Effects of moisture, temperature and decomposition stage on respirational carbon loss from coarse woody debris (CWD) of important European tree species

Steffen Herrmann [a] & Jürgen Bauhus [a]

[a] Institute of Silviculture , University of Freiburg , Freiburg im Breisgau , Germany
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RESEARCH ARTICLE

Effects of moisture, temperature and decomposition stage on respirational carbon loss from coarse woody debris (CWD) of important European tree species

STEFFEN HERRMANN & JÜRGEN BAUHUS

Institute of Silviculture, University of Freiburg, Freiburg im Breisgau, Germany

Abstract
Coarse woody debris (CWD) is critical for forest ecosystem carbon (C) storage in many ecosystems. Since the turnover of CWD is mostly driven by mineralization, changes in temperature and precipitation may influence its pools and functions. Therefore, we analysed, under controlled conditions, the effect of wood temperature and moisture on carbon respiration from CWD for the important European tree species *Fagus sylvatica* L., *Picea abies* (L.) Karst. and *Pinus sylvestris* L. in different stages of decay, represented by different wood densities. Additionally, we measured CWD respiration of individual *F. sylvatica* and *P. abies* logs over one year to analyse the effects of micro-climatic variables in the field. CWD respiration rates under controlled lab conditions were about two times higher for beech than for spruce and pine and similar for the latter two species. In addition, wood moisture exerted a stronger influence on respiration than wood temperature. In contrast, respiration in the field was most strongly controlled by temperature. Average Q_{10} values under controlled conditions were 2.62 for *F. sylvatica* and 2.32 for *P. abies* across all temperature and moisture levels, while no significant relationship between temperature and CO_2 flux was observed for *P. sylvestris*. About 80% of the variation in respiration under controlled conditions could be explained by species, wood density, moisture and temperature and their interactive effects. Temperature alone explained 96% (beech) and 94% (spruce) of the variation in respiration in the field. Furthermore, we predicted average monthly temperatures of CWD in the field very accurately from air temperature ($r^2 = 0.96$), which is relevant for modelling CWD carbon dynamics under climate change scenarios. Our results indicate that species identity, decay stage and micro-climatic conditions should be considered when predicting CWD decay rates.

Keywords: *Coarse woody debris, carbon, respiration, decomposition.*

Introduction

In addition to its importance for biodiversity and ecosystem functioning, coarse woody debris (CWD) can be a major component of the ecosystem carbon (C) balance (Harmon et al. 1986; Lindenmayer et al. 2002; Kimmins 2004; Pregitzer & Euskirchen 2004; Harmon et al. 2011). According to Turner et al. (1995), about 10% of the sequestered carbon in the forests of the USA is in CWD and 33% in living trees. In some forests, the mass and carbon storage of decaying logs and snags considerably exceeds the mass and carbon storage in live trees (Kimmins 2004). Furthermore, woody litter can contribute up to 75% to the total soil carbon store (Hyvonen & Agren 2001). Therefore, assessing the amount of

carbon in CWD is critical to account for carbon stored in forests. However, the carbon pool in CWD undergoes temporal fluctuations (Harmon 2009), which are to a large extent influenced by CWD mineralization. Until now, detailed knowledge in particular about its temporal dynamics as influenced by climatic variation is insufficient to accurately consider CWD in ecosystem carbon models (Cornwell et al. 2009). Thus, the carbon flux from woody debris remains a crucial uncertainty within global carbon-climate models (Woodall & Liknes 2008; Weedon et al. 2009).

The longevity and turnover of carbon stored in CWD is determined by its decomposition rate, which in turn determines the amount of CO_2 release (net emission) from CWD.

Correspondence: Steffen Herrmann, Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland.
E-mail: steffen.herrmann@wsl.ch
Current address: Steffen Herrmann, Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland.

Respirational carbon loss is usually the main process of dead wood decomposition (Mackensen et al. 2003). For example, up to 76% of the whole carbon in CWD logs is lost through respiration in the tropics over the whole decomposition period (Chambers et al. 2001).

The decomposition rate (and thus respirational carbon loss) is primarily related to activity of micro-organisms, chiefly fungi, which can degrade lignin and cellulose. The activity of these micro-organisms in CWD is mainly dependent on climatic (wood temperature and wood moisture) and substrate specific (tree species, decay stage and diameter) variables. According to Harmon et al. (1995), the substrate specific variables may possibly dominate the climatic variables. In other studies, climatic variables had been identified as the main driver of CWD decomposition determined as respirational carbon loss (Chambers et al. 2001; Mackensen et al. 2003; Müller-Using 2005; Liu et al. 2006). Climate change with its possible effects on decomposition rates will probably influence the function of dead wood as a carbon sink (Mackensen & Bauhus 1999). The detailed extent of this effect is not known. Therefore, it is critical to develop a better understanding of the climatic controls on CWD decomposition. In addition, to model CWD carbon dynamics under climate change scenarios, it is further necessary to understand the relationship between CWD temperature (T_{CWD}) and air temperature (T_{AIR}).

So far, relatively few studies have quantified CWD respiration (Marra & Edmonds 1996; Wang et al. 2002; Bond-Lamberty et al. 2003; Mackensen & Bauhus 2003; Liu et al. 2006; Jomura et al. 2008; Hagemann et al. 2010; Wu et al. 2010; Forrester et al. 2012; Olajuyigbe et al. 2012) compared to the many studies that have investigated the effect of temperature and moisture on soil respiration (e.g. Raich & Schlesinger 1992; Howard & Howard 1993; Kirschbaum 1995; Reichstein et al. 2000). The consensus of these studies is that soil respiration increases exponentially with temperature, when soil moisture or other factors are not limiting (see also Davidson & Janssens 2006 for review and theoretical background).

