by roots than by decomposition in balsam fir ecosystems. *Canadian Journal of Forest Research* 33: 1744-1753.

Lavigne M. B., Foster R. J. and Goodine G. (2004). Seasonal and annual changes in soil respiration in relation to soil temperature, water potential and trenching. *Tree Physiology* 24: 415-424.

Lee M. S., Nakane K., Nakatsubo T. and Koizumi H. (2003). Seasonal changes in the contribution of root respiration to total soil respiration in a cool-temperate deciduous forest. *Plant and Soil* 255: 311-318.

Lloyd J. and Taylor J.A. (1994). On the temperature dependence of soil respiration. *Functional Ecology* 8: 315-323.

Longdoz B., Yernaux M. and Aubinet M. (2000). Soil CO₂ efflux measurements in a mixed forest: impact of chamber disturbances, spatial variability and seasonal evolution. *Global Change Biology* 6: 907-917.

Ohashi M., Gyokusen K. and Saito A. (2000). Contribution of root respiration to total soil respiration in a Japanese cedar (*Cryptomeria japonica* D. Don) artificial forest. *Ecological Research* 15: 323-333.

Parton W.J., Schimel D.S., Cole C.V. and Ojima D.S. (1987). Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal* 51: 1173-1179.

Pregitzer K.S., Lakowski M.J., Burton A.J., Lessard V.C. and Zak D.R. (1998). Variation in sugar maple root respiration with root diameter and soil depth. *Tree Physiology* 18: 665-670.

Raich J.W. and Schlesinger W.H. (1992). The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B: 81-99.

Reichstein M., Tenhunen J., Roupsard O., Ourcival J. M., Rambal S., Miglietta F., Peressotti A., Pecchiari M., Tirone G. and Valentini A. (2003). Inverse modeling of seasonal drought effects on canopy CO₂/H₂O exchange in tree Mediterranean ecosystems. *Journal of Geophysical Research* 108.

Reichstein M., Subke J.A., Angeli A.C. and Tenhunen J.D. (2005). Does the temperature sensitivity of decomposition of soil organic matter depend upon water content, soil horizon, or incubation time. *Global Change Biology* 11: 1-14.

Reth S., Reichstein M. and Falge E. (2005). The effect of soil water content, soil temperature, soil pH-value and the root mass on soil CO₂ efflux - A modified model. *Plant and Soil* 268: 21-33.

Rochette P., Flanagan L.B. and Gregorich E.G. (1999). Separating soil respiration into plant and soil components using analyses of the natural abundance of carbon-13. *Soil Science Society of America Journal* 63: 1207-1213.

Russell C.A. and Voroney R.P. (1998). Carbon dioxide efflux from the floor of a boreal aspen forest. I. Relationship to environmental variables and estimates of C respired. *Canadian Journal of Soil Science* 78: 301-310.

Subke J.A., Reichstein M. and Tenhunen J.D. (2003). Explaining temporal variation in soil CO₂ efflux in a mature spruce forest in Southern Germany. *Soil Biology Biochemistry* 35: 1467-1483.

Tang J., Baldocchi D. and Xu L. (2005). Tree photosynthesis modulates soil respiration on a diurnal time scale. *Global Change Biology* 11: 1298-1304.

Thierron V. and Laudelout H. (1996). Contribution of root respiration to total CO₂ efflux from the soil of a deciduous forest. *Canadian Journal of Forest Research* 26: 1142-1148.

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., Guomundsson J., Thorgeirsson H., Ibrom A., Morgenstern K., Clement R., Moncrieff J.B., Montagnani L., Minerbi S. and Jarvis P.G. (2000). Respiration as the main determinant of carbon balance in European forests. *Nature* 404: 861-864.

Yuste C.J., Nagy M., Janssens I.A., Carrara A. and Ceulemans R. (2005). Soil respiration in a mixed temperate forest and its contribution to total ecosystem respiration. *Tree Physiology* 25: 609-619.

Yuste J. C., Janssens I. A., Carrara A. and Ceulemans R. (2004). Annual Q(10) of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Global Change Biology* 10: 161-169.

Tables

	H1	H2
Leaf area index ($m^2.m^{-2}$)	6.9	7.4
Tree density (stems ha^{-1})	7015	17938 (7337)
Ground area ($m^2.ha^{-1}$)	47.5	12.6 (7.9)
Mean annual temperature ($^{\circ}C$)	9.7	
Mean annual precipitations (mm)	913	

Table 1. Main characteristics of studied sites. Numbers in brackets indicate specific value for beech (*Fagus sylvatica* L.).

	H1		H2	
	CP	TP	CP	TP
R_{10} ($\mu mol_{CO_2}.m^{-2}.s^{-1}$)	1.39 (0.14)	0.92 (0.09)	1.36 (0.08)	1.08 (0.09)
Q_{10}	3.14 (0.58)	2.42 (0.44)	3.11 (0.29)	2.51 (0.31)
R^2	0.76	0.68	0.90	0.83
RMSE	0.47	0.29	0.32	0.31

Table 2. Fitted parameters (R_{10} , Q_{10}), determination coefficient (R^2) and root mean square error (RMSE) derived from least mean square non-linear regression of equation (1) given for control (CP) or trenched (TP) plots in H1 and H2 sites. Standard errors are given under brackets.

	H1		H2	
	CP	TP	CP	TP
Microbial C ($\mu g_C.g^{-1}$)	136 (11)*	98 (4)	112 (5)	104 (12)
DOC ($\mu g_C.g^{-1}$)	132 (5)	125 (5)	167 (8)*	150 (15)*
Microbial N ($\mu g_N.g^{-1}$)	38 (3)*	29 (1)	31 (2)	29 (3)

Table 3. Microbial C and N, and dissolved organic carbon (DOC) contents from soil cores sampled inside the trenched plots. The * symbol indicates a significant difference among plots at $p=0.05$ level. Standard errors are given under brackets.

Figures

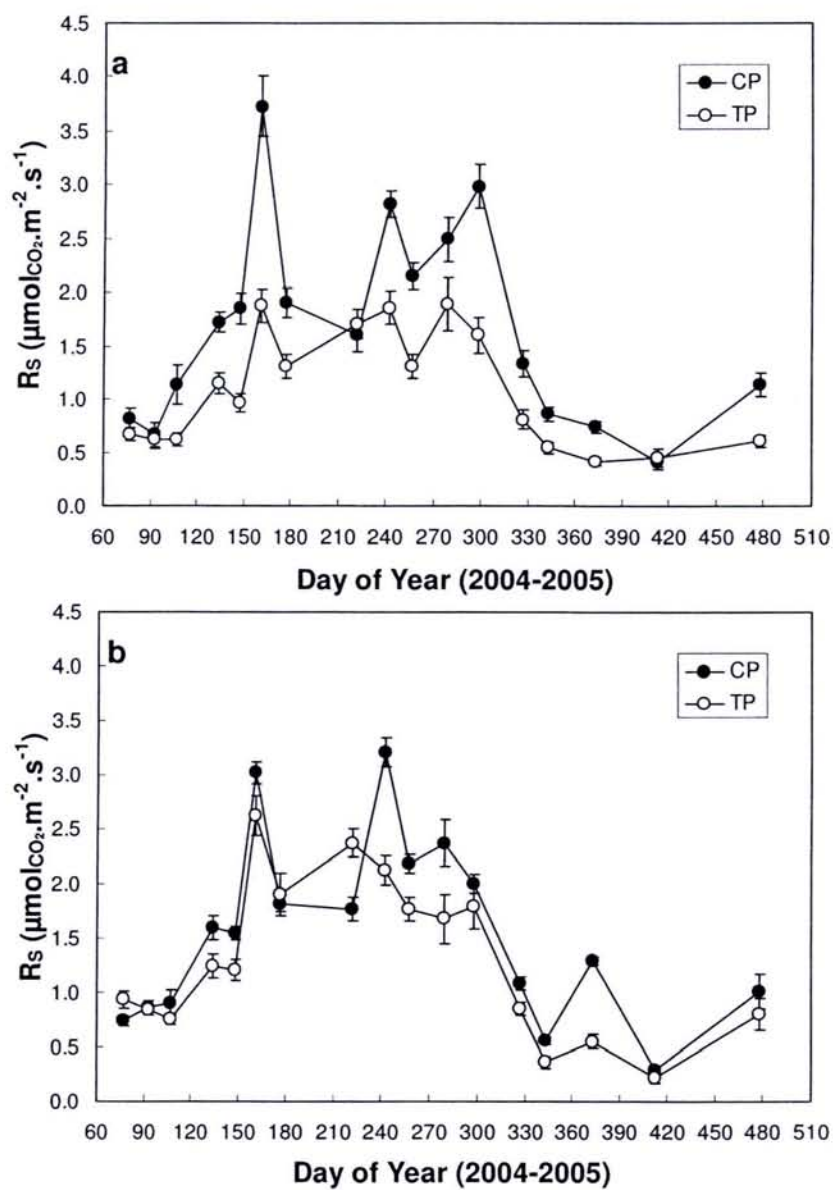


Figure 1. Seasonal evolution of R_s in control (CP) or trenched (TP) plots in H1 (a) or H2 (b) sites. Errors bars, when larger than symbols represent standard errors.

