Comparison of methods to quantify respirational carbon loss of coarse woody debris

Article *in* Canadian Journal of Forest Research · November 2008

DOI: 10.1139/X08-115

CITATIONS
24

READS
246

2 authors:

Jürgen Bauhus
University of Freiburg
471 PUBLICATIONS **15,803** CITATIONS
SEE PROFILE

Steffen Herrmann
Thünen Institute of Forest Ecosystems, Eberswalde, Germany
14 PUBLICATIONS **234** CITATIONS
SEE PROFILE

Comparison of methods to quantify respirational carbon loss of coarse woody debris

Steffen Herrmann and Jürgen Bauhus

Abstract: Carbon (C) loss from coarse woody debris (CWD) may be important in forest ecosystem C budgets, yet there are no standard methods of quantifying it. Here we assessed respirational C loss of log segments of European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.), to compare the two main measurement approaches (the static and dynamic methods using soda lime and an infrared gas analyser, IRGA) with three different measurement options for CWD logs. These included (*i*) incubation of the whole log segment, (*ii*) the use of small in situ chambers on the curved log surface, and (*iii*) extracted wedges of wood. On average, significantly higher amounts of CO_2 were measured with the IRGA (125%) compared with soda lime. In addition, the soda lime method requires careful calibration of incubation length and amounts of soda lime used. Regardless of the measurement method and tree species, substantially higher amounts of CO_2 were measured for whole log segments than for the other two options. Measuring respiration with small in situ chambers on logs or extracted wedges might underestimate real CO_2 flux by up to 74%. We therefore recommend measurement of CWD respiration using gas analysers for large log segments.

Résumé : La perte de carbone due aux débris ligneux grossiers (DLG) est potentiellement importante dans le bilan du carbone des écosystèmes forestiers mais il n'existe pas de méthode standard pour la quantifier. Nous avons évalué la perte de carbone due à la respiration de segments de billes de hêtre commun (*Fagus sylvatica* L.) et d'épicéa commun (*Picea abies* (L.) Karst.) dans le but de comparer les deux principales approches de mesure, soit les méthodes statique et dynamique qui utilisent la chaux sodée et un analyseur à infrarouge, ainsi que trois façons différentes de prendre les mesures pour les billes de DLG. Cela inclut (*i*) l'incubation d'un segment entier de bille, (*ii*) l'utilisation in situ de petits réceptacles sur la surface courbe de la bille et (*iii*) des morceaux de bois extraits de la bille. En moyenne, des quantités significativement plus grandes de CO_2 ont été mesurées avec l'analyseur à infrarouge (125 %) comparativement à la chaux sodée. De plus, la méthode à la chaux sodée nécessite une calibration minutieuse de la durée d'incubation et des quantités de chaux sodée utilisées. Peu importe la méthode de mesure et l'essence, des quantités substantiellement plus grandes de CO_2 ont été mesurées avec des segments entiers de bille qu'avec les deux autres façons. La mesure de la respiration avec des petits réceptacles in situ sur les billes ou avec des morceaux de bois pourrait sous-estimer le flux réel de CO_2 et donner des résultats jusqu'à 74 % inférieurs au flux réel. Nous recommandons par conséquent de mesurer la respiration des DLG à l'aide d'analyseurs à infrarouge en utilisant de gros segments de bille.

[Traduit par la Rédaction]

Introduction

Coarse woody debris (CWD) has been recognized as a key structural element of forests (Lindenmayer and McCarthy 2002) and as an indicator of ecologically sustainable forest management (MCPFE 2003). It is of particular importance for biodiversity (Koehler 2000; Lindenmayer et al. 2002; Alexander 2003) and ecosystem carbon (C) balance (Harmon et al. 1986; Turner et al. 1995; Kimmins 2004), as either a sink or a source. Therefore, it has also been considered in C accounting systems (Mackensen and Bauhus 1999; Larsson et al. 2007). To incorporate it in C accounting systems and to manage CWD as a resource, that is, to maintain certain levels of CWD in different decay stages in the landscape, detailed knowledge particularly about its temporal dynamic (decomposition process) is required. Up to now this is only rudimentary.

The main process involved in CWD decay is the loss of organic matter through respiration by microorganisms. According to Chambers et al. (2001), up to 76% of the whole C in CWD logs is lost through respiration in the tropics over the whole decomposition period. The C respiration of CWD can also be quite significant in the context of forest ecosystem C budgets. According to Müller-Using and Bartsch (2004), respiration from dead logs in a central German European beech (*Fagus sylvatica* L.) forest amounted to approximately 20% of the level of soil respiration.

Despite the importance of CWD respiration, so far there are no established or recognized methods for its measurement. Different methods and sampling designs have been used in various studies (Marra and Edmonds 1996; Chambers et al. 2001; Mackensen and Bauhus 2003). However, the effectiveness of the different methods commonly used to measure CWD respiration and the errors associated with them are not known. It is therefore also impossible to compare measurements that have been made with different techniques. Whereas there is a large body of literature on soil

Received 15 February 2008. Accepted 12 August 2008. Published on the NRC Research Press Web site at cjfr.nrc.ca on 9 October 2008.