In this study, we analysed the effect of varying wood temperature and moisture on the current respirational carbon loss of CWD of *Fagus sylvatica* L., *Picea abies* (L.) Karst. and *Pinus sylvestris* L. in different stages of decay under controlled laboratory conditions. Additionally, using a case study approach, we measured CWD respiration continuously over one year in the field on one *F. sylvatica* L. and one *P. abies* (L.) Karst. log to analyse the effect of micro-climatic variables.

Specifically we hypothesised that:

1. CWD respiration rates differ among tree species and decay stages.
2. CWD respiration increases with temperature in a temperature range normally encountered in forests; this increase is dependent on the moisture content of CWD.
3. Wood temperature can be predicted from T_{AIR}.

Materials and Methods

General CO_2 measurements

All CO_2 measurements were carried out with a dynamic or flow-through non-steady-state (FT-NSS) chamber (Livingston & Hutchinson 1995) using an IRGA. We used the LICOR 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 average value of the last three 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, chamber air concentration was automatically scrubbed down to 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).

Incubation experiment

The effects of different, constant wood temperatures (5, 10 and 20°C) and moisture (from water saturated to dry in three steps) on the respirational carbon loss of CWD of *F. sylvatica*, *P. abies* and *P. sylvestris* was analysed under controlled conditions for wood of different density representing early, intermediate and late stages of wood decomposition, analogue to decay stages 1, 3 and 5 of a 5-class decay classification system (Sollins 1982).

For this experiment, we used small samples (four replicate pieces), i.e. extracted wedges from discs for early and intermediate decay stages (ca. 10-cm long, 7-cm wide at the bark end, and 7-cm thick; similar to the ones described in Herrmann & Bauhus 2008) or a certain amount of wood mass from logs at late stages of decomposition, where no wedges could be cut. Samples were collected in southern German nature reserves (beech: "Roettlerwald" for decay

stage 3, "Hofstatt" for decay stages 1 and 5; spruce and pine: "Silbersandgrube"). Wood samples representing different decay stages were cut from different logs. Here, it was not our intention to sample the whole variation within the decay classes of each species, since we used density and not decay class as independent variable in the statistical models. Therefore, samples representing one decay class were collected from different positions of one or two logs per species depending on availability. Hence, the samples stemming from the same log may be regarded as not being independent. However, the variations in wood density among the replicates of the same decay class and species were comparable to the variations within decay class of these species, when collected from a large population of logs in the field (Müller-Using & Bartsch 2009).

Directly after cutting, all samples were initially placed in water until water saturation was achieved. Water saturation is the point, where all the water is bound in the cell walls (fibre saturation) and all cell cavities are filled with water. This was asserted through repeated weighing of immersed samples until constant weight was achieved, which took up to two months for some samples. Maximum water contents, in relation to dry weight, ranged from 99–1131% in beech, 138–656% in spruce and 140–671% in pine between decay classes 1 and 5, respectively. With the very high water contents adjusted here, the results from the lab incubation cannot be directly extrapolated to field conditions. However, the major purpose of the lab experiment was to assess the relative and not the absolute importance of temperature and moisture on decomposition rates and to compare the different tree species.

The experiment was conducted in two climate chambers with constant temperature and air moisture. The air humidity was set to maximum for all temperatures to minimise drying of the samples. Samples were allowed to equilibrate under the specific temperature in the lab 24 h before the start of the respiration measurements. Measurements were conducted in a small chamber with a closed lid on the bottom; similar to the ones described by Herrmann and Bauhus (2008). Samples were rewetted (i.e. sprayed with water) after each measurement step to maintain a constant moisture level. The experiment started with the lowest temperature (5°C) and the highest moisture level of the sample (i.e. maximum water content; "wet"). After this, the temperature was increased to 10 and 20°C while the moisture level was kept constant. This was followed by a second measurement period under the same moisture level with the same varying room temperatures, starting with 10, then 20 and finally

5°C. Here, it was our intention to account for possible effects related to a constant measurement order. Therefore, temperatures were applied in a different order compared to the first sequence. This procedure was repeated for the two remaining moisture levels ("medium" and "dry"). The samples were dried in a fan-forced oven to moisture levels "medium" (ranging from 76–316% in beech, 100–192% in spruce, and 91–227% in pine) and "dry" (ranging from 35–81% in beech, 19–90% in spruce and 26–59% in pine between decay classes 1 and 5, respectively).

After completion of all CO_2 measurements, the samples were dried to constant mass at 105°C to determine the gravimetric moisture content for the different moisture levels as well as dry density via volume measurements using the water displacement method.

Case study "Conventwald"

Study site

The experiment was conducted in a nature reserve called "Conventwald", which has been set aside since 1970. The reserve is located in the Central Black Forest in southwest Germany at 700–860 m a.s.l [latitude: 48.021261°(N), longitude: 7.965628°(E)]. Average annual precipitation is about 1400 mm. The mean annual T_{AIR} is 6.6°C. The exposition is south oriented with an inclination of about 20°. The geological substrate is Paragneis covered by Cambisol soils with a deep profile. The vegetation consists of closed mixed mature forest (about 170 years old) with European beech (*F. sylvatica*), Silver fir (*Abies alba*) and Norway spruce (*P. abies*). Since 1984, the "Conventwald" has been a long-term forest ecosystem research site, and more information about the experiments can be found in Wilpert and Puhlmann (2007). At the site, temperature and precipitation were monitored continuously at a tower.

Sampling design

We measured CWD respiration continuously over one year (October 2007–September 2008; and on three additional days in April and May 2007) for one *F. sylvatica* and one *P. abies* log to analyse the effect of wood moisture and wood temperature in the field. Here, it was not our intention to make broader inferences about decomposition rates by species. Instead, we aimed to use these case studies to assess the effects of seasonal fluctuations of climatic factors on respiration.

