Stem and branch respiration of beech: from tree measurements to estimations at the stand level

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Summary

• Stem and branch respiration of 30-yr-old \textit{Fagus sylvatica} trees was measured in a temperate forest for 1 yr to estimate the annual flux at the stand level.
• The seasonal response of respiration to air temperature was determined using infra-red gas analysis (IRGA) systems. Annual respiration was derived from half-hourly temperature recording and allometric relations established for the same forest.
• The basal respiration rate at 15°C (R\textsubscript{15}) increased greatly during the growing season. On a volume basis, monthly means of R\textsubscript{15} were higher for branches than for stems. For stems, Q\textsubscript{10} was relatively constant throughout the year, with an annual average of 1.7. Estimated annual respiration was approx. 325 g C m\textsuperscript{-2} ground surface area yr\textsuperscript{-1} with 50% of this amount attributed to growth respiration.
• Stem and branch respiration played a major role in the annual carbon balance of the beech stand. It represented approx. one third of the ecosystem-level carbon loss from respiration. The magnitude of crown respiration makes it obvious that information on branch respiration characteristics is required for reliable estimations at the stand level.

Key words: \textit{Fagus sylvatica} (beech), trunk respiration, temperature, seasonal change, scaling, annual carbon budget.

Introduction

Interest in stem respiration is increasing as many quantitative estimates show that it is a large component of the annual carbon balance of forest ecosystems, and therefore partly determines the capacity of forests to stock carbon. Total autotrophic respiration can consume > 50% of the carbon fixed by leaves in forests (Ryan, 1991). Nevertheless, estimates of the proportion of woody tissue respiration vs gross primary production show large variations (from 7% to 50%, see Ryan et al., 1994a). Many studies suggest that respiration is a key process in explaining variations in ecosystem productivity (Valentini \textit{et al.}, 1996). Its importance relative to CO\textsubscript{2} assimilation could explain some variations in forest ecosystem production depending on climate (Ryan \textit{et al.}, 1995) and fertilization (Stockfors & Linder, 1998). The decline of productivity in ageing forests has been attributed to increasing amounts of respiring woody tissue (Kozlowski \textit{et al.}, 1991; Yoder \textit{et al.}, 1994), but several studies also have shown that only a small fraction of the decline can be explained by sapwood respiration (Ryan & Waring, 1992; Murty \textit{et al.}, 1996; Ryan \textit{et al.}, 1997).

Differences in stem respiration could be the result of differing site characteristics, but evaluations of stem respiration also depend on measurement and calculation methods. Quantifying the stem respiration of a forest ecosystem requires CO\textsubscript{2} efflux measurements in the field to build or validate simulation models. Respiration strongly depends on temperature; therefore, this environmental parameter is generally used to simulate temporal variation. Some difficulties are involved in scaling up from local and noncontinuous field respiration measurements to estimates of carbon loss at the ecosystem level for the duration of one year. These difficulties can be summarized in four major issues:

1. Quantifying the evolution of CO\textsubscript{2} through the different seasons. Few studies have examined the seasonal respiration
throughout an entire year. Some have shown that the response of respiration to temperature clearly varies among months (Paembonan et al., 1991).

2. Quantifying the intra- and intertree variability. Several previous studies have shown differences between stems and branches for volume-based or area-based respiration (Moller et al., 1954; Sprugel, 1989; Sprugel, 1990), but these differences are rarely considered when scaling up to the stand level. Many studies have shown differences among trees for stem maintenance and growth respiration, which were correlated to live cell volume and annual dry-matter production, respectively (Ryan, 1990).

3. Determining the best unit of scale. The unit chosen (surface area, sapwood volume, sapwood dry mass) can greatly affect the final results. Surface area, for instance, was found to be the best unit for expressing maintenance respiration of *Picea abies* (Stockfors & Linder, 1998) because the living cells were concentrated in the outer wood. Nevertheless, Ryan (1990) found maintenance respiration of *Pinus contorta* and *Picea engelmannii* was better estimated by sapwood volume.

4. Obtaining accurate estimates of stem and branch volume or surface area at the stand level. Small errors in these volume or area estimates could lead to large errors in scaled-up values, especially if respiration rates are heterogeneous within and among trees. Stand-level estimations have been developed with and without allometric relationships (Yoda et al., 1965; Ryan & Waring, 1992; Edwards & Hanson, 1996).