S. Herrmann[1] and J. Bauhus. Institute of Silviculture, University of Freiburg, Tennenbacherstr. 4, 76106 Freiburg i. Br., Germany.

[1]Corresponding author (e-mail: steffen.herrmann@waldbau.uni-freiburg.de).

 doi:10.1139/X08-115

respiration and the different methods to measure it (Lund et al. 1999; Janssens et al. 2000; Pumpanen et al. 2004; Rochette and Hutchinson 2005), the general findings from those studies and the methodological developments may not be directly transferable to the measurement of CWD respiration. To measure CWD respiration, it is, for example, possible to incubate entire log sections (e.g., Müller-Using 2005). In addition, the diffusion patterns in logs, in particular with regard to variation between circular and cross-sectional surfaces of logs, may differ greatly from those of soils.

In this study we compared the two main measurement approaches, the static method, based on absorption of CO_2 within a closed chamber using soda lime, and the dynamic method, in which CO_2 evolution is determined with an infrared gas analyser (IRGA). This comparison first required an assessment of the amount of soda lime required for efficient absorption of CO_2. In addition, we compared three different measurement options for logs, in which CWD respiration was measured through (*i*) incubation of a whole log segment, (*ii*) the use of small in situ chambers on the curved log surface area (without circular cross-sectional areas at the end of the log cylinders), or (*iii*) incubation of wooden wedges extracted from the log.

Materials and methods

Static method for CWD respiration measurements

CO_2 was absorbed within a static or non-flow-through steady-state (NFT-SS) chamber (Livingston and Hutchinson 1995), using soda lime ($NaOH + Ca(OH)_2$). Soda lime was dried before use in a fan-forced oven for at least 12 h at 100 °C. After drying, it was placed in a desiccator for 2–3 h to allow for temperature equilibration. Before incubation, the amount of soda lime used was weighed. After incubation, soda lime (remaining in the Petri dish) was dried as before and weighed after equilibration in the dessicator. The gain in mass, corrected for the chemically released water by the factor 1.69 (Grogan 1998), equalled the amount of CO_2 absorbed.

Since there is insufficient published information on the optimal duration of incubation and the amount of soda lime required for efficient absorption of CO_2, these two parameters were determined in experiments using an artificial CO_2 source. The CO_2 absorption was tested in PVC buckets (12.3 L volume) with associated lids as well as in small PVC chambers (1.3 L volume). The latter consisted of one tube (approximately 10 cm in diameter and 15 cm long) and two lids (approximately 2 cm thick), which were sealed with O-rings placed in circular cut grooves. The lids of the PVC buckets were sealed using aluminium sealing tape. The two sizes were chosen to simulate the experimental conditions for the assessment of CO_2 evolution on CWD. A defined quantity of CO_2 was produced using Na_2CO_3 and HCl (4 $mol \cdot L^{-1}$). Two different quantities of CO_2, 0.2 and 4 g, were chosen because these represented possible quantities produced by placing chambers on logs or by incubating stem wedges and log segments. The HCl was frozen in liquid N to have sufficient time for the installation before the start of the reaction and to ensure that none of the CO_2 produced could escape before the system was sealed. The acid was placed in a small plastic bottle before freezing. Before starting the experiment, the bottle with the frozen HCl was placed upside down with the lid open in a metal rack above a plastic dish containing the Na_2CO_3. This permitted a reasonably slow titration and, thus, release of the CO_2. The size of plastic bottle and dish varied according to the amount of HCl and Na_2CO_3 used. For the small PVC chamber, this installation was placed on a metal grid above the Petri dish containing the soda lime. In case of the PVC bucket, it was placed next to the soda lime. We aimed to use the largest possible Petri dish area in relation to the chamber. In the case of the small chamber, it had a diameter of 7.5 cm. In case of the PVC bucket, a Petri dish of 14.5 cm diameter was used, which made up 33.6% of the bottom surface area.

The experiment started by increasing the amount of soda lime in 5 g steps under a constant incubation time of 24 h until 100% capture of the produced CO_2 was reached. Using this amount, the incubation time increased in 6 h intervals. To test whether CO_2 absorption efficiency could be increased with rewetting dried soda lime (Keith and Wong 2006), 5 mL H_2O was added to 20 g of soda lime when 4 g CO_2 was produced (12.3 L volume). The calibration experiment was carried out under constant temperature of approximately 18 °C.

The soda lime was handled as described above. Each measurement was repeated two times and the CO_2 absorption in empty containers, which were used as blanks, was subtracted from the mean mass gain.

Dynamic method

Measurements were carried out with a dynamic or flow-through non-steady-state (FT-NSS) chamber (Livingston and Hutchinson 1995) using an IRGA. We used the LI-COR LI 6400-09 portable photosynthesis system combined with soil CO_2 flux chamber (LI-6400-09, LI-COR, Inc., Lincoln, Nebraska).