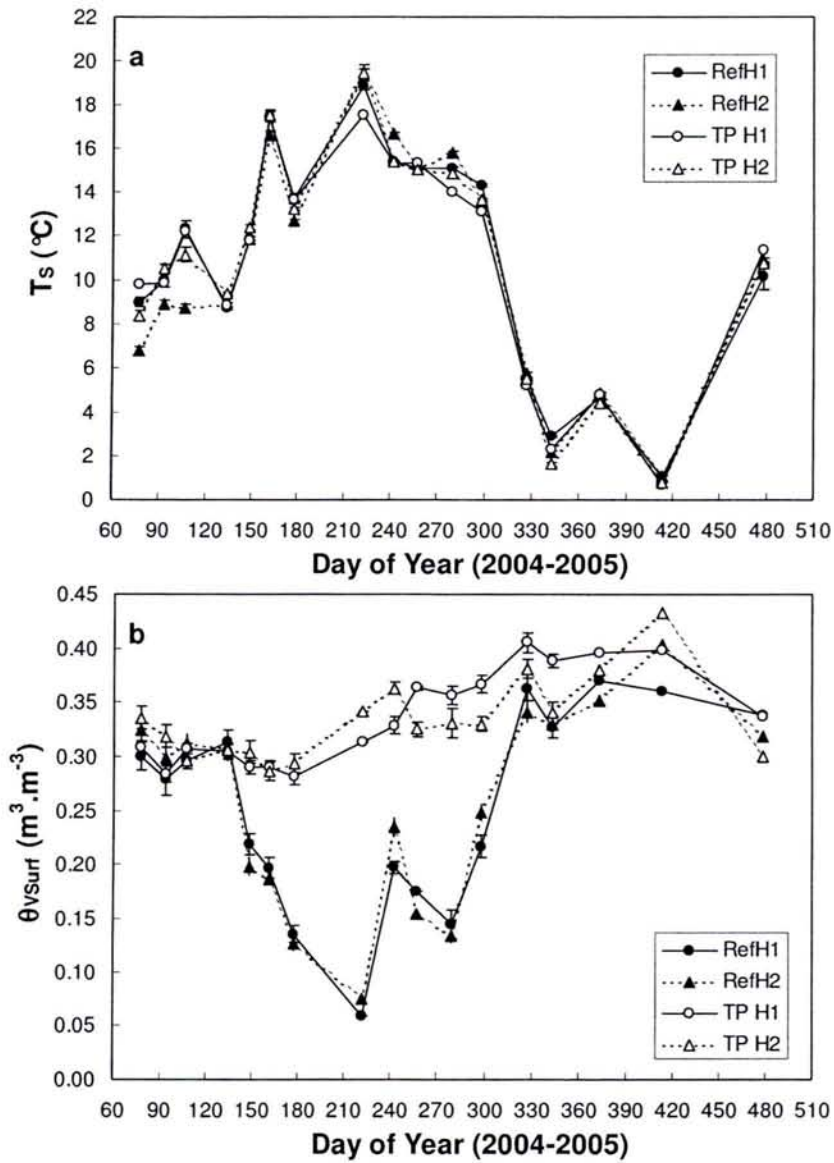


Figure 2. Seasonal evolution of soil temperature at -10 cm (T_s , a) and soil volumetric water content (θ_{surf} , b) in the four treatments (control or trenched plots, H1 or H2 sites). Errors bars when larger than symbols represent standard errors.

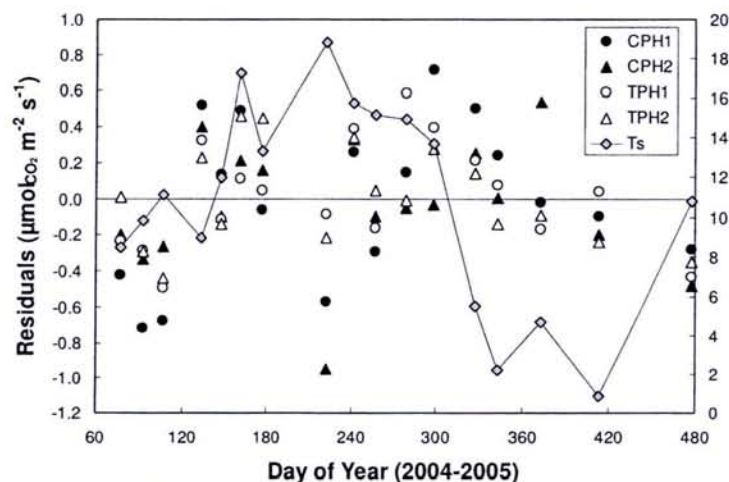


Figure 3. Temporal evolution of residual for the four treatments, and evolution of mean soil temperature at -10 cm (T_s) calculated from daily mean of all plots.

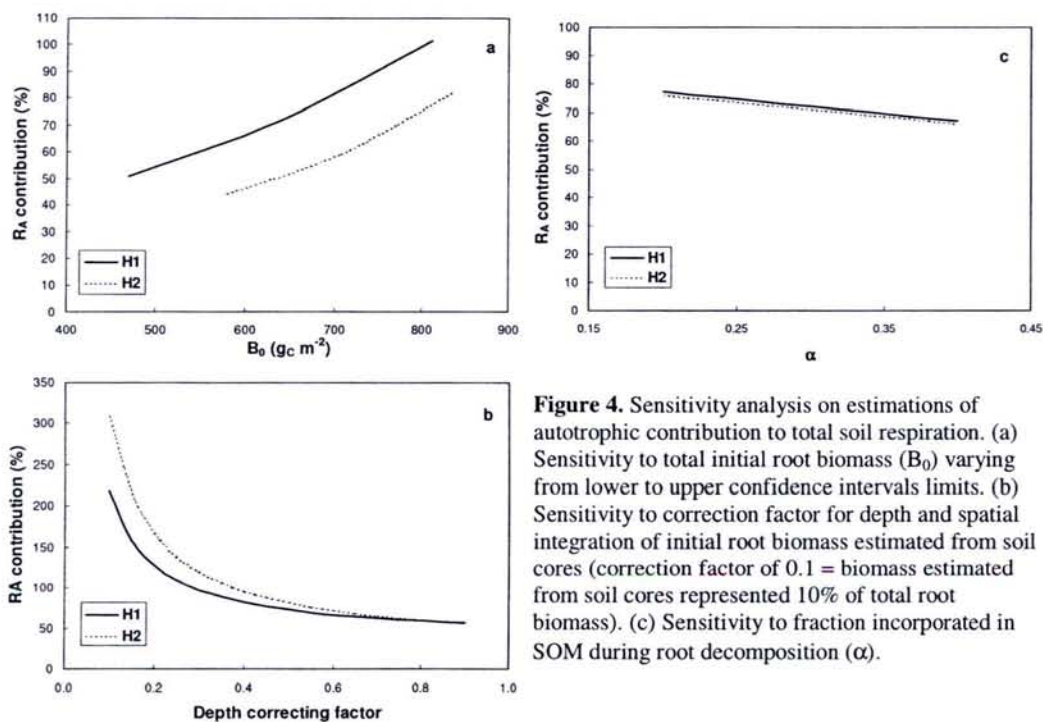


Figure 4. Sensitivity analysis on estimations of autotrophic contribution to total soil respiration. (a) Sensitivity to total initial root biomass (B_0) varying from lower to upper confidence intervals limits. (b) Sensitivity to correction factor for depth and spatial integration of initial root biomass estimated from soil cores (correction factor of 0.1 = biomass estimated from soil cores represented 10% of total root biomass). (c) Sensitivity to fraction incorporated in SOM during root decomposition (α).