The logs were selected in order to provide a range of conditions regarding decay stage and diameter as well as ground contact and suspended positions. The

logs originated from trees that fell in 1996 (*F. sylvatica*) and in 1990 (*P. abies*). The detailed characteristics of the two logs and the different measurement locations are described in Table I.

Small *in situ* chambers (Herrmann & Bauhus 2008), distributed along the length of the two logs in order to capture the different measurement options were used to measure CO_2 evolution. In total, six small *in situ* chambers were installed (in circular cut grooves) on the European beech log and nine on the Norway spruce log. Installation of the chambers was conducted in autumn 2006. Respiration measurements were done twice a month starting in October 2007 until September 2008 (and three additional days in April and May 2007). Measurements were conducted in a varying order. Following the completion of respiration measurements, wood samples were taken with a drill (28 mm in diameter) at all measurement positions to assess the dry density. Wood samples were dried to constant mass at 105°C in a fan-forced oven. Dry weight was measured and related to dry volume, which was determined via water displacement method for density assessment.

Temperature and moisture measurement

Wood temperature was measured using GREISINGER EASYLOG 40KH temperature logger (GREISINGER electronic GmbH, Regenstauf, Germany). Measurements were recorded in hourly time steps. Temperature probes were installed in the wood in small holes at 5-cm depth. Three temperature loggers were used in the European beech log and four in the Norway spruce log. They were distributed along the stem axis in order to represent the different measurement locations.

Wood moisture content was assessed using time domain reflectometry (TDR) soil moisture probes (TRIME-IT, UP GmbH, Ibbenbüren, Germany), installed in the same way as for the temperature probes at a depth of 7 cm. TDR probes were connected to an on-site data logger. Volumetric wood moisture content was measured and logged every hour. One TDR probe was installed in the spruce log and three were used for the beech log. For the beech log, the two extra probes were used to capture differences in moisture content between less decomposed and highly decomposed wood as well as between log sections that were either suspended or had soil contact.

Analysis

Although some samples used for the incubation experiment originated from the same log, these were regarded as independent replicates. These samples were taken from different positions within the same log and differed substantially in density and presumably also in composition of the microflora, as has been shown by others (Shigo 1986; Schwarze et al. 1999; Vetrovsky et al. 2011).

Following square root transformation of original data, CO_2 flux from incubated samples was normally distributed according to Kolmogorov–Smirnov tests.

A one-way analysis of variance (ANOVA) was conducted to analyse possible differences in CO_2 flux between the three species.

A non-parametric correlation matrix (Spearman-Rho) was used to assess possible correlations between the CO_2 flux and the independent variables.

Table I. Log characteristics of European beech and Norway spruce in the case study "Conventwald" (0: without soil contact, 1: with soil contact; overall length, beech: 25.85 m, spruce: 29.32 m).

Fagus sylvatica

	Measurement location					
Parameter	B1	B2	B3	B4	B5	B6
Dry density (g cm^{-3})	0.354	0.397	0.515	0.443	0.435	0.320
Diameter (cm)	55.5	42.7	37.4	36.7	25.5	24.7
Decay class (1–4)	2	2	2	2	4	3
Soil contact	1	0	1	0	1	0

Picea abies

	Measurement location								
Parameter	S1	S2	S3	S4	S5	S6	S7	S8	S9
Dry density (g cm^{-3})	0.338	0.345	0.292	0.310	0.359	0.309	0.283	0.345	0.279
Diameter (cm)	28.5	29.3	35.3	38	39.2	39.9	44.3	48.4	48.3
Decay class (1–4)	4	4	3	2	2	2	2	2	2
Soil contact	1	1	1	0	0	1	0	0	0

An analysis of covariance (ANCOVA; 4-way) was conducted to assess the overall importance of each experimental factor (wood density, temperature and moisture content as continuous variables and tree species as a factor). Linear regressions of square root transformed CO_2 flux against temperature were fitted for each combination of species, moisture and decay class. Q_{10} values (between 5 and 20°C) and decomposition constants (k; at 10°C as a standard temperature) were derived for each regression. Differences in Q_{10} and k values between species were compared using Mann–Whitney U test.

Annual decomposition constants (k) for incubation experiments and field studies were calculated by converting the CO_2 flux per area into a carbon flux per unit of carbon in CWD. For that purpose, it was assumed that carbon density of CWD is 0.5, a value that had been determined in other analyses (Herrmann unpublished). To calculate the dry mass and CWD carbon related to the CO_2 flux measured in small *in situ* chambers on logs, the ratio of the surface area of the chamber to the surface area of the log segment was multiplied with the calculated dry mass (based on measurements of volume and density) of the whole log segment; see also Herrmann and Bauhus (2008).

k (yr^{-1}) was calculated according to the Equation (1):

$$k(\text{yr}^{-1}) = \text{g } CO_2 - \text{C kg CWD} - \text{C}^{-1}\text{d}^{-1}$$
$$\times\ 365/1000, \tag{1}$$

where

$$\text{gCO}_2 - \text{C kg CWD} - \text{C}^{-1}\text{d}^{-1}$$
$$= (\text{g } CO_2 \text{ kg DM}^{-1} \text{ d}^{-1} \times 12/44)/0.5$$

The Q_{10} values, which represent the factor by which respiration increases with a temperature increase of 10°C, were calculated as:

$$Q_{10} = (R_2/R_1){}^{\wedge}[10/(T_2 - T_1)] \tag{2}$$

where R_1 and R_2 were the CWD respiration at temperatures T_1 and T_2 (Ellert & Bettany 1992).