Each measurement was repeated four times and the mean value of the last three times was taken for further analyses. The minimum measurement time for each cycle was 90 s. Before the start of the four cycles, a target value for ambient CO_2 concentration was set. This was measured by placing the open soil chamber near the location where it was used. After this, a measurement range ("Δ value," e.g., 10 ppm below and above ambient) dependent on the flux value was chosen. At the beginning of each cycle the chamber concentration was automatically scrubbed down below ambient and then measured as it rose through the measurement range. Following each measurement, the CO_2 flux for the target ambient CO_2 concentration was calculated automatically (LI-COR 2007).

Sampling design

The experiment was carried out on log segments (three replicate pieces) of decay stage 2 (Albrecht 1990) of *F. sylvatica* and Norway spruce (*Picea abies* (L.) Karst.) (Table 1). The segments were cut from one log per species. Log segments were stored at approximately 10 °C and brought to the lab 24 h before the start of the experiment. All preparations were done before the samples were brought to the lab.

Three different possibilities for measuring CO_2 evolution

Table 1. Log segment characteristics.

Sample	Density ($g \cdot cm^{-3}$)	Length (cm)	Diameter (cm)
Fagus sylvatica			
1	0.28	30	19.0
2	0.31	30	19.3
3	0.32	30	20.2
Picea abies			
1	0.26	28.8	20.0
2	0.24	29.7	20.1
3	0.26	29.5	19.3

on the log segment were compared: (*i*) whole log segment, (*ii*) small in situ chamber, and (*iii*) extracted wedge (Fig. 1).

Measurements of CO_2 emission using small in situ chambers and wedges were repeated three times at three separate measurement locations per log segment. The measurement locations were selected randomly. In case of small in situ chambers on log segments of spruce, only two repeated measurements could be conducted. For each measurement option, soda lime was incubated with three blank measurements without CO_2 evolution into the chamber and the resulting average amount was subtracted from the measured CO_2 evolution.

The experiment started with the CO_2 assessment of the whole log segment, followed by assessment in small in situ chambers. After measurements in the small in situ chambers were completed, wedges were extracted at these positions (diameter 10 cm, length ranging from log surface to the pith) and CO_2 evolution was again assessed. Wooden wedges were measured inside a small PVC chamber, applying the same system as for soda lime calibration. The soda lime incubations with small in situ chambers had to be done in two terms because only the two cylinders with vertical orientation could be filled with soda lime at the same time (Fig. 1). Between the two measurement terms the log was turned by 90°.

To minimize bias related to temporal dynamics in CO_2 evolution from the material, the IRGA measurements were conducted before and after the soda lime incubation and the mean value was used for further analysis and comparison.

To measure CO_2 evolution of entire log segments, these were placed in PVC chambers consisting of a PVC tube (40 cm long, 25 cm in diameter, and 7 mm thick) and two lids. One lid was sealed permanently at the bottom of the tube using PVC adhesive. The second lid was sealed temporarily with Terostat (Terostat IX, Teroson GmbH, Heidelberg, Germany) car body sealant for incubation with soda lime. For measurements with the IRGA, the lid was prepared according to the soil chamber mounting plate and directly connected to the sensor head. For IRGA measurements of log segments, air was distributed inside the chamber similar to the soil chamber system using a flexible perforated PVC tube, which was twisted around the inside walls of the chamber in a spiral pattern. A battery-driven fan was installed at the bottom of the chamber below the log segment (which was placed on four plastic poles) to ensure air mixing. Since the log segment was producing more CO_2 than could be sufficiently scrubbed down with the system pump, synthetic air from a gas bottle (approximately 300 ppm CO_2) was used to adjust the chamber CO_2 concentrations. This air was introduced into the chamber with a flexible PVC tube. During air introduction, a second flexible tube was used for pressure compensation and flow control. It was led inside a glass of water and flow was slowed down when bubbles occurred.

For the measurements using small in situ chambers, circular grooves (three on each log segment) approximately 10 cm in diameter were cut and PVC rings (approximately 5 cm tall and 2 mm thick) were installed. The LI-COR soil CO_2 flux chamber was directly connected to these PVC rings.

For soda lime incubation, the rings were sealed with the same lids as used for the soda lime calibration, but foam rings (LI-COR) were used instead of O-rings and sealing was achieved using strong rubber bands connected with the PVC tube by metal clips and placed around the lid.

For soda lime incubations with entire log segments, 63 g dried soda lime was used and for small in situ chambers and wedges, 15 g dried soda lime was used. These quantities were determined on the basis of the calibration experiment. Sizes of Petri dishes and their relation to the surface area were the same as used for the calibration of the soda lime method. For each measurement option, soda lime measurements were taken using an incubation time of 48 h. This time was chosen according to the results of the soda lime calibration experiment and to permit sufficient time for CO_2 evolution. The temperature was constant throughout the experiment at approximately 18 °C.

After completion of all CO_2 measurements, all parts of the log segments and extracted wedges were dried to constant mass at 105 °C and dry density of wedges was determined following volume measurements using the water displacement method.