**ARTICLE 5: Spatial variation of soil CO₂ efflux in a beech forest
in relation with soil and stand characteristics**

J. Ngao¹, B. Longdoz^{1*}, D. Epron², N. Breda¹, A. Granier¹

¹ UMR Ecologie et Ecophysiologie Forestière, Centre INRA de Nancy, 54280 Champenoux, France

² UMR Ecologie et Ecophysiologie Forestière, Université Henri Poincaré Nancy 1, 54506 Vandoeuvre-les-Nancy cedex, France

*Corresponding author:

Bernard Longdoz (longdoz@nancy.inra.fr)

Fax: (+33) 383 394 069

Phone: (+33) 383 394 038

Running title: Spatial variation of soil respiration

Abstract

This study aimed to characterize the spatial variability of soil respiration (R_S) within across an European beech stand by determining the main soil and stand factors potentially driving R_S . We aimed to explain the seasonal variations of R_S through an empirical model. We conducted R_S measurements in 2003 and 2004 in 9 plots differing in their soil type and, occasionally in tree age. The fitted model explained 69% of seasonal variability of R_S when data from all plots were used. The basal respiration at 10°C (R_{10i}) varied among plots. Correlation analyses revealed that root biomass did not allow explaining spatial variability of R_{10i} , as like as litter C and soil C contents, stand basal area and density. Basal respiration is significantly correlated with topsoil bulk density and C/N ratio, and with leaf area index. When LAI was not taken into account in a multiple regression analysis because of a partial correlation with C/N ratio, the latter and topsoil bulk density would explain 87% of spatial variability of R_{10i} . This study highlighted the spatial variability of R_S and addressed the potential need to consider spatially varying factors in soil respiration models and

Introduction

In the global changing climate context and increasing atmospheric CO₂ concentration, European forest ecosystems act as carbon sink (Valentini *et al.*, 2000; Janssens *et al.*, 2003). Several evidences showed that the sink strength depends more upon total ecosystem CO₂ efflux (R_{ECO}), as its variations among ecosystems would much vary than gross primary production (GPP) (Grace and Rayment, 2000; Valentini *et al.*, 2000; Granier *et al.*, 2002). Soil CO₂ efflux (R_S) is the second C flux after GPP and the main component of R_{ECO} (Raich and Schlesinger, 1992; Granier *et al.*, 2000; Janssens *et al.*, 2001). Modeling and predicting changes in R_S in relation with a forest carbon (C) balance context is still subject to uncertainties mainly due to both temporal and spatial variability of R_S.

Determinism of temporal variability of R_S has been assessed at the interannual scale (Savage and Davidson, 2001; Raich *et al.*, 2002; Epron *et al.*, 2004a), but seasonal variability remained the most common time scale approach. In a given site in temperate climate, soil temperature is the main determinant of R_S seasonal evolution (Lloyd and Taylor, 1994; Longdoz *et al.*, 2000), and several evidences highlighted the predominant role of root respiration (also called autotrophic respiration) in temperature sensitivity of R_S (Boone *et al.* 1998; Widén and Majdi, 2001; Epron *et al.*, 2001; Lavigne *et al.*, 2004). Temperature sensitivity of R_S is often described through the Q₁₀ factor (van't Hoff, 1898), whereas it is calculated on measurements taken across the entire year during which different processes may seasonally change in both intensity and differ in temperature responses, leading to misestimate actual temperature sensitivity of R_S (Janssens and Pilegaard, 2003; Curiel Yuste *et al.*, 2004). However, with Arrhenius function (Lloyd and Taylor, 1994), Q₁₀ function is one of the most used and provides useful description of temporal variability when the latter have to be consider. Soil water content (θ_v) also exerts a strong influence on R_S, limitation occurring at low or high θ_v values (Janssens *et al.*, 2003). Both soil temperature and θ_v are able to explain a large part of seasonal variations that generally comprised 60-90% of total variance (Davidson *et al.*, 1998; Epron *et al.*, 1999; Janssens *et al.*, 2003; Curiel Yuste *et al.*, 2003; Lavigne *et al.*, 2004; Reth *et al.*, 2005) in particular in drought sites or periods during which θ_v controls R_S (Reichstein *et al.*, 2002; Rey *et al.*, 2002; Epron *et al.*, 2004b; Ciais *et al.*, 2005). Moreover when considering that soil temperature covary with θ_v as dependent variables (Davidson *et al.*, 1998). Other abiotic and biotic factors have been investigated to explain temporal variability, such as precipitation, photosynthesis, litter decomposition, soil-pH and root mass through empirical models (Rout and Gupta, 1989; Buchmann, 2000; Högberg *et al.*, 2001; Hanson *et al.*, 2003; Gough and Seiler, 2004; Reth *et al.*, 2005; Tang *et al.*, 2005).

Contrary to temporal variations, sources of spatial variations were reported but poorly investigated (Lankreijer, 2003). All approaches for measuring R_S addressed the spatial variability that have to be taken into account for accurate R_S estimation and scaling up: number of measurements by chamber techniques (Adachi *et al.*, 2005), footprint of fluxes determined by eddy covariance method (Schmid, 1994; Schuepp *et al.* 1990), spatial relevance of CO₂ concentration profiles. At a global scale, productivity and precipitations seemed to explain differences in R_S (Janssens *et al.*, 2001; Raich *et al.*, 2002). At smaller scales, sites variations highlighted differences in R_S in relation with soil temperature, roots biomass, litter layer, C and nutrient contents in mineral soil, and leaf area index (LAI) (Stoyan *et al.*, 2000; Borken *et al.*, 2002; Reichstein *et al.*, 2003; Gough et Seiler, 2004). However, few studies focused on intra-site variability of R_S, on which soil and stand structure at a stand scale would therefore influence. Thus this concern is crucial for comparing annual R_S and annual R_{ECO} when these fluxes are not sampled from the same

spatial sources, and moreover when contribution of R_S to R_{ECO} change seasonally (Curiel Yuste *et al.* 2005).

This study aimed to assess the spatial variability of R_S within a European beech stand by determining the main factors potentially driving R_S . We aimed to explain the seasonal variations of R_S through an empirical model. We conducted R_S measurements in 9 plots differing in their soil type and, occasionally in tree age. From plot data, model parameters as well as annual estimations of R_S were compared with main soil and plot characteristics, in the aim to model spatial variations of R_S .

Material and methods

Sites

The study was conducted in the Hesse state forest (48°40'N, 7°05'E, altitude 305m) in the Northeast of France. European beech (*Fagus sylvatica* L.) and oaks (*Quercus petraea* (Matt.) Lielb. and *Q. robur* L.) are the main species. We focused on dominated 35-year old beech stands, even if a part of the study was located in a 20-year beech area mixed with hornbeam (*Carpinus betulus* L.) and oaks (*Quercus petraea* (Matt.) Lielb. and *Q. robur* L.). Table I gives main characteristics for 2003 and 2004. Mean annual temperature and precipitations are 9.2°C and 820 mm, respectively (Granier *et al.*, 2000). In the studied area, soil type is between luvisol and stagnic luvisol (FAO classification) covered by a mull (see below) humus type (almost no O_F and no O_H layers below the O_L layer), highlighting a high biological activity. However, a hydromorphic gradient induce a variation of soil type following the depth at which appears a silt-clay layer and the degree of winter water excess as revealed by oxydo-reduction spots (Quentin *et al.*, 2001, Bouriaud *et al.*, 2003): The BO type had no silt-clay layer. In opposition, The BOR type has a superficial silt-clay layer (65-100 cm layer) and oxydo-reduction spots appear at -35 cm, defining the most pronounced hydromorphic type. The BRe type is in an intermediate range with oxydo-reduction spots appearing at -60 cm. BO and BRe soils are covered by oligo-mull humus, while the BOR type is covered by meso-mull humus. All types are acidic soil (mean pH_{H_2O} and pH_{KCl} reaching 4.5 and 3.8 for the 0-10 cm layer respectively) that does not contain carbonate (Quentin *et al.*, 2001).

Soil respiration measurements

Measurements of R_S were conducted with a closed dynamic chamber system (Li 6000-9, Licor, Lincoln, USA) connected to an infrared gas analyzer (IRGA) Li-6252 (Licor, Lincoln, USA). Air circulation inside the chamber is provided by the pump of the Li-6252 (flow rate 1.5 l.min⁻¹) and drives the air inside the chamber through a drilled ring that allows air mixture and homogenization. Once the chamber laid on a PVC collar (110 mm diameter), we waited 10 s before starting the record of CO₂ concentration ([CO₂]) during 60 s. Collars were inserted into soil (1.5 cm depth) two weeks before the first measurements, and left during the entire experiment time. A foam gasket ring provided an airtight seal between the chamber and the collar. No significant difference of pressure between the inside and the outside of the chamber was found, thus major risks of air leak were avoided (Longdoz *et al.*, 2000). Slopes values ($\mu\text{mol}_{CO_2} \text{ mol}^{-1}$) calculated by the Licor system were selected in field regarding to slope standard deviation (SD) less than 0.04 $\mu\text{mol}_{CO_2} \text{ mol}^{-1}$, considering that SD above this threshold reflected an irregular increase of [CO₂] within the chamber.