For the case study "Conventwald", a non-parametric correlation matrix (Spearman-Rho) was calculated to assess possible correlations between the CO_2 flux and the independent variables.

Following square root transformation of the CO_2 flux, a simple linear regression of average temperature per log against average CO_2 flux per log was calculated. Q_{10} (between 5 and 20°C) and k values were calculated based on the linear regression model and based on mass loss (k value) and compared with those from the incubation experiment.

To investigate the relationship between T_{CWD} and T_{AIR} in the field (measured on a continuous basis nearby), we conducted regression analyses.

The statistical analysis was conducted using SPSS Statistics 17.0 (SPSS Inc., Chicago, IL, USA). All significance testing was done with $p < 0.05$.

Results

Incubation experiment

On average, the CO_2 flux of beech woody debris (0.351 g CO_2 kg DM^{-1} d^{-1}) was significantly higher ($p < 0.01$) than that of spruce and pine (0.122 and 0.119 g CO_2 kg DM^{-1} d^{-1}, respectively) (Table II). The CO_2 flux of spruce was not different from that of pine ($p > 0.9$). Therefore, the two conifers were pooled for some further analyses. The corresponding k values were 0.07 yr^{-1} and 0.024 yr^{-1} for beech and spruce/pine, respectively (Table II).

In addition, the CO_2 flux variation increased with increasing temperature and moisture content for all species (Figure 1).

The positive relationship between moisture and CO_2 flux for beech ($r = 0.75$, df $= 106$, $p < 0.001$) and spruce/pine ($r = 0.63$, df $= 214$, $p < 0.001$) was stronger than the positive relationship between temperature and CO_2 flux for both species (beech: $r = 0.4$, df $= 106$, $p < 0.001$; spruce/pine: $r = 0.44$, df $= 2\ 14$, $p < 0.001$). Furthermore, a significant negative relationship between moisture and density was detected for beech ($r = -0.42$, df $= 106$, $p < 0.001$) and spruce/pine ($r = -0.32$, df $= 214$, $p < 0.001$).

Wood density as well as wood temperature interacted with species ($F = 24.1$, df $= 2.3$, $p = 0.000$; $F = 5.6$, df $= 2.3$, $p < 0.01$) and wood moisture content ($F = 127.2$, df $= 1.3$, $p = 0.000$; $F = 47.6$, df $= 1.3$, $p = 0.000$) to influence CO_2 flux from CWD (Table III).

About 80% of the variation in CO_2 flux could be explained by species, density, moisture and temperature and their interactive effects. The most important share of the variation (29%) was explained by the interaction of moisture and density. Moisture alone explained additional 17%, followed by the interactive effects of species and density (14%), moisture and temperature (13%) and species (12%; Table III).

In comparison with beech and spruce, the linear regressions between temperature and CO_2 flux were not significant for woody debris of pine for most of the combinations of density and moisture content (Table IV).

Mean Q_{10} (between 5 and 20°C) and k values of beech (2.62 and 0.07 yr^{-1}) were higher than those of spruce (2.32 and 0.03 yr^{-1}), indicating a higher sensitivity of mineralization in beech CWD to

Table II. Density, moisture content, CO_2 flux (g CO_2 kg DM^{-1} d^{-1}), and annual decomposition constant (k) (derived from CO_2 flux) of dead wood samples of European beech, Norway spruce and Scots pine in the laboratory incubation experiment (average temperature: 11.67 (7.07)°C).

Species	Dry density (g cm^{-3})	Moisture (% dry weight)	CO_2 flux (g CO_2 kg DM^{-1} d^{-1})	Decomposition constant k (yr^{-1})
Fagus sylvatica	0.409 (0.24)	247 (366)	0.35 (0.51)	0.070 (0.102)
Picea abies	0.391 (0.15)	181 (202)	0.12 (0.12)	0.024 (0.024)
Pinus sylvestris	0.366 (0.1)	173 (210)	0.12 (0.15)	0.024 (0.030)

Note: Values are means with SDs given in parantheses ($n = 108$).

changes in temperature and moisture. Note that mean moisture content was also higher for beech (247%) compared to spruce (181%). Generally, Q_{10} values decreased with increasing wood density and increasing moisture level for beech and spruce. Maximum Q_{10} values were higher for beech (3.52) than for spruce (3.05), and minimum Q_{10} values were also higher for beech (1.41) than for spruce (1.28) (Table IV). In contrast to Q_{10} values, k values increased with decreasing wood density and increasing moisture level for beech (0.021–0.186 yr^{-1}) and with increasing moisture level for spruce (0.007–0.045 yr^{-1}). Differences between beech and spruce were not significant for Q_{10} ($p > 0.4$) and k ($p > 0.05$).

Case study "Conventwald"

In the field, respiration rates of spruce CWD tended to be slightly more temperature-dependent ($Q_{10} =$

2.78) than those of beech ($Q_{10} = 2.54$). The average annual decomposition constant (k) calculated from the respiration measurements was about twice as high (190% for beech and 211% for spruce, respectively) than the one calculated from mass loss based on time since death (Table V).

Based on respiration measurements, the k-value of beech CWD (0.113 yr^{-1}) was about 2.1 times higher than that of spruce (0.054 yr^{-1}). Based on mass loss, the one for beech CWD (0.052 yr^{-1}) was 2.3 times higher than that of spruce (0.023 yr^{-1}).

A strong positive relationship between temperature and CO_2 flux was observed for beech ($r = 0.98$, df $= 23$, $p = 0.000$) and spruce ($r = 0.97$, df $= 23$, $p = 0.000$) (Figure 2).

No relationship was observed between moisture and CO_2 flux for both species.