Analysis

The CO_2 evolution measured with the IRGA and soda lime methods were expressed as g CO_2 per kilogram dry mass and day. To calculate the dry mass related to the CO_2 measured in small in situ chambers, the ratio of the surface area of the chamber to the curved surface area (without circular cross-sectional areas at the end of the log cylinders) of the whole log segment was multiplied with the dry mass of the whole log segment.

To analyse for differences between the two methods of CO_2 measurements, Wilcoxon's signed-ranks test (Storm 1995) was applied. The different sampling designs were compared for *F. sylvatica* and *P. abies* individually. We first tested for equal variances using Levene's test. Since in most cases the variances were significantly different, Welch's ANOVA followed by Tukey–Kramer's honestly significant difference test (if a significant difference was detected) was performed (Sall et al. 2001). All significance testing was done with $p < 0.05$.

Results

Soda lime calibration

To effectively capture 0.2 g CO_2 in a confined space of 1.3 L volume, 15 g soda lime was needed (Table 2). To cap-

Fig. 1. Sample types of coarse woody debris (CWD): whole log segment and small in situ chamber (*a*) and extracted wedge (*b*).

ture 100% of 4 g CO_2 in a confined space of 12.3 L volume, 30 g soda lime was needed. Thus, the mass of the CO_2 absorbed comprised 1.3%,and 13.3% of the initial soda lime masses, respectively. Smaller amounts of soda lime resulted in incomplete CO_2 absorption. Adding moisture to the dry soda lime did not influence the efficiency of adsorption.

Comparing different incubation times (in a confined space of 12.3 L volume) showed that after 6 h, approximately 50% of 4 g of CO_2 produced was absorbed by 30 g soda lime and after 12 h, 90% was already captured. Ninety-eight percent absorption was reached after 18 h and 100% was absorbed after an incubation time of 24 h (Table 2).

Comparison of IRGA and soda lime method

There were considerable differences between the CO_2 measurements with soda lime and IRGA across all sampling designs for both tree species. On average, significantly higher CO_2 fluxes were measured with the IRGA compared with soda lime (0.7 and 0.56 g CO_2·kg dry mass^{-1}·d^{-1}; p = 0.03; SD 0.49 and 0.4). The slope of the regression line was not significantly different from the 1:1 line, showing that the difference between the two methods was constant over the entire measurement range (Fig. 2). Analysing the differences between soda lime and IRGA values separately for CWD from both tree species showed that the differences were only significant for *F. sylvatica* (0.75–0.62 g CO_2·kg dry mass^{-1}·d^{-1}; p = 0.04). Owing to the greater variation, no significant difference was detected for *P. abies*, but the absolute differences between means for the two methods were equally high (0.61–0.47 g CO_2·kg dry mass^{-1}·d^{-1}). Comparing differences in CO_2 measurements between the two methods separately for the different types of wood samples showed that the differences were only significant for wedges (p = 0.001).

The effect of sample type on CO_2 measurements

Comparing the different CWD samples and sample locations for *F. sylvatica* revealed significantly lower amounts of CO_2 for only small in situ chambers when compared with whole log segments and only when using the IRGA (Fig. 3). The coefficient of variation increased for soda lime and IRGA from log segments (5.9% and 7.2%) to small in situ chambers (68.9% and 59.7%) and wedges (87.2% and 88%). Compared with whole log segments, CO_2 evolution for small in situ chambers and wedges was 53% and 66% with soda lime and 36% and 59% with the IRGA.

For *P. abies*, the amount of CO_2 measured using small in situ chambers and wedges was significantly lower than for log segments in case of soda lime, and the amount of CO_2 measured with small in situ chambers was significantly lower than for log segments and wedges when using the IRGA method. The variation, expressed as coefficient of variation, generally increased for soda lime and IRGA from log segments (2.1% and 1.9%) to small in situ chambers (49.6% and 46.2%) and wedges (73.2% and 35.7%). Compared with whole log segments, CO_2 evolution for small in situ chambers and wedges was 41% and 26% with soda lime and 29% and 87% with the IRGA.