We conducted R_S measurements in 3 plots selected by in each soil type. Seven plots were installed in a 35-year old beech area (H1A, H1B, H1C, H1D, H1E, H1F and H1G) while the 2 other plots were installed in the 20-year old mixed beech area (H2B and H2I). Maximum distance between 2 plots is 700 m. Within each plot, 12 collars were inserted in soil following 2 transects, and distance between collars were arbitrary set to 1 m. R_S was measured in all plots every 2-3 weeks during 18 months from August 2003 to January 2005. Measurements performed from 8:00 a.m. to sunset were averaged by plot and mean value is assumed to represent daily mean R_S since previous measurements highlighted that there were no significant diurnal variations of R_S (unpublished data). Daily R_S per plot were calculated with their 95% confidence intervals.

Soil temperature and water content

Continuous measurements of soil temperature at -10 cm (T_{SC}) are made by 5 and 4 copper-constantan thermocouples in H1 and H2 sites, respectively. Data were acquired every 10 s and 30-min averages were stored (Model CR7 datalogger, Campbell Scientific, Courtaboeuf, France). Continuous measurement of volumetric soil water content at -10 cm (θ_v) are made by a time-domain reflectance (TDR) TRAS system (SoilMoisture Equipement Corp., Santa Barbara, USA). Data were acquired every hour. Daily T_{SC} and θ_v per plot were calculated for 2003 and 2004 (Figure 1). T_S and soil water content in the 0-6 cm layer (θ_{surf}) were also measured concurrently with R_S in the vicinity of soil respiration chamber by using a homemade copper-constantan thermocouple (M. Yernaux, Faculty of Agronomy of Gembloux, Belgium), and an ML2x ThetaProbe (Delta-T Device, Cambridge, UK), respectively.

Stand and soil characterization

Maximum LAI in plots were determined with a LAI2000 (Licor, Lincoln, USA) in mid summer 2003 and 2004. Diameter at breast height (DBH) was measured in January 2005 in all plots on all living trees inside a 7 m-diameter circle centred on the collars transects. In spite of a smaller sampling area than previous studies (Granier *et al.*, 2000; Bouriaud *et al.*, 2003) basal area (G) and tree density (N) deduced from these measurements allowed a rather good description of plots. The G/N ratio, that represents the mean individual basal area, was computed in order to describe the effect of tree

In order to determine C compartments within each plot, 6 soil cores (15 cm height, 8 cm diameter) were sampled in January 2005 following the collar transects, but we avoided zones of soil compaction resulted from frequent measurements. Leaf and woody litters were coarsely separated in field from bulk soil. In laboratory, remaining leaf fragments and bud scales were easily retrieved, since there was almost no O_F and no O_H layers below the O_L layer. Then, we measured the A_0 layer depth and gently isolated it following a visual transition from highly organic black-colored top layer to brown colored core. During both litter and A_0 layer isolation, both living and dead roots were retrieved. Soil was sieved (2 mm mesh size), while roots were manually retrieved, dead roots being recognized by black color, low rigidity and density, and disaggregating cortex. Remaining aggregates were partly dissolved in distilled water for 24 hours and sieved (2 and 1 mm mesh size) for retrieving the remaining roots. All organic materials were oven-dried during 5 days at 65°C, A_0 and bulk soil were dried at 30°C during 5 days. Carbon and nitrogen (N) contents of materials (litter, roots, bulk soil organic matter (SOM) and A_0 OM) were determined in a NCS2500 elemental analyzer (CE Instrument ThermoQuest, Italy). Concurrently to soil coring, topsoil density

was assessed by specific cylinders. In each plot, we removed standing litter in the vicinity of previous soil cores, and took 6 soil samples using steel cylinders (5 cm height, 8 cm diameter) following the collar transects, too. In addition three other soil samples were taken following a third transect within the plot.

Data analysis

We analyzed data of 2003 and 2004 together because in 2003, we covered a range of T_S and θ_{surf} that did not allow an extrapolation to the whole year. In addition, 2003 summer drought give us the opportunity to describe accurately the effect of θ_{surf} on R_S . In a first step, an empirical model was fitted to daily R_S , T_S and θ_{surf} data by each plot with least square non linear regression (SAS 8.1, SAS Institute Inc., USA),

$$R_S = R_{10} Q_{10}^{\frac{T_S - 10}{10}} e^{-e^{(a - b \theta_{\text{surf}})}} \quad (1)$$

Where R_{10} is the basal respiration at 10°C, Q_{10} is the parameter which multiply R_S when T_S increases by 10°C and is assumed to reflect the temperature sensitivity of R_S , a and b are the parameter of the simplified Gompertz function, which allowed a positive influence on R_S at low θ_{surf} , and no-limiting θ_{surf} range (Janssens *et al.*, 2001). Then, equation (1) was fitted to the entire dataset where R_{10} was allowed to vary among plots and the other parameters were not allowed to vary among plots following:

$$R_S = \sum_i y_i R_{10i} Q_{10}^{\frac{T_S - 10}{10}} e^{-e^{(a - b \theta_{\text{surf}})}} \quad (2)$$

Where R_{10i} is the R_{10} parameter of the plot i and y_i a dummy variable equal to 0 or 1 according to the plot i (Epron *et al.*, 2004a). Equation (1) was applied using parameters determined with equation (2) to simulate daily R_S in field in each plot with continuously monitored T_{SC} and θ_V . θ_V values (-10 cm) were corrected for soil depth through polynomial regression with θ_{surf} values (0-6 cm) recorded in the vicinity of TDR probes. Annual R_S values were calculated by summing simulated daily R_S from 1st January 2004 to 31st December 2004.

One-way ANOVA analysis was used for comparing litter, roots, SOM, A_0 OM and soil density among plots (Statview 5.1, SAS Institute Inc., USA). Two-way ANOVA and further Fischer's protected least significant difference (PLSD) post-hoc tests were performed for comparing R_S , T_S and θ_{surf} among plots and date as independent variables at $p=0.05$ level. Correlation analysis was used in order to investigate relationships among soil parameters, stand characteristics, model parameters (R_{10i} , Q_{10} , a and b) and annual R_S . Among significantly correlated explicative parameters, partial correlation analyses were performed in order to discard covarying parameters. Finally, we performed a stepwise regression analysis aiming at modeling R_S spatial variation.

Results

Soil respiration, soil temperature and soil water content

Soil CO_2 efflux classically showed seasonal variations (Figure 1a) among which daily means per plot ranged from $0.24 \pm 0.10 \mu\text{mol}_{\text{CO}_2} \text{m}^{-2} \text{s}^{-1}$ (mean \pm 95% confidence interval) to $4.1 \pm 0.94 \mu\text{mol}_{\text{CO}_2} \text{m}^{-2} \text{s}^{-1}$. Two-way ANOVA revealed significant differences in R_S among date and plots with a significant interaction date*plot, excepted at DOY 274 and 386 while R_S did not differ significantly among plots. At a given date, when differences were

significant among plot, H1C plot showed the lowest R_S (PLSD, $p < 0.0001$), while plot showing the highest flux value varied between H1B and H1F. Both T_S and θ_{Surf} showed seasonal variations (Figure 1b and c). Seasonal range of daily values of T_S was comprised between $-0.1 \pm 0.2^\circ\text{C}$ and $22.1 \pm 0.7^\circ\text{C}$. Although significant, inter-plot differences in T_S were less than 2°C . Seasonal range of θ_{Surf} was comprised between $0.02 \pm 0.01 \text{ m}^3 \text{ m}^{-3}$ and $0.4 \pm 0.01 \text{ m}^3 \text{ m}^{-3}$, with significant differences among plots.

As expected, lowest R_S values corresponded to low T_S values in winter (around 1°C and 2°C in 2003 and 2004, respectively), while higher R_S values were recorded for rather warm soil (T_S around 15°C) combined with not limiting θ_{Surf} values that ranged between $0.18 \text{ m}^3 \text{ m}^{-3}$ to $0.27 \text{ m}^3 \text{ m}^{-3}$ for the same date. The response of R_S to T_S evolution was best predicted by an exponential function (Q_{10} , $R^2 = 0.25-0.63$; $\text{RMSE} = 0.24-0.50$) but residuals of this relationship showed that (1) Q_{10} function underestimated actual R_S when T_S was above 17°C (Figure 3a), and (2) a significant non-linear relation with θ_{Surf} on which the Gompertz function can be applied (Figure 3b). Thus, modeling R_S with both T_S and θ_{Surf} lead to no major biases in residuals (Figure 3c). Table 2 presents parameters values of equation (1) per plot, which explained 53% to 90% of seasonal variance of R_S . Adding θ_{Surf} as independent variable allowed improving performance of model by from 11% to 45%. No significant relationship between R_{10} (Q_{10}) and mean annual soil temperature among plots was found. As Q_{10} , a and b parameters showed low deviations among plots, equation (2) was fitted to all dataset and determined Q_{10} , a and b parameters at $2.70 (\pm 0.29)$, $0.87 (\pm 0.29)$ and $18.06 (\pm 5.20)$, respectively ($\text{RMSE} = 0.45$, $R^2 = 0.69$). R_{10i} values are reported in Table 2. Residuals of equation (2) were unbiased against neither T_S nor θ_{Surf} , but they evolved with a seasonal trend independent to climatic variations of T_S and θ_{Surf} when plotted against time, (Figure 4). Applying equation (2) with T_{SC} and θ_V corrected for depth ($R^2 = 0.95$, $p < 0.0001$) from Figure 1 lead to large spatial differences in annual R_S that ranged from $470 \text{ gC m}^{-2} \text{ y}^{-1}$ (H2I) and $763 \text{ gC m}^{-2} \text{ y}^{-1}$ (H1B, Table 2).