The linear regression model between square root transformed CWD respiration and temperature

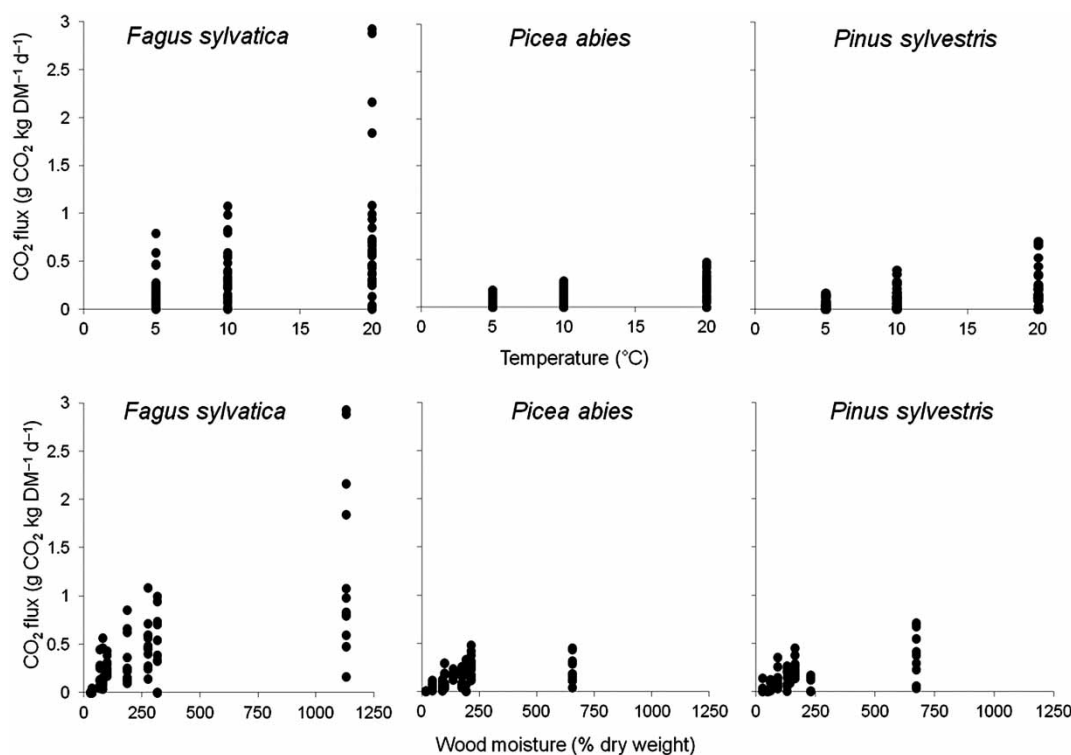Figure 1. Amounts of CO_2 (g CO_2 kg DM^{-1} d^{-1}) measured in relation to temperature (°C) and wood moisture content (% dry weight) for *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris* in the laboratory incubation experiment; $n = 108$.

Table III. Analysis of covariance (ANCOVA) between square root of EFFLUX and the explaining variables in the laboratory incubation experiment.

Source	Type III sum of squares	df	Mean square	F	Significance	Partial Eta squared
Corrected model	20.167	12	1.681	102.877	0.000	0.799
Intercept	0.148	1	0.148	9.068	0.003	0.028
Species	0.712	2	0.356	21.799	0.000	0.123
Density	0.095	1	0.095	5.823	0.016	0.018
Moisture	1.025	1	1.025	62.752	0.000	0.168
Temperature	0.242	1	0.242	14.800	0.000	0.045
Species × temperature	0.183	2	0.091	5.601	0.004	0.035
Species × density	0.788	2	0.394	24.114	0.000	0.134
Density × temperature	0.060	1	0.060	3.686	0.056	0.012
Moisture × temperature	0.777	1	0.777	47.592	0.000	0.133
Density × moisture	2.077	1	2.077	127.171	0.000	0.290
Error	5.080	311	0.016			
Total	63.881	324				
Corrected total	25.247	323				

explained 96% (beech; sqrt [CO_2 flux (g CO_2 kg DM^{-1} d^{-1})] $= 0.372 + 0.038 \times$ temp, $p = 0.000$) and 94% (spruce; sqrt [CO_2 flux (g CO_2 kg DM^{-1} d^{-1})] $= 0.232 + 0.029 \times$ temp, $p = 0.000$; "temp" = temperature) of the whole variation in CO_2 flux. No interactive effect of moisture and temperature was observed.

Prediction of CO_2 flux from T_{AIR} and estimated T_{CWD} in the field

The temperature in CWD (T_{CWD}) followed the T_{AIR} closely (Figure 3).

T_{CWD} was less variable than T_{AIR} but showed a similar average annual maximum and minimum. T_{AIR} explained 69% of the variation in T_{CWD} ($T_{CWD} = 0.776 \times T_{AIR} + 1.5985$).

The prediction of T_{CWD} could be improved, when average T_{AIR} from four previous days were included in the model in addition to T_{AIR} from the same day.

This model explained 74% of the variation in T_{CWD} ($T_{CWD} = 0.870 + 0.577 \times AvT_{AIR4} + 0.280 \times T_{AIR}$).

The prediction of average monthly T_{CWD}s from average monthly T_{AIR}s was very accurate. The linear regression between these two parameters ($T_{CWD} = 0.9693 \times T_{AIR} - 0.0101$) had a goodness of fit of $r^2 = 0.96$.

The distance between the CO_2 flux estimated from T_{AIR} and the one estimated from measured T_{CWD} increased with increasing temperature (from 0.03 g CO_2 kg DM^{-1} d^{-1} at 5°C to 0.11 g CO_2 kg DM^{-1} d^{-1} at 20°C) for *P. abies* (Figure 4). Similar results were observed for *F. sylvatica*.