Discussion

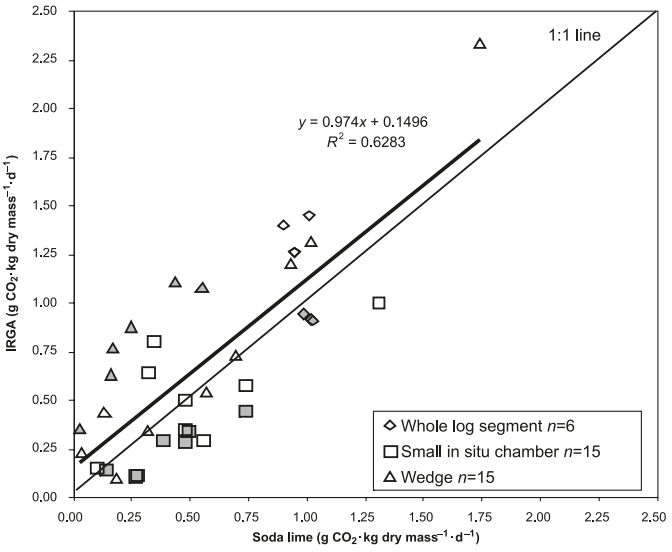
Soda lime calibration

Our study showed the importance of preliminary assessment of incubation times and the amounts of soda lime required for effective capture of CO_2 evolved. Relatively more soda lime was needed for small amounts of CO_2 and small incubation volumes than for larger amounts of CO_2 and larger incubation volumes. One explanation could be that there is some threshold or minimum amount of soda lime required to become receptive for CO_2 absorption. According to Edwards (1982), the saturation point of soda lime is reached when the mass of the CO_2 absorbed is 28% of the initial soda lime mass, but he generally suggested that the mass of CO_2 absorbed should be <7% of the initial mass of soda lime used for incubation. In a study by Keith and

Table 2. Calibration of soda lime in terms of amount and incubation time.

Volume (L)	Amount of CO_2 produced (g)	Amount of soda lime (g)	Incubation time (h)	Percent capture of CO_2
1.3	0.203	5	24	74
1.3	0.203	10	24	84
1.3	0.201	15	24	100
12.3	4.002	30	6	48
12.3	4.002	30	12	92
12.3	4.004	30	18	98
12.3	4.002	30	24	100

Fig. 2. Amounts of CO_2 (g CO_2·kg dry mass^{-1}·d^{-1}) measured with soda lime (x) and infrared gas analyser (IRGA) (y) for three different sample types of coarse woody debris (CWD) of *Fagus sylvatica* (open symbols) and *Picea abies* (solid symbols). The bold line represents the linear regression between the two measurement techniques across all sample types.



Wong (2006), mass increase of exposed soda lime was <3% (amount of soda lime used, 50 g; range of efflux, 1–10 g C·m^{-2}·d^{-1}; incubation volume, 6.9 L). Janssens et al. (2000) stated that their mass ratio of absorbed CO_2 to exposed soda lime was never >10%.

Our results indicated that 12–24 h are necessary for complete CO_2 absorption, which concurs with the study by Rochette and Hutchinson (2005). Owing to the temperature dependency of soda lime absorption, the period of time required for complete absorption may be related to the diurnal variation in temperature during field studies. However, this was not an issue in our study, which was conducted at constant temperature.

Comparison of IRGA and soda lime method

Generally we measured greater CO_2 evolution with the IRGA than with the soda lime method, which is consistent with findings from other studies (Haynes and Gower 1995; Keith and Wong 2006). In this study IRGA values were on average 20% greater than soda lime values. Reported differences in other comparable studies were in the range of 5% and 20%. In contrast, Janssens et al. (2000) found soil CO_2 evolution measured with the soda lime technique to be 36% greater when compared with an IRGA, but they also stated that both methods were not directly comparable because of their experimental designs.

The high variation in measured CO_2 fluxes observed in this study may be partially attributed to the finding that static methods are generally less accurate than dynamic methods (Lund et al. 1999). This also points to possible errors associated with the incubation method or soda lime handling. In a laboratory soil CO_2 flux simulation (with known CO_2 fluxes and simulated soil consisting of polyurethane foam), Nay et al. (1994) found that the soda lime method tended to overestimate CO_2 flux at low rates (<1.6 g CO_2-C·m^{-2}·d^{-1}) and severely underestimated CO_2 flux at high flux rates (5 g CO_2-C·m^{-2}·d^{-1}). In contrast, our results showed a consistent difference between methods across the range of CO_2 flux rates, indicating that there was no problem with CO_2 saturation at high flux rates.