Spatial variation of soil characteristics

Stand and soil characteristics are summarized in Table 3. One-way ANOVA and PLSD tests showed that topsoil density was significantly higher in H2I than in other plots ($p = 0.0036$), while topsoil density in H1C was significantly higher density than H1F. $A_0\text{-C}$ layer was significantly higher in H1F and significantly lower in H1C, H1D and H1G plots than in other plots ($p = 0.0024$). Litter-C was significantly lower in H1D and H1E plots ($p = 0.0027$). No significant differences were found in either living, dead or total roots pools among plots. Bulk soil-C was significantly higher in H1E, H1F and H1G plots than in other plots ($p < 0.0001$). $A_0\text{-N}$ content was significantly higher in H1F and H2I ($p = 0.0164$). Litter-N content was significantly higher in H1A, H1E, H1G and H2B ($p = 0.0018$). As for root-C, root-N did not differ significantly among plots. Bulk soil-N showed significantly higher amounts in ($p = 0.0002$) in H1A, H1F and H1G plots than in other plots. Thus, these results highlighted the large spatial variability in soil parameters, enabling us to investigate spatial variability of R_S model parameters.

Influence of stand and soil characteristics on soil respiration

Correlation analysis revealed that R_{10i} was significantly correlated to topsoil density ($r = -0.81$, $p = 0.0056$). R_{10i} was also significantly correlated with LAI ($r = -0.83$, $p = 0.0035$) as well with C/N ratio of A_0 layer ($r = 0.85$, $p = 0.0020$). LAI and C/N ratio were related ($r = -0.79$, $p = 0.0091$). Partial correlation coefficient between LAI and C/N was rather high (-

0.69), whereas partial correlations topsoil density-LAI and topsoil density-C/N were low (-0.32 and 0.16, respectively). Basal area was significantly correlated with both bulk soil-C ($r = 0.71$, $p = 0.031$) and bulk soil-N ($r = 0.73$, $p = 0.0244$). We also observed a significant positive correlation between C content and N content in A_0 layer, litter and roots, but none of these variables were related with R_{10i} .

When considering parameters from fit by each plot, Q_{10} parameter was significantly correlated with stem density ($r = 0.86$, $p = 0.0018$), while both a and b were positively correlated with stem density ($r = 0.84$ and 0.70 , respectively) and negatively related to basal area ($r = -0.86$ and -0.70 , respectively). However, strong significant correlation of parameters among plot were observed, such as Q_{10} was related to a ($r = 0.76$; $p = 0.0142$) and a with b ($r = 0.92$, $p < 00001$).

A stepwise regression lead to the following equation modeling R_{10i} :

$$R_{10i} = -1.472 \text{ density} + 0.192 \text{ C/N} \quad (3)$$

Where density is the topsoil density and C/N is the C/N ratio of A_0 layer ($p = 0.0022$; $R^2 = 0.87$).

Discussion

Modeling seasonal variations of soil respiration

Soil respiration, as well as soil temperature and soil water content showed both seasonal and spatial variations. Our model was shown to explain a large part (69%) of seasonal variations of R_S . Q_{10} value (2.70) was rather lower than the one previously reported in Epron *et al.* (1999) for the same forest but remained within the range of those already published for temperate forests (Davidson *et al.*, 1998; Buchmann, 2000; Janssens *et al.*, 2003a; Epron *et al.*, 2004a; Hashimoto, 2005). Integrating measurements made in 2003 during the summer drought enabled us to emphasize the effect of soil water content on soil respiration (Figure 3). Adding θ_{Surf} improved greatly performance of R_S model and allowed to explain 23% of total variance, confirming if necessary the important role of soil moisture (Rey *et al.*, 2002; Curiel Yuste *et al.*, 2003; Epron *et al.*, 2004b). However, residuals of fitted equation (2) revealed a seasonal trend that is, by definition, independent to climatic variations of T_S and θ_{Surf} . This may be partly due to the fact that the Q_{10} function underestimates actual respiration at low temperature (Llyod and Taylor, 1994), but the Gompertz function would also underestimate respiration value at low temperature due to his mathematical definition: in our plots, the Gompertz function described well response of R_S for θ_{Surf} ranged between $0.2 \text{ m}^3 \text{ m}^{-3}$ and around $0.07 \text{ m}^3 \text{ m}^{-3}$, below which the function would be unadapted at fitting data.

Our temporal analysis did not take into account inter-annual variability of either R_S values itself (Raich *et al.*, 2001; Epron *et al.*, 2004a) or sensitivity of R_S to empirical models (Janssens *et al.*, 2003a). Especially Figure 4 would suggest other processes varying in time but independently of T_S and θ_{Surf} . McLean and Huhta (2000) showed that temporal fluctuations in soil moisture affect microfungus community structure, while [CF DED]. [suggestion of variations in biomass of respiratory compartments i.e. autotrophic and / or heterotrophic compartment] Schimel *et al.* (1999) natural variations of moisture induced changes in microbial and structure. Further improvements would be possible if several driving variables were integrated into this model, such as rain events (Curiel Yuste *et al.*, 2003; Lee *et al.*, 2004). In particular, modeling R_S for phenology events such as spring and fall root activities and foliar resorption before litterfall, would therefore improve the temperature sensitivity of these processes that are still confounded in the Q_{10} parameter

(Davidson *et al.*, 1998; Epron *et al.*, 2001; Bååth and Wallander, 2003; Janssens *et al.*, 2003b; Curiel Yuste *et al.*, 2004).

Spatial variation of R_S and plot characteristics

Large spatial variations of annual R_S were observed. These variations were directly related to the R_{10i} parameters variations as annual R_S were calculated with R_{10i} . Most of stand and soil variables also varied among plot, and would potentially affect spatial variability of R_{10i} through its autotrophic or/and heterotrophic component.

Spatial variation of T_S would almost affect for root respiration as root and rhizospheric Q_{10} have been shown to be higher than SOM decomposition Q_{10} (Boone *et al.*, 1998; Epron *et al.*, 2001; Lavigne *et al.*, 2004). In our study, no significant relationship between R_{10i} (Q_{10}) and mean annual soil temperature was fortunately found, indicating that potential spatial variations of T_S would not affect spatial variability of R_S .

Variations of topsoil density would result from influences of both forest management and intrinsic variability as soil hydromorphy. Indeed, soils with the higher density values (H1C and H2I) were historically compacted by thinning and regeneration operations. Compaction would reduce topsoil porosity and thus reduce CO_2 diffusion. In addition, Jordan *et al.* (2003) showed that soil compaction could induce a greater N loss of soil microbial biomass, reduce soil microbial activity by reducing acid phosphatase, and decrease oaks seedling height and dry mass production. In the other hand, except for H1C, H1B and H1F, having the lower density value, presented a pronounced hydromorphy (BOR soil type). This would induce a greater root and earthworm activity to counterbalance effect of relative anoxia occurring at low depth (-35 cm), and thus enhancing both microbial and autotrophic CO_2 production and topsoil diffusivity.

Acknowledgements

M. F. Willm, B. Clerc and F. Geremia are warmly thanked for their valuable help in field. M. M. Yernaux (FUSAGx, Belgium) is friendly thanked for providing us in temperature probes. M. Y. Lefevre is also thanked for his precious knowledge in soil determination. Ms J. Marchand is thanked for her precise chemical analysis. M. P. Gross and P. Courtois are greatly thanked for their continuous maintenance of field instruments and collecting micrometeorological data. A special thank for M. O. Ryk for his valuable help in soil core sorting. This study was supported by the European project CarboEurope IP and the French National Forest Service (ONF).