Discussion

Incubation experiment

Our incubation experiment demonstrated that wood moisture exerted a stronger influence on carbon

Table IV. Q_{10} and k values for *F. sylvatica*, *P. abies* and *P. sylvestris* derived from linear regressions (sqrtEFFLUX $= a + b \times$ temperature) for each combination of species, moisture and decay class in the laboratory incubation experiment; mean Q_{10} values were 2.62 for *F. sylvatica* and 2.32 for *P. abies*, mean k values (yr^{-1}) were 0.07 for *F. sylvatica* and 0.03 for *P. abies* (mean density (g cm^{-3}): 0.41 for *F. sylvatica*, 0.39 for *P. abies*; mean moisture content (% dry weight): 247 for *F. sylvatica*, 181 for *P. abies*).

Decay class	Moisture level	Q_{10}			k (yr^{-1}; at 10°C)		
		F. sylvatica	*P. abies*	*P. sylvestris*	*F. sylvatica*	*P. abies*	*P. sylvestris*
1	1	—[b]	2.64	—[b]	—[b]	0.007	—[b]
	2	2.95	3.05	—[b]	0.021	0.017	—[b]
	3	1.41	1.28	—[b]	0.05	0.03	—[b]
3	1	3.52	—[b]	—[b]	0.028	—[b]	—[b]
	2	3.04	2.82	—[b]	0.046	0.016	—[b]
	3	1.78	1.88	1.6	0.085	0.045	0.04
5	1	—[a]	—[a]	—[a]	—[a]	—[a]	—[a]
	2	—[b]	—[b]	—[b]	—[b]	—[b]	—[b]
	3	3.01	2.24	—[b]	0.186	0.034	—[b]

[a]No CO_2 flux.
[b]Regression coefficients not significant ($p > 0.05$).

Table V. CO_2 flux (g CO_2 kg DM^{-1} d^{-1}) of coarse woody debris of European beech and Norway spruce in the case study "Conventwald".

Species	Diameter (cm)	Density (g cm^{-3})	Temperature (°C)	Moisture (Vol%)	CO_2 flux (g CO_2 kg DM^{-1} d^{-1})	Decomposition constant k (yr^{-1}) based on	
						CO_2 flux[a]	Mass loss[b]
F. sylvatica	37 (11.5)	0.411 (0.07)	7.7 (6.3)	26 (8)	0.5 (0.51)	0.113	0.052 (0.019)
P. abies	39 (7.3)	0.318 (0.03)	7.4 (6.1)	25 (5)	0.24 (0.26)	0.054	0.023 (0.007)

Note: Values are means with SDs given in parantheses ($n = 24$ for beech and spruce).
[a]Calculated from linear regression model.
[b]The original dry mass was calculated based on the average dry density (g cm^{-3}) of 0.68 (beech) and 0.43 (spruce), for the time period between 2009 and tree death: 1996 for beech (13 years) and 1990 for spruce (19 years). The original diameter was reconstructed if necessary, via the estimation of the thickness of already decomposed parts.

mineralisation than wood temperature and that the effect of moisture was more pronounced in beech than in the two conifer species. Similar results, with moisture content as the dominant environmental control over CWD respiration, were also found in a boreal black spruce forest in Canada (Hagemann et al. 2010). In contrast, a lab incubation with black spruce CWD logs showed a stronger influence of temperature ($R^2 = 0.37$) than moisture ($R^2 = 0.18$) on CO_2 flux (Wang et al. 2002). However, in that study, the temperature range was considerably wider than in our study, 5–42°C, whereas the variation in moisture content of CWD samples was much smaller (10–190% dry weight). Similar to our results, the variability in CO_2 flux increased with temperature or water content (Wang et al. 2002). Temperature explained 67–76% of the variation in respiration from downed logs in an old-growth temperate forest in north-eastern China (Wu et al. 2010). In that study, wood moisture content varied between 0.2 and 1.9 g H_2O g^{-1} dry wood over one year. In another study of woody debris respiration, in

which temperatures ranged between -10 and 33°C and moisture content between 0.1 and 6.8 g H_2O g^{-1} dry wood, T_{AIR} and wood moisture were of similar importance; each variable explained about 20% of the variation in respiration (Liu et al. 2006). This comparison indicates that the importance attributed to the influence of temperature and moisture in CWD decomposition, depends on the range of these factors that is applied. Since the temperature and moisture ranges have been so variable in previous studies, it is not possible to arrive at general conclusions about the relative importance of these factors.

In the incubation experiment, we observed mostly linear relationships between wood temperature as well as wood moisture and CO_2 flux. Commonly, an exponential relationship between temperature and CO_2 flux is assumed, as long as moisture or other factors are not limiting (see "Introduction" section). We found that the influence of temperature on CO_2 flux was dependent on wood moisture content. Similarly, declining temperature sensitivity of soil
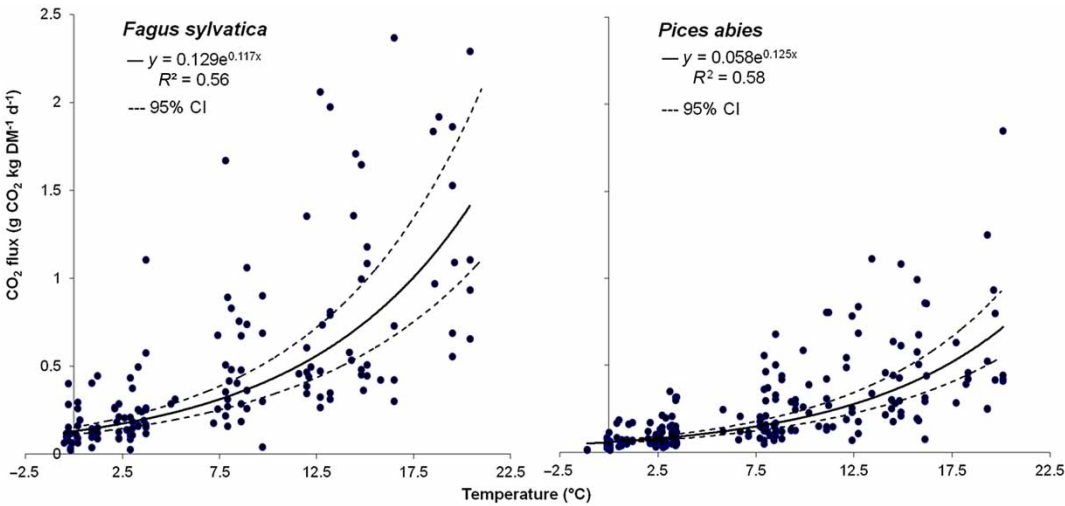