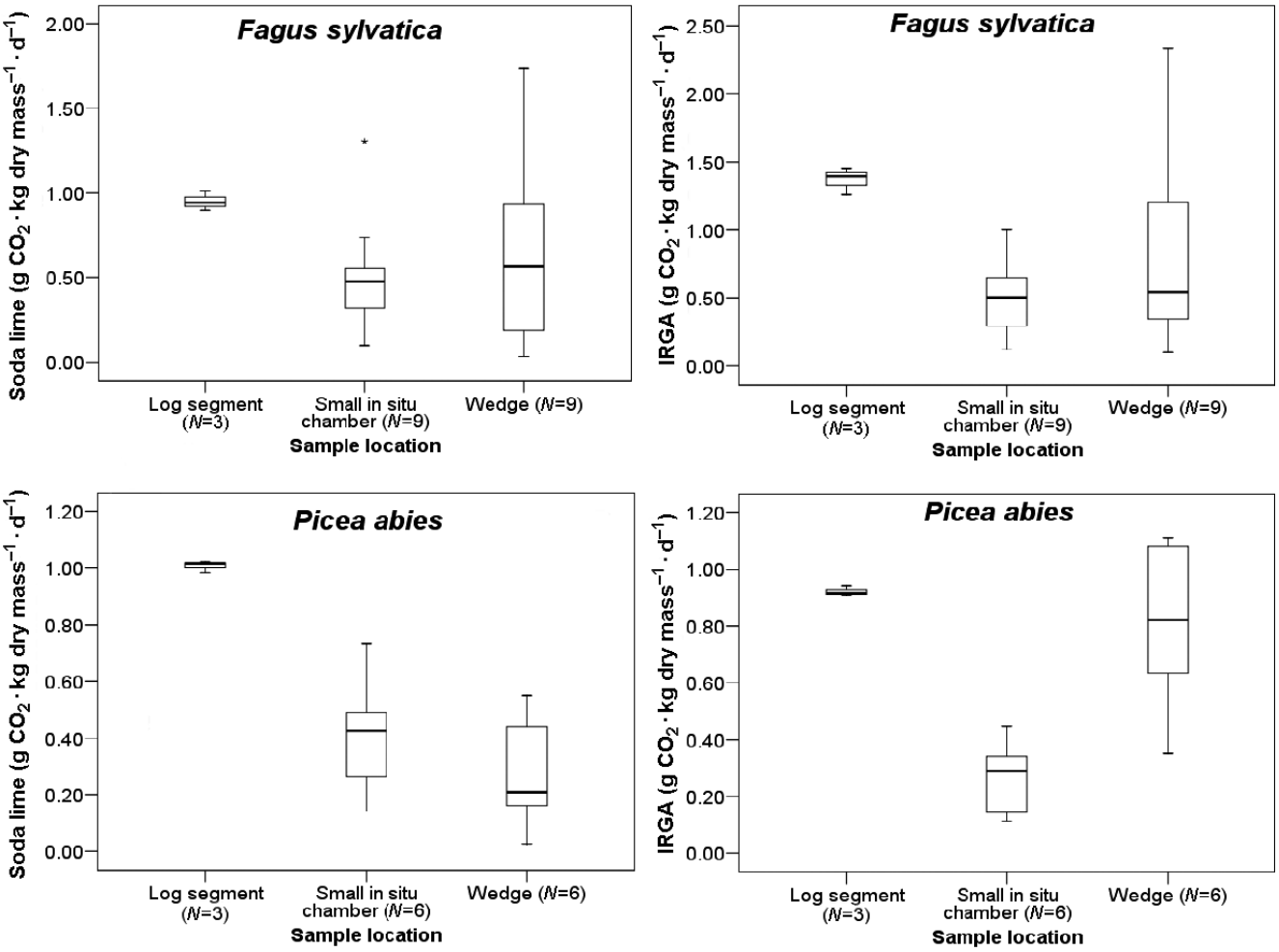
These results demonstrate that while soda lime may be easier and cheaper to use than an IRGA, CWD respiration may be consistently underestimated. Given the great variation between measurements, this underestimation could not be accurately captured by a correction factor.

Effect of sample type

Our study clearly showed that measuring respiration with small in situ chambers on logs (Marra and Edmonds 1996; Progar et al. 2000) or extracted wedges (Chambers et al. 2001) is not representative of whole log segments. The same may be true for cross-sections cut from log segments (Liu et al. 2006). Assuming that measurements of log segments resemble the real CO_2 flux from entire logs most accurately, extrapolations from measurements of small in situ chambers on the stem surface and stem wedges might underestimate real CO_2 flux up to 74%, depending on the method and the type of sample used. This would introduce a considerable error in ecosystem C budgets.

Quantities of CO_2 fluxes measured on wedges were on average 20% above those measured with small in situ chambers, suggesting that the former gave a closer picture of the respiration rate of the log segment. The small in situ chambers are more likely susceptible to gas leakages than the other two sample types, which were completely contained in chambers. While every care was taken to fit the in situ chambers as tightly as possible to the log surface, CO_2 that evolved beneath the chambers might pass the chambers through cracks in the wood. In addition, the in situ chambers did not capture the CO_2 flux from cross-sectional surfaces. Individual values of the CO_2 evolution measured on wedges with the highest ratio of cross-sectional to surface area ex-

Fig. 3. Amounts of CO_2 (g CO_2·kg dry mass^{-1}·d^{-1}) measured for log segments, small in situ chambers, and wedges with soda lime and IRGA for *Fagus sylvatica* (*a*) and *Picea abies* (*b*); box plots display median, 95% confidence interval, and minimum and maximum values; points outside box plots represent outliers.



ceed those measured on log segments, whereas CO_2 evolution measured with small in situ chambers was generally below the one of whole log segments. This suggests that the proportion of cross-sectional surface area may be important and that the bark may act as a barrier for gaseous diffusion. Along with the heterogeneity of the decomposition process on the log this may at least partly explain our results.

Our study was not designed to estimate the proportion of CO_2 evolution from logs that diffuses through the cross-sectional surfaces. For this purpose, a comparison of respiration from logs with sealed and unsealed cross-sections should be done. However, if we assume that the measurements with small in situ chambers adequately capture the CO_2 flux from the circular surface of cylindrical logs, then the CO_2 evolution from the circular ends were between 46% and 59% of total log respiration for soda lime measurements and between 64% and 71% using the IRGA. Presumably, that proportion will increase with decreasing log length and it should be considered in CWD respiration measurements.