References

- Adachi M., Bekku Y.S., Konuma A., Kadir W.R., Okuda T. and Koizumi H. (2005). Required sample size for estimating soil respiration rate in larges area of forests and of two types of plantation in Malaysia. *Forest Ecology and Management* 210: 455-456.
- Bååth E. and Wallander H. (2003). Soil and rhizosphere microorganisms have the same $Q(10)$ for respiration in a model system. *Global Change Biology* 9: 1788-1791.
- Boone R.D., Nadelhoffer K.J., Canary J.D. and Kaye J.P. (1998). Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature* 396: 570-572.
- Borken W., Muhs A. and Beese F. (2002). Application of compost in spruce forests: effects on soil respiration, basal respiration and microbial biomass. *Forest Ecology and Management* 159: 49-58.

-
- Bouriaud O., Soudani K. and Bréda N. (2003). Leaf area index from litter collection: impact of specific leaf area variability within a beech stand. *Canadian Journal remote sensing* 29: 371-380.
- Buchmann N. (2000). Biotic and abiotic factors controlling soil respiration rates in *Picea abies* stands. *Soil Biology and Biochemistry* 32: 1625-1635.
- Curjel Yuste J., Nagy M., Janssens I.A., Carrara A. and Ceulemans R. (2005). Soil respiration in a mixed temperate forest and its contribution to total ecosystem respiration. *Tree Physiology* 25: 609-619.
- Curjel Yuste J., Janssens I. A., Carrara A. and Ceulemans R. (2004). Annual Q(10) of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Global Change Biology* 10: 161-169.
- Davidson E.A., Belk E. and 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 Biology* 4: 217-227.
- Epron D., Farque L., Lucot E. and Badot P.M. (1999). Soil CO₂ efflux in a beech forest: dependence on soil temperature and soil water content. *Annals of Forest Science* 56: 221-226.
- Epron D., Le Dantec V., Dufrene E. and Granier A. (2001). Seasonal dynamics of soil carbon dioxide efflux and simulated rhizosphere respiration in a beech forest. *Tree Physiology* 21: 145-152.
- Epron D., Nouvellon Y., Roupsar O., Mouvondy W., Mabilia A., Saint-Andre L., Joffre R., Jourdan C., Bonnefond J.M., Berbigier P. and Hamel O. (2004). Spatial and temporal variations of soil respiration in a Eucalyptus plantation in Congo. *Forest Ecology and Management* 204: 149-160.
- Gough C. M. and Seiler J. R. (2004). The influence of environmental, soil carbon, root, and stand characteristics on soil CO₂ efflux in loblolly pine (*Pinus taeda* L.) plantations located on the South Carolina Coastal Plain. *Forest Ecology and Management* 191: 353-363.
- Granier A., Ceschia E., Damesin C., Dufrene E., Epron D., Gross P., Lebaude S., Le Dantec V., Le Goff N., Lemoine L., Lucot E., Ottorini J.M., Pontailler J.Y. and Saugier B. (2000). The carbon balance of a young Beech forest. *Functional Ecol.* 14: 312-325.
- Hanson P. J., O'Neill E. G., Chambers M. L. S., Riggs J. S., Joslin J. D. and Wolfe M. H. (2003). Soil respiration and litter decomposition. *North American Temperate Deciduous Forest Responses to Changing Precipitation Regimes* 166: 163-189.
- Hashimoto S. (2005). Q₁₀ values of soil respiration in Japanese forests. *Journal Forest Research* 10: 409-413.
- 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., Gudmundson J., Minerbi S., Berbigier P., Ibrom A., Moncrieff J.B., Aubinet M., Bernhofer C., Jensen N.O., Vesala T., Granier A., Schulze E.D., Lindroth A., Dolman A.J., Jarvis P.G., Ceulemans R. and Valentini R. (2001). Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology* 7: 269-278.
- Janssens I. A., Dore S., Epron D., Lankreijer H., Buchmann N., Longdoz B., Brossaud J. and Montagnani L. (2003). Climatic influences on seasonal and spatial differences in soil CO₂ efflux. *Fluxes of Carbon, Water and Energy of European Forests*. Berlin, Springer-Verlag Berlin. 163: 233-253.
- Janssens I. A. and Pilegaard K. (2003). Large seasonal changes in Q(10) of soil respiration in a beech forest. *Global Change Biology* 9: 911-918.
- Jordan D., Ponder F. and Hubbard V. C. (2003). Effects of soil compaction, forest leaf litter and nitrogen fertilizer on two oak species and microbial activity. *Applied Soil Ecology* 23: 33-41.
- Lavigne M. B., Foster R. J. and Goodine G. (2004). Seasonal and annual changes in soil respiration in relation to soil temperature, water potential and trenching. *Tree Physiology* 24: 415-424.

-
- Lloyd J. and Taylor J.A. (1994). On the temperature dependence of soil respiration. *Functional Ecology* 8: 315-323.
- Longdoz B., Yernaux M. and Aubinet M. (2000). Soil CO₂ efflux measurements in a mixed forest: impact of chamber disturbances, spatial variability and seasonal evolution. *Global Change Biology* 6: 907-917.
- McLean M.A. and Huhta V. (2000). Temporal and spatial fluctuations in moisture affect humus microfungus community structure in microcosms. *Biology and Fertility of Soils* 32: 114-119.
- Raich J.W. and Schlesinger W.H. (1992). The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B: 81-99.
- Reichstein M., Rey A., Freibauer A., Tenhunen J., Valentini R., Banza J., Casals P., Cheng Y., Grünzweig J.M., Irvine J., Joffre R., Law B.E., Loustau D., Miglietta F., Oechel W., Ourcival J.M., Pereira J.S., Peressotti A., Ponti F., Qi Y., Rambal S., Rayment M., Romanya J., Rossi F., Tedeschi V., Tirone G., Xu M. and Yakir D. (2003). Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. *Global Biogeochemical cycles* 17: 1104.
- Reichstein M., Tenhunen J., Roupsard O., Ourcival J. M., Rambal S., Dore S. and Valentini R. (2002). Ecosystem respiration in two Mediterranean evergreen Holm Oak forest: drought effects and decomposition dynamics. *Functional Ecology* 16: 27-39.
- Reichstein M., Tenhunen J. D., Roupsard O., Ourcival J. M., Rambal S., Miglietta F., Peressotti A., Pecchiari M., Tirone G. and Valentini R. (2002). Severe drought effects on ecosystem CO₂ and H₂O fluxes at three Mediterranean evergreen sites: revision of current hypotheses? *Global Change Biology* 8: 999-1017.
- Reth S., Reichstein M. and Falge E. (2005). The effect of soil water content, soil temperature, soil pH-value and the root mass on soil CO₂ efflux - A modified model. *Plant and Soil* 268: 21-33.
- Rey A., Pegoraro E., Tedeschi V., Deparri I., Jarvis P. G. and Valentini R. (2002). Annual variation in soil respiration and its components in a coppice oak forest in Central Italy. *Global Change Biology* 8: 851-866.
- Rout S.K. and Gupta S.R. (1989). Soil respiration in relation to abiotic factors, forest floor litter, root biomass and litter quality in forest ecosystems of Siwaliks in northern India. *Acta Oecologica* 10: 229-244.
- Stoyan H., De-Polli H., Böhm S., Robertson G.P. and Paul E.A. (2000). Spatial heterogeneity of soil respiration and related properties at the plant scale. *Plant and Soil* 222: 203-214.
- 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., Guomundsson J., Thorgeirsson H., Ibrom A., Morgenstern K., Clement R., Moncrieff J.B., Montagnani L., Minerbi S. and Jarvis P.G. (2000). Respiration as the main determinant of carbon balance in European forests. *Nature* 404: 861-864.

Tables

	T _{Air} (°C)	P (mm)	
2003	10.8	660	
2004	9.7	917	
Plot	Soil type	Age	Species
H1A	BRe	35	FS
H1B	BOR	35	FS
H1C	BOR	35	FS
H1D	BRe	35	FS
H1E	BO	35	FS
H1F	BOR	35	FS+PA
H1G	BRe	35	FS
H2B	BO	20	FS+Q+CB
H2I	BO	20	FS+Q+CB

Table 1. Main characteristics of studied plots. Mean annual air temperature (T_{Air}) and precipitations (P) are given for 2003 and 2004. Studied plots are defined for their soil type, tree age (years) and their main specific composition (>95%): FS = *Fagus sylvatica* L.; PA = *Picea abies* L.; Q = *Quercus* sp.; CB = *Carpinus betulus* L.).