Figure 2. Amounts of CO_2 (g CO_2 kg DM^{-1} d^{-1}) measured in relation to temperature for *Fagus sylvatica* and *Picea abies* in the case study "Conventwald".
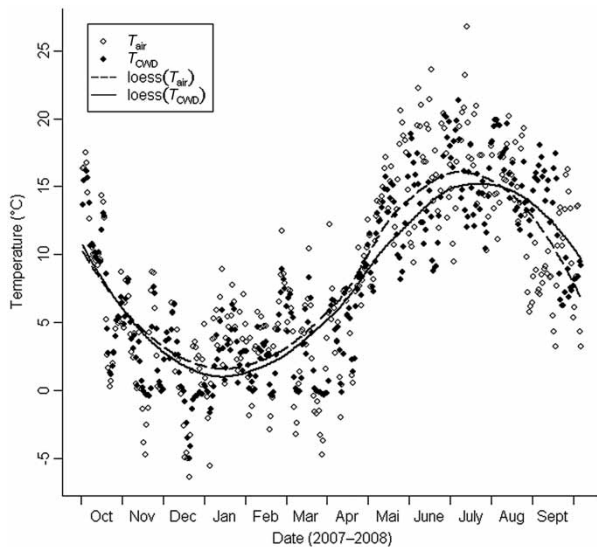
Figure 3. CWD temperature (T_{CWD}) and air temperature (T_{AIR}) measured in the case study "Conventwald"; fitted lines are loess smoothed values.

respiration (expressed as Q_{10}) was observed with increasing soil water deficit in a study by Reichstein et al. (2002). In contrast to Reichstein et al. (2002), we observed decreasing Q_{10} values with increasing wood moisture content for *F. sylvatica* and *P. abies* (Table IV). Similar results, decreasing Q_{10} values with increasing decay class and wood moisture content, were also observed in the study by Wu et al. (2010). On the other hand, *k* values increased with increasing moisture content.

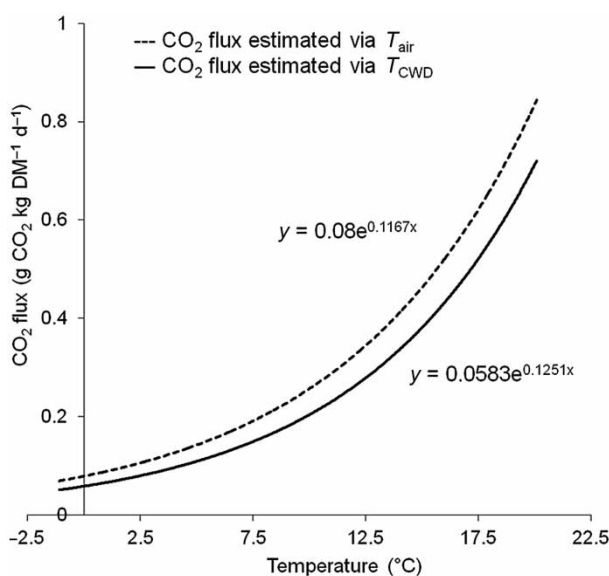The very dry and saturated moisture conditions under which CWD samples were measured in our

Figure 4. CO_2 flux estimated from T_{AIR} in relation to the CO_2 flux estimated from measured T_{CWD} for *Picea abies* in the case study "Conventwald".

incubation study might be one reason why exponential relationships were not observed. Here, we aimed to assess respiration across the maximum moisture range. While the absolute moisture contents achieved in our lab experiment are unlikely to occur under natural conditions, the general pattern (i.e. the observed interactive effects of wood temperature and moisture content) should be applicable. However, owing to the few moisture levels used, it was not possible to identify an optimum. Optimal moisture levels around 200% dry weight for decay classes 3 and 4, with restricted respiration at lower and higher moisture contents were observed for decomposing Sitka spruce logs in Ireland (Olajuyigbe et al. 2012). Similar, maximum respiration at intermediate wood water contents (0.4 m^{-3} m^{-3} related to void volume) were also observed in a broad-leaved forest in Japan (Jomura et al. 2008).

In accordance with Liu et al. (2006) and Wang et al. (2002), we conclude that the influence of one variable, moisture or temperature, can outweigh the other at extreme values. The high sensitivity to these factors in our study may also be related to the small sample sizes used, which would have placed less limitations of the decomposition process on oxygen availability, which may be more important in larger logs.

Furthermore, we found that the effect of temperature on CO_2 flux in our incubation study was dependent on species. Our regression analysis revealed a non-significant effect of temperature on CO_2 flux for woody debris of pine for all but one combination of density and moisture content. This might be attributed to a higher decay resistance of pine wood. Similar to our results, Yatskov et al. (2003) observed a strong effect of mean annual temperature on decomposition rate only for decay susceptible species (e.g. *Betula pendula*), whereas tree species with more decay resistant heartwood (such as *Pinus sylvestris* in our study) were less responsive.