Most studies concerning stem respiration have been done on conifers. Investigations of other woody species, especially deciduous broadleaved trees, need to be expanded. In the current study, we measured stem CO$_2$ efflux of a temperate deciduous species, beech (*Fagus sylvatica*). The study was conducted in a young forest stand. Measurements were taken over 1 yr on trees of various diameters, and at different heights within the trees (at 1.3 m and higher on stems, and on branches in the crown). Our objectives were: to determine the response of respiration to air temperature over the different seasons; to examine inter- and intratree variability; to determine the relative importance of maintenance and growth respiration; and to estimate the annual carbon flux from stem and branch respiration at the stand level.

**Materials and Methods**

**Site description**

The experimental site is a 0.63-ha plot located 5 km south of Sarrebourg, eastern France, in the Hesse Forest (48°40' N, 7°05' E, 300 m elevation, slope < 2%). This forest is an EUROFLUX site equipped with electricity (220 V). It has a temperate climate. Annual temperature and precipitation means are 9.2°C and 820 mm, respectively. The soil is a gley luvisol according to the Food and Agriculture Organization (FAO) classification (depth > 120 cm). The predominant woody species is *Fagus sylvatica* L., with a minor component of *Quercus petraea*, *Betula pendula* and *Carpinus betulus*. In 1997, the trees were aged 25–35 yr with a density of 3480 trees ha$^{-1}$, a mean height of 13 m, and a mean diameter of 8 cm at 1.30 m height. The histogram of tree diameters at the site is presented in Fig. 1. The canopy was closed to a large extent with a maximum leaf area index (LAI) of 5.6 in 1997 (Granier et al., 2000). For *F. sylvatica*, leaf emergence reached 100% at the end of April (Lebaube et al., 2000). Trees were not subjected to a water constraint. The predawn water potential measured in the crown was approx. –0.5 MPa throughout the summer, except during the first 2 wk of September when it dropped to –1.1 MPa (Lemoine, 2000).

**Field respiration measurements**

Respiration was measured at two locations: on stems at 1.30 m height and on branches in the crown.

**Stem respiration at 1.30 m height**

Stem CO$_2$ efflux measurements were done using temporary clamp-on chambers made of two half-cylinders of transparent, hard plastic Acrylic resin. We used five 20-cm-long chambers with variable-diameter openings in the endwalls. Chambers were attached to the stem at approx. 1.30 m height. The two halves of the chambers were sealed together and to the bark with gasket and rubber sealant (Terostat-7, Teroston, Ludwigburg, Germany). The seals were tested by blowing along the joints and measuring the CO$_2$ evolution in the chamber. The chambers were covered with aluminium foil to prohibit bark photosynthesis and overheating from direct sun exposure. There were no visible mosses or algae on stems. Carbon dioxide efflux was measured on the airtight closed system using a solid-state IRGA detector (PP Systems, CIRAS-1, Hitchin, UK; response time
approx. 1 s). The chambers were connected to the IRGA by 80 cm of flexible tubing (BEV-A LINE IV, polyethylene lined Tygon). A constant flow rate (10⁻⁴ m³ min⁻¹) was maintained by the IRGA pump. The air in the chamber was homogenized by a fan. The CO₂ efflux measurement was stopped either when CO₂ variation reached 50 ppm or when measurement time reached 120 s. The rate of CO₂ evolution was verified as linear for the duration of the measurements. Between measurements, to avoid artificially high CO₂ efflux, the air in the chamber was purged with ambient air for several minutes.

Stem respiration measurements were conducted each month from March 1997 to February 1998 (except January) on 15 different trees. These 15 trees were pooled into five diameter classes which corresponded to the following inner diameters of the respiration chambers: 4, 7.5, 10, 11, and 13.5 cm. Empty chamber volumes ranged from 1313 to 5856 cm³, and chamber volumes with the stems inside ranged from 1092 to 2861 cm³. Sample trees encompassed the range of diameters and dominance status present at the site (see Fig. 1). The three smallest trees (in the 4 cm diameter class) were 9 m high; the others were 12–15 m high. The trees of the two smallest diameter classes were suppressed, the others were either codominant or dominant. The monthly measurements were performed over 3 d. The chambers were not left on the stems at the same position during each sampling date. For each tree, the chamber remained in place all day long, and three measurements were recorded every 1.5 or 2 h from predawn to at least sunset. Between measurement sets, the stoppers were removed from the chambers to allow air ventilation and avoid CO₂ accumulation in the chambers.