Plot	H1A	H1B	H1C	H1D	H1E	H1F	H1G	H2B	H2I
R ₁₀	1.63	2.37	1.44	1.62	1.46	2.1	1.78	1.46	1.4
Q ₁₀	2.49	2.73	2.35	2.4	2.54	2.45	2.89	3.27	2.89
a	0.97	1.13	1.17	1.34	0.27	0.25	0.89	3.49	1.94
b	25.30	17.52	21.97	25.54	15.70	14.74	19.56	46.33	24.35
R ²	0.68	0.75	0.53	0.61	0.66	0.72	0.68	0.9	0.89
RMSE	0.42	0.5	0.46	0.41	0.38	0.49	0.47	0.29	0.24
R _{10i}	1.72	2.20	1.38	1.63	1.50	2.11	1.83	1.59	1.36
Annual R _s	599	788	506	583	516	733	633	557	475

Table 2. Parameters of the empirical model (Equation (1), see Material and Methods) fitted on all soil respiration, temperature and water content data per plot. All parameters were significant at p = 0.05 level. Applying equation (1) with parameters determined by equation (2) lead to annual R_s (gC m⁻² y⁻¹).

	H1A	H1B	H1C	H1D	H1E	H1F	H1G	H2B	H2I
N	7016	7535	4158	3898	3638	3638	7276	17968	17968
G	47.5	35.7	44.3	30.0	45.3	53.9	48.7	16.6	16.6
LAI	6.9	5.6	7.2	5.8	8.1	4	6.9	7.4	7.4

	H1A	H1B	H1C	H1D	H1E	H1F	H1G	H2B	H2I
<i>Soil density</i>	0.81	0.69	0.88	0.75	0.87	0.75	0.85	0.85	1.02
<i>A₀</i>	8.5	8.1	5.9	5.8	4.7	13.4	9.6	6.8	9.0
<i>Litter</i>	5.0	1.7	3.3	4.1	5.0	3.3	4.2	4.3	1.5
C									
<i>Roots</i>	1.1	1.30	0.8	1.6	1.0	0.7	1.8	1.0	1.2
<i>Bulk soil</i>	24.5	26.0	26.5	22.7	32.1	34.0	31.2	24.5	24.2
<i>Total</i>	41.3	40.3	37.9	36.1	44.0	52.1	51.0	39.7	38.7
<i>A₀</i>	0.37	0.37	0.37	0.15	0.29	0.41	0.19	0.18	0.23
<i>Litter</i>	0.05	0.02	0.03	0.05	0.05	0.04	0.05	0.05	0.03
N									
<i>Roots</i>	0.01	0.02	0.01	0.03	0.01	0.01	0.04	0.02	0.01
<i>Bulk soil</i>	0.36	0.22	0.45	0.23	0.37	0.44	0.29	0.20	0.12
<i>Total</i>	3.8	3.3	3.1	3.3	3.3	4.3	4.2	3.2	3.5

Table 3. Tree density (N, stem ha⁻¹), basal area (G, m² ha⁻¹) and leaf area index (LAI, m² m⁻²) of different studied plots. Mean carbon (upper panel) and nitrogen (lower panel) contents (t ha⁻¹) determined in the different pools in the 0-15 cm soil layer, and bulk density of 0-5 cm soil layer (g cm³). Total mean C and N content were calculated directly by summing C and N content of different pools by each core. Root pool integrated both living and dead roots.

Figures

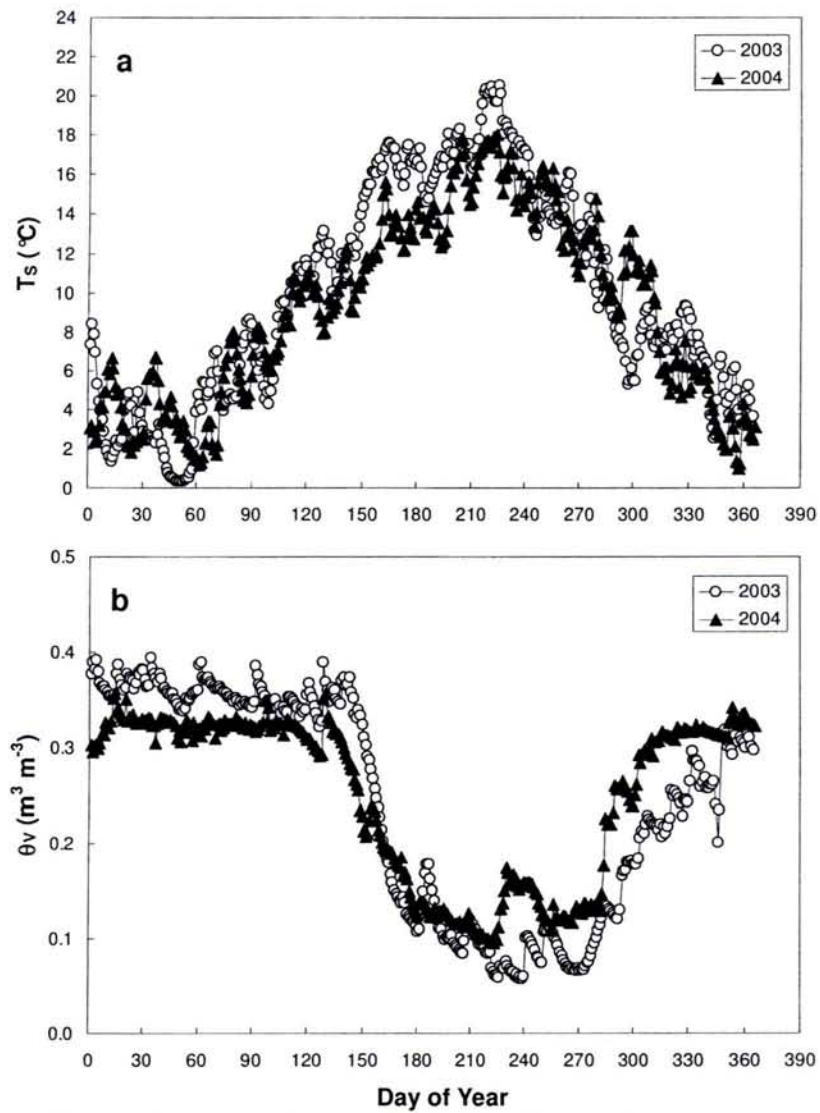


Figure 1. Daily mean soil temperature (at -10cm, T_s) and soil water content (0-6 cm, θ_v) in 2003 and 2004.

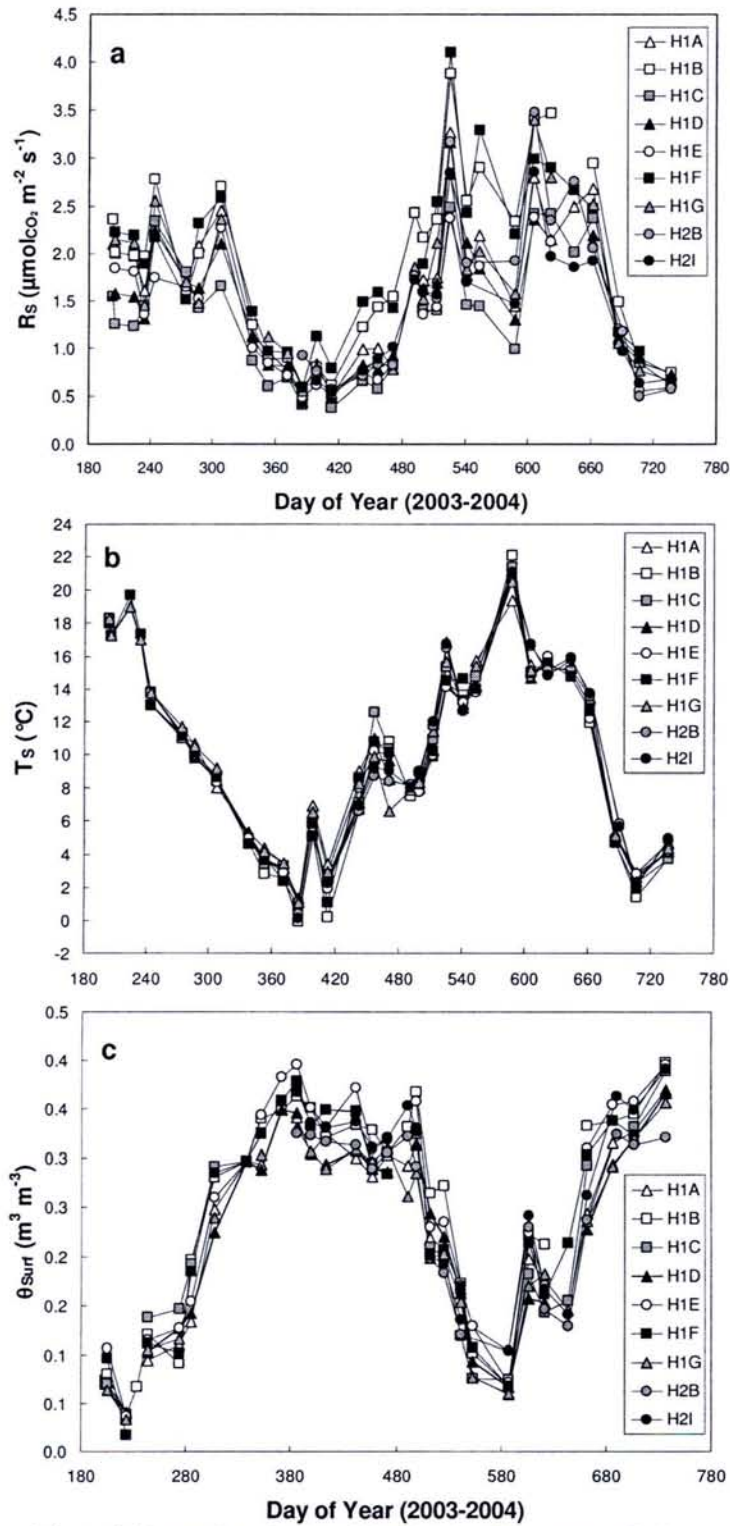


Figure 2. Mean soil respiration efflux R_s (a), soil temperature T_s (b) and soil water content θ_{Surf} (c) seasonal variation by each plot.