CWD respiration rates in the lab incubation were significantly affected by the interactive effect of wood density (and hence also the decay status), species, as well as moisture content. A significant effect of density on CWD respiration has also been observed in other studies (Wang et al. 2002; Bond-Lamberty et al. 2003; Liu et al. 2006; Wu et al. 2010; Olajuyigbe et al. 2012). Similar to our results, T_{CWD} and water content interactions explained 74% of the observed variation (Wang et al. 2002) and between 78 and 87% (Olajuyigbe et al. 2012). While only 61% of the variation in respiration of snags and logs was explained in the study by Jomura et al. (2008). This indicates that CWD moisture and temperature are likely more important for CWD

mineralisation than other factors such as fungal species composition, CWD size or plant traits (see Cornwell et al. 2009).

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In contrast to the lab incubation experiment, wood moisture content was neither limiting nor excessive (ranging from 5–41% and 11–30% on a volume basis for beech and spruce, respectively) in the field experiment. Therefore, we observed the biggest influence on the CO_2 flux for temperature (ranging from about -1–$20°C$ for both species), which explained about 96% of the variation in CO_2 flux for beech and 94% for spruce. A similar effect, with a positive correlation for temperature ($R^2 = 0.11$) and no correlation for wood moisture ($R^2 = 0.02$) were found in a CWD respiration study in experimental forest canopy gaps (Forrester et al. 2012).

The Q_{10} values (between 5 and $20°C$) measured in the field (2.54 for beech and 2.78 for spruce) were similar (beech) or slightly higher (spruce) compared to those determined under controlled conditions (2.62 for beech and 2.32 for spruce). For comparison, a Q_{10} value of 4.1 was observed for black spruce for a similar temperature range (Wang et al. 2002). Between $20°C$ and $42°C$, the Q_{10} value for black spruce equalled 1.7 and for the whole temperature range of 5–$42°C$ a Q_{10} of 2.5 was calculated. In other studies, Q_{10} values between 2.41 and 2.95 (Wu et al. 2010) and between 3.35 and 4.76 have been determined (Olajuyigbe et al. 2012). The analysis of a global data-set comprising CWD decay rates and average annual temperatures yielded an average Q_{10} value of 2.53 (Mackensen et al. 2003). For CWD in a European beech forest in Central Germany, a Q_{10} value of 2.2 for decay stage 1 and 2.7 for decay stage 3 was observed between temperatures of 0 and $20°C$ (Müller-Using 2005). The Q_{10} value was 2.5 for decay stages 2 and 4. This shows that the Q_{10} values determined in this study are comparable to those reported in the literature, and that the global value of Mackensen et al. (2003) might be a good approximation also for the species studied here in the absence of better information. However, this comparison also shows that in particular cases (species, decay status, etc.), approaches to model CWD respiration with an average or default Q_{10} value might be associated with high errors.

The average decomposition constants (k) calculated from the respiration measurements in the field were about twice as high (190% for beech and 210% for spruce) than k-values calculated from mass loss (Table V). This is not surprising, because these respiration measurements did not include lag times

due to initially slow colonisation by fungi. In addition, respiration measurements may be conducted over a period that is more favourable for decomposition than the long-term average, and respiration rates may change with decomposition stage. Similar to our results, the k-values based on respiration rates were 6–12 times higher than the k-values derived from density loss in a study by Mackensen and Bauhus (2003). However, in another study, it was proposed that decay rates derived from respiration measurements should be lower than the overall decay rate based on mass loss, which also comprises fragmentation and leaching in the mass loss rate (Liu et al. 2006).

In cases, where fragmentation and leaching contribute substantially to mass loss from CWD, or where respiration and decomposition rates vary substantially with decomposition stage, the accuracy of approaches to model CWD mass loss based on instantaneous measurements of respiration rates will be limited.

Prediction of CO_2 flux from T_{AIR} and estimated T_{CWD} in the field

T_{AIR} explained 69% of the variation in T_{CWD} in the field. In a similar study, T_{CWD} was positively correlated to T_{AIR} ($R^2 = 0.79$), with a hysteresis effect that correlated with decay status and leaf area index (Wang et al. 2002). Similar results and decreasing correlation strength with increasing depth from CWD surface to bottom were found by Hagemann et al. (2010). An even higher correlations between wood and T_{AIR} ($R^2 = 0.9$) was observed by Forrester et al. (2012).

Our results showed that T_{CWD} and T_{AIR} were best correlated for monthly averages ($R^2 = 0.96$). Therefore, a prediction of T_{CWD} from T_{AIR} to model respirational carbon loss of CWD based on monthly averages seems to be feasible. In contrast, the use of large time steps in CWD respiration models underestimated annual CWD respiration because of the non-linear relationship among CWD respiration, T_{CWD} and water content (Wang et al. 2002). In the same study, the use of T_{AIR} instead of T_{CWD} in models with an hourly time step introduced a much greater error to annual CWD respiration rates compared to models with weekly time steps. Thus, the temporal scale that is most useful for predictions of annual CWD respiration and thus annual decomposition rates might have to be determined for specific situations. However, monthly temperature averages are commonly available data from meteorological stations.

Conclusion

Our study showed that CWD respiration rates were dependent on tree species and decay stages and were strongly controlled by wood temperature and wood moisture content. Therefore, it may be too simple to model CWD mass loss with constant decay rates for the entire decomposition process (see also Herrmann & Prescott 2008). The relationship between T_{AIR} and T_{CWD} offers an approach of modelling temperature influence on respiration and may, therefore, be included in models of forest carbon emissions.

Acknowledgements

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