The high variation of CO_2 measurements from small in situ chambers and wedges points to a high spatial variability of the decomposition process on different positions along the log. It also suggests that it is more appropriate to determine the CO_2 evolution for larger log sections. However, measuring CWD respiration of entire log sections in the field remains a great technical challenge for which practical solutions need to be developed. There are obvious limits on the size and decomposition stages of logs that can be lifted in and out of large respiration chambers. If logs are wrapped in nylon mesh or other netting, disintegration and fragmentation through their handling may be prevented when using log sections for incubation. However, the effect that repeated lifting of logs has on the fungal mycelia network between logs and soil and hence respiration has not been investigated. For these reasons, the development of large chambers to be mounted onto logs may be the more promising solution. All of the above approaches will be increasingly difficult to use as the decomposition stage of logs advances.

The methods examined here are designed to measure short-term CWD respiration and hence mass loss. Scaling up from CWD respiration measurements to the long-term dynamics of CWD mass loss is difficult, since the combined effects of temperature, moisture, and interactions between substrate quality and microorganisms need to be considered.

The quantification of mass loss in long-term studies (e.g., Stone et al. 1998; Herrmann and Prescott 2008) is likely to be more appropriate for this purpose. However, this approach, unless supported by appropriate instrumentation and measurements, does commonly not distinguish between C losses through respiration, leaching, and fragmentation.

Acknowledgements

This research was funded by the German Science Foundation (DFG - BA 2821/4-1).

References

Albrecht, L. 1990. Grundlagen, Ziele und Methodik der waldökologischen Forschung in Naturwaldreservaten. Naturwaldreservate in Bayern 1. München, 1990.

Alexander, K.N.A. 2003. The British saproxylic invertebrate fauna. *In* Proceedings of the 2nd Pan-European Conference on Saproxylic Beetles, June 2002, Egham, Surrey, UK. *Edited by* C. Poland Bowen. People's Trust for Endangered Species, Cloisters House, London. pp. 8–10.

Chambers, J.Q., Schimel, J.P., and Nobre, A.D. 2001. Respiration from coarse woody litter in central Amazon forests. Biogeochemistry, **52**: 115–131. doi:10.1023/A:1006473530673.

Edwards, N.T. 1982. The use of soda-lime for measuring respiration rates in terrestrial systems. Pedobiologia (Jena), **23**: 321–330.

Grogan, P. 1998. CO_2 flux measurement using soda lime: correction for water formed during CO_2 adsorption. Ecology, **79**: 1467–1468. doi:10.1890/0012-9658(1998)079[1467:CFMUSL]2.0.CO;2.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Lienkaemper, G.W., Cromack, K.J., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res, **15**: 133–302. doi:10.1016/S0065-2504(08)60121-X.

Haynes, B.E., and Gower, S.T. 1995. Below-ground carbon allocation in unfertilised and fertilised red pine plantations in Northern Wisconsin. Tree Physiol. **15**: 317–325. PMID:14965955.

Herrmann, S., and Prescott, C.E. 2008. Mass loss and nutrient dynamics of coarse woody debris in three Rocky Mountain coniferous forests: 21 year results. Can. J. For. Res. **38**: 125–132. doi:10.1139/X07-144.

Janssens, I.A., Kowalski, A.S., Longdoz, B., and Ceulemans, R. 2000. Assessing forest soil CO_2 efflux: an *in situ* comparison of four techniques. Tree Physiol. **20**: 23–32. PMID:12651523.

Keith, H., and Wong, S.C. 2006. Measurement of soil CO_2 efflux using soda lime absorption: both quantitative and reliable. Soil Biol. Biochem. **38**: 1121–1131. doi:10.1016/j.soilbio.2005.09.012.

Kimmins, J.P. 2004. Forest ecology — a foundation for sustainable management. 3rd ed. Prentice-Hall, Upper Saddle River, N.J.

Koehler, F. 2000. Totholzkäfer in Naturwaldzellen des nördlichen Rheinlandes. Vergleichende Studien zur Totholzkäferfauna Deutschlands und deutschen Naturwaldforschung. Naturwaldzellen Teil VII. – Schrr. LÖBF/LAfAO NRW (Recklinghausen), **18**: 1–351.

Larsson, T.-B., Barbati, A., Bauhus, J., Van Brusselen, J., Lindner, M., Marchetti, M., Petriccione, B., and Petersson, H. 2007. The role of forests in carbon cycles, sequestration, and storage. IUFRO Newsletter, **5**: 1–10.

LI-COR. 2007. Soil CO_2 flux chamber. Available from www.licor.com/env/PDF_Files/6400-09.pdf. [Accessed 9 November 2007.]

Lindenmayer, D.B., and McCarthy, M.A. 2002. Congruence between natural and human forest disturbance: a case study from Australian montane ash forests. For. Ecol. Manage. **155**: 319–335. doi:10.1016/S0378-1127(01)00569-2.