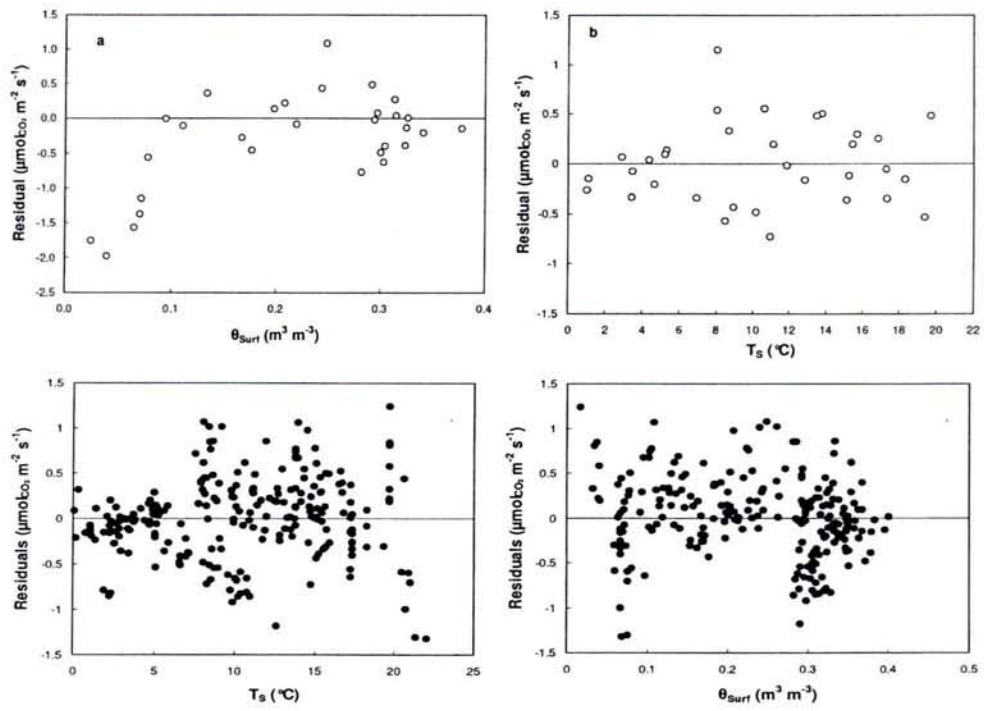


Figure 3. Residuals of the temperature function plotted against showed significant biases. Taking into account the effect of soil water content (a) in soil respiration model as given in equation (1) lead to unbiased residuals either when fitting separately (b) or all plots together (c and d).

Monsieur NGAO Jérôme

DOCTORAT DE L'UNIVERSITE HENRI POINCARÉ, NANCY 1

en BIOLOGIE VEGETALE & FORESTIERE

VU, APPROUVÉ ET PERMIS D'IMPRIMER N° 1143

Nancy, le 23 décembre 2005

Le Président de l'Université



☎☎☎☎☎☎☎☎☎☎

RESUME

Le but de notre travail a été d'approfondir la connaissance des principaux compartiments participant à la respiration d'un écosystème (R_{ECO}) afin d'en dégager les facteurs majeurs influençant sa variabilité dans deux hêtraies (H1 et H2) de la forêt de Hesse. Différents suivis du flux de CO_2 du sol (R_S) ont été initiés, ainsi que des expériences de décomposition de litière de feuilles et de débris ligneux. Ainsi, la respiration du sol autotrophe (R_{Auto}) représente 38% et 42% de R_{ECO} dans les sites H1 et H2 respectivement. La respiration du sol hétérotrophe (R_{Hetero}) représente 14% et 29% de R_{ECO} dans H1 et H2 respectivement. Le flux de CO_2 issu de la décomposition de la nécromasse ligneuse (R_B) contribue à 14% de R_{ECO} dans H1. La contribution annuelle de la décomposition de la litière (R_L) est estimée à 8% de la respiration annuelle total du sol. Pour le site H1, en considérant une valeur annuelle de R_S de $529 \text{ g}_C \text{ m}^{-2} \text{ an}^{-1}$ (2004) et une valeur annuelle de R_{Hetero} de $147 \text{ g}_C \text{ m}^{-2} \text{ an}^{-1}$, la contribution de R_L à R_{Hetero} est ramenée à 29%. Nos résultats confirment que la température du sol est un facteur essentiel influençant grandement la variabilité temporelle des différents flux de CO_2 , mais laisse une grande part de la variabilité (notamment spatiale) à d'autres facteurs susceptibles d'être confondus ou cachés derrière le pattern général imposé par elle. L'effet du contenu volumique en eau du sol (θ_{Surf}) à Hesse est globalement positif sur R_S et R_B , notamment aux faibles valeurs d'humidité. Mais il est plus difficile de prévoir l'effet des variations de θ_{Surf} à plus long terme sur la biomasse microbienne notamment. La variabilité spatiale de R_S peut être décrite à travers la respiration basale normalisée avec des paramètres liés au sol comme la densité apparente ou le rapport C/N du sol superficiel. Les paramètres du peuplement tels que la surface terrière, la densité en nombre tiges ou l'indice de surface foliaire n'expliquent apparemment pas cette variabilité. La biomasse racinaire en elle-même ne permet pas non plus d'expliquer la variabilité spatiale de R_S . Ces différentes approches permettent de mieux cerner les variabilités influençant R_{ECO} et ses composantes. Les limites et incertitudes des méthodes employées durant ce travail sont discutées.

Mots-clefs : autotrophe, carbone, compartiment, contenu en eau, écosystème, flux CO_2 , hétérotrophe, hêtraie, racines, respiration, sol, température, variabilité.

ABSTRACT

The aim of this work was to improve knowledge on the main components of ecosystem respiration (R_{ECO}), and to emphasize the main variables driving its variability within two beech stands of Hesse Forest. Different surveys of soil CO_2 efflux (R_S) were initiated, as well as decomposition experiment of leaf litter and woody debris. Thus, autotrophic respiration (R_{Auto}) represented 38% and 42% of R_{ECO} in the H1 and H2 sites, respectively. Heterotrophic respiration represented 14% and 29% of R_{ECO} in the H1 and H2 sites, respectively. CO_2 efflux from woody debris (R_B) contributed to 14% of R_{ECO} in H1 site. Annual contribution of leaf litter decomposition (R_L) was estimated to 8% of annual R_S . For the H1 site, when considering an annual R_S value of $529 \text{ g}_C \text{ m}^{-2} \text{ y}^{-1}$ (2004) and an annual R_{Hetero} value of $147 \text{ g}_C \text{ m}^{-2} \text{ y}^{-1}$, contribution of R_L to R_{Hetero} was 29%. Our results confirmed that soil temperature was an essential factor having a major influence on temporal variability of CO_2 efflux, but it left a large part of variability that could be explained by confounded or hidden other factors. The effect of soil water content (θ_{Surf}) at Hesse was globally positive on R_S and R_B , in particular for low values of θ_{Surf} . Spatial variability of R_S could be described through the basal respiration rate with soil parameters as soil bulk density or the C-to-N ratio of superficial soil layer. At a first sight, neither stand parameters (basal area, stand density or leaf area index) nor root biomass did not explain spatial variability of R_S . These results provided substantial information and allowed a better understanding of variability of R_{ECO} and its components. Limits and uncertainties of methods employed during this work are discussed.

Keywords: autotrophic, beech, carbon, compartment, CO_2 flux, ecosystem, heterotrophic, respiration, root, soil, temperature, variability.