In rare cases when replicates differed by > 10%, further measurements were taken. Additionally, in July, respiration was monitored through a 24-h period to assess the change in respiration with temperature during day and night. The circumstances of stems enclosed by the chambers were measured manually each month. The total radial area increment at the three locations measured. The branch radial increment at the three locations was measured manually each month.

Vertical profile of respiration along the stem. Four times a year, on the tree used for branch measurements, the CO₂ efflux from the stem was measured at three heights using the chambers and system described above for 1.30 m height. Three chambers were attached at 12.25, 6.5, and 0.5 m of height (corresponding to diameters of 4, 7.5, and 10 cm). The highest chamber was in the live crown; the remaining two chambers were below the crown. Measurements were taken every 1.5 h during daytime, for a total of approx. five times per day. The vertical profile of respiration was recorded in July, August, September and December (on days 192, 234, 269 and 345).

Respiration data analysis

The respiration rates recorded in the field were adjusted for temperature variation using a simple exponential equation (eqn 1). Respiration rates (i.e. CO₂ efflux, R) were expressed in terms of Q₁₀ that is, the change in rate with a 10°C change in temperature as follows:

$$ R = R_{15} Q_{10}^{(T-15)/10} $$  

(eqn 1)

(R₁₅, the basal respiration rate.) In our case, a basal temperature (Tb) of 15°C (R₁₅ = R₁₅) was chosen. Respiration was either the total CO₂ efflux measured, or the estimated maintenance or growth respiration. Either air or stem temperatures, measured in °Celsius, were used for the variable, T. The stem temperature is the more biologically relevant reference but only air temperature was monitored over the full year. For each measurement site on the sample trees, daily R₁₅ and Q₁₀ values were calculated for the 24-h period using eqn 1. Data analyses were computed using

We calculated the growth respiration by subtracting the estimated maintenance respiration adjusted for temperature from the total CO$_2$ efflux measured. We calculated stem construction costs by relating stem increment and growth respiration. For each tree measured, the instantaneous growth respiration for the growing period (mol CO$_2$ s$^{-1}$ per chamber), the total annual growth respiration (mol CO$_2$ yr$^{-1}$ per chamber) and the total annual stem volume increment (cm$^3$ yr$^{-1}$ per chamber) were calculated for the part of the stem enclosed in the chambers at 1.30 m height. The total annual growth respiration per chamber was calculated using individual monthly $Q_{10}$ and $R_{15}$ values, and half-hourly air temperature data recorded at the site at a height of 18 m in 1997 (A. Granier, pers. com.). Linear regressions forced through the origin (SAS, 1994; regression procedure with the NOINT option) were used to relate growth respiration values to the stem volume increment and to calculate the construction cost of stem organic matter.

Stem volume and area

Allometric relationships for stems Twenty-three additional trees which represented the population of sample trees used for respiration measurements were felled in the vicinity of the Hesse experimental stand to provide dimensional and biomass data. Each tree stem, including all fork arms, was cut into segments of < 1.2 m, and the exact length of each segment was recorded. A sample disk was cut from the base of each stem segment for measurements in the laboratory. The accurate length of each disk (c. 10 cm) was recorded and its radius was calculated as the mean of four radii (not including the bark which is quite thin in P. petraea) measured at 90° intervals from the major axis. From these measurements, the total volume and surface area of the stem was computed. Moreover, the woody biomass of each sample disk was measured after oven-drying to constant weight at 105°C to allow calculations of green wood specific gravity (dry mass per volume of fresh wood). Also for each tree, an inventory of branches originating directly from the stem (first-order branches) was done, and basal branch diameters (bark not included) were measured. These diameters were used to obtain the branch biomass.

Allometric relationships for branches Three trees of differing crown status (two codominant, one suppressed) were selected to establish the total areas and volumes of the branch fractions of the different diameter classes. Based on the observed diameter distributions, and the branch diameters used for respiration measurements, we designated the following cross-sectional diameter classes ($d$) for branches: $d = 0.5$ cm; $0.5 < d \leq 2.0$ cm; $d > 2.0$ cm. No branch diameters larger than 3 cm were observed in our plot. For each of the three trees, two first-order branches were chosen from each third of the crown. Additionally, one second-order branch was selected from every third of each first-order branch.