Lindenmayer, D.B., Claridge, A.W., Gilmore, A.M., Michael, D., and Lindenmayer, B.D. 2002. The ecological roles of logs in Australian forests and the potential impacts of harvesting intensification on log-using biota. Pac. Conserv. Biol. **8**: 121–140.

Liu, W.H., Bryant, D.M., Hutyra, L.R., Saleska, S.R., Hammond-Pyle, E., Curran, D., and Wofsy, S.C. 2006. Woody debris contribution to the carbon budget of selectively logged and maturing mid-latitude forests. Oecologia (Berl.), **148**: 108–117. doi:10.1007/s00442-006-0356-9.

Livingston, G.P., and Hutchinson, G.L. 1995. Enclosure-based measurement of trace gas exchange: applications and sources of error. *In* Biogenic trace gases: measuring emissions from soil and water. *Edited by* P.A. Matson and R.C. Harriss. Blackwell Science, Cambridge, UK. pp. 14–50.

Lund, C.P., Riley, W.J., Pierce, L.L., and Field, C.B. 1999. The effects of chamber pressurization on soil-surface CO_2 flux and the implications for NEE measurements under elevated CO_2. Glob. Change Biol. **5**: 269–281. doi:10.1046/j.1365-2486.1999.00218.x.

Mackensen, J., and Bauhus, J. 1999. The decay of coarse woody debris. National Carbon Accounting System Tech. Rep. 6. Australian Greenhouse Office, Commonwealth of Australia, Canberra.

Mackensen, J., and Bauhus, J. 2003. Density loss and respiration rates in coarse woody debris of *Pinus radiata*, *Eucalyptus regnans* and *Eucalyptus maculata*. Soil Biol. Biochem. **35**: 177–186. doi:10.1016/S0038-0717(02)00255-9.

Marra, J.L., and Edmonds, R.L. 1996. Coarse woody debris and soil respiration in a clearcut on the Olympic Peninsula, Washington, U.S.A. Can. J. For. Res. **26**: 1337–1345. doi:10.1139/x26-149.

Ministerial Conference on the Protection of Forests in Europe (MCPFE). 2003. State of Europe's Forests 2003. The MCPFE Report on Sustainable Forest Management in Europe. MCPFE Liaison Unit, Vienna; United Nations Economic Comission for Europe, Geneva; and Food and Agricultural Organization of the United Nations, Rome. Available from www.mcpfe.org/content/index.php?lang. [Accessed 20 December 2003.]

Müller-Using, S. 2005. Totholzdynamik eines Buchenbestandes im Solling. Berichte des Forschungszentrums Waldökosysteme, Reihe A, Bd. 193 2005.

Müller-Using, S., and Bartsch, N. 2004. Dynamics of woody debris in a beech (*Fagus sylvatica* L.) forest in central Germany. *In* Improvement and Silviculture of Beech — Proceedings of the 7th International Beech Symposium. IUFRO Research Group 1.10.00, 10–20 May 2004, Teheran, Iran. *Edited by* K. Sagheb-Talebi, P. Madsen, and K. Terazawa. Published by Research Institute of Forests and Rangelands (RIFR), Iran. pp. 83–89.

Nay, M.S., Mattson, K.G., and Bormann, B.T. 1994. Biases of chamber methods for measuring soil CO2 efflux demonstrated with a laboratory apparature. Ecology, **75**: 2460–2463. doi:10.2307/1940900.

Pumpanen, J., Kolari, P., Ilvesniemi, H., Minkkinen, K., Vesala, T., Niinistö, S., Lohila, A., et al. 2004. Comparison of different chamber techniques for measuring soil CO_2 efflux. Agric. For. Meteorol. **123**: 159–176. doi:10.1016/j.agrformet.2003.12.001.

Progar, R.A., Schowalter, T.D., Freitag, C.M., and Morrell, J.J. 2000. Respiration from coarse woody debris as affected by moisture and sapotroph functional diversity in Western Oregon. Oecologia (Berl.), **124**: 426–431. doi:10.1007/PL00008868.

Rochette, P., and Hutchinson, G.L. 2005. Measurement of soil

respiration in situ: chamber techniques. Agron. Monogr. **47**: 247–286.

Sall, J., Lehmann, A., and Creighton, L. 2001. JMP® start statistics. A guide to statistics and data analysis using JMP® and JMP IN® software. SAS Institute Inc., Duxbury, Pacific Grove, Calif.

Stone, J.N., MacKinnon, A., Parminter, J.V., and Lertzman, K.P. 1998. Coarse woody debris decomposition documented over 65 years on southern Vancouver Island. Can. J. For. Res. **28**: 788–793. doi:10.1139/cjfr-28-5-788.

Storm, R. 1995. Wahrscheinlichkeitsrechnung, mathematische Statistik und statistische Qualitðtskontrolle. Fachbuchverlag, Leipzig, Germany.

Turner, D.P., Koerper, G.J., Harmon, M.E., and Lee, J.J. 1995. A carbon budget for forests of the conterminous United States. Ecol. Appl. **5**: 421–436. doi:10.2307/1942033.