Branch profile equations were established for first- and second-order branches. These equations related the cross-sectional diameter at a given point on a branch to the distance from this point to the apex of the branch and to the branch length. Surface and volume equations for first- and second-order branches were obtained by integrating the suitable branch profile equation. The same procedure was applied to the third-order branches by using the branch profile equation established for second-order branches. Branches at higher orders of ramification were scarce and short and were ignored. For each sampled first-order branch, the surface areas and volumes of the different branch diameter classes were estimated with the surface and volume equations established for branches of different orders. Allometric relations between the total area (or volume) of each diameter class of branches and the basal diameter (or length) of the first-order branches were then established.

The allometric relations obtained for branches were used to estimate the area and volume of the different branch diameter classes at tree level. This was done using the diameter inventory of first-order branches and the relation established between diameter and length of first-order branches. Finally, estimates of stem and branch volume and area were made at
tree level and linked to tree diameter. These estimations were summed up, using tree diameter inventories on the site, to obtain volume and area estimations at the stand level.

Data analysis for allometric relationships The relationships used to estimate the surface areas and volumes of stems and branches were established with one of the following software applications: StatView II™ (Abacus Concepts Inc., Berkeley, CA, USA), Data Desk 4.1 (Data Description Inc., Ithaca, NY, USA) and S-PLUS (Data Analysis Division of MathSoft Inc., Seattle, WA, USA). Linear and nonlinear regression models were used. Depending on the model, several statistics were used to assess reliability: the coefficient of determination ($r^2$), the residual mean square error (MSE), and the $P$-values.

Scaling-up stem respiration to annual and stand-level bases

Stem respiration throughout the year was estimated using monthly derived $Q_{10}$ and $R_{15}$ values, half-hourly air temperature data, and stem areas or volumes of four compartments (stems plus the three diameter classes of branches). All wood was considered to be sapwood because trees at the site had live cells throughout their stems (E. Ceschia, unpublished). The annual maintenance and growth components were calculated separately using $Q_{10}$ and $R_{15}$ obtained from maintenance and growth respiration, respectively.

For the stems, we used $Q_{10}$ and $R_{15}$ calculated by averaging the values obtained for the different trunk diameter classes (using individual $Q_{10}$ and $R_{15}$ values gave similar results). We did not take any measurements in January, so for this month we used $Q_{10}$ and $R_{15}$ derived from averaged December and February values.

For the crown, we used $Q_{10}$ and $R_{15}$ derived from each data set obtained from the three branches of different diameter. Results from the smallest diameter ($0.25$ cm) were applied to the thin branch category ($d \leq 0.5$ cm). For the larger branches, the results from the 1.25- and 2.5-cm-diameter branches were applied to diameter classes $0.5 < d \leq 2.0$ cm and $d > 2.0$ cm, respectively. For December, January and February (there were no measurements on branches for these months), we derived $Q_{10}$ and $R_{15}$ from values averaged over September, October and November. All the calculations were made either on a volume or an area basis.

Results

Daily variations

Diurnal stem respiration generally increased with air temperature (Fig. 2a). It reached a maximum during or after air temperature was highest, then decreased during the afternoon. One day in February when the minimum temperature was $-4.5^\circ$C, respiration started to increase only after air temperature had reached its maximum (data not shown). Measurements recorded at 1.30 m height in relation to air (a) or stem (b) temperature. Measurements were recorded over 24 h in July 1997 on three trees. Data obtained from two additional trees gave similar results but are omitted for clarity of the figure. Tree diameters were 4 cm (closed triangles), 7.5 cm (open circles) and 10 cm (closed circles). The arrows indicate the direction of temperature fluctuation at the time of respiration measurements ($T_{incr}$, increasing temperature from point 1 to point 2; $T_{decr}$, decreasing temperature from point 2 to point 3). Note: small error bars may be hidden by symbols for the means.

Seasonal trends

On most days, the relationship between air temperature and respiration was well described by an exponential equation, although a linear relation occasionally fit slightly better. On average, the coefficient of determination ($r^2$) was equal to 0.6 and 0.8 for adjustments from stem ($n = 27$) or branch ($n = 9$) measurements, respectively. Values for $Q_{10}$ obtained by fitting either volume-based or area-based respiration data were
similar; therefore, we showed only those obtained from volume-based values. For stems at 1.30 m height, the monthly mean \( Q_{10} \) (using air temperature) calculated with all sample trees was quite stable all year long (Fig. 3a). The annual mean was 1.7 (SD = 0.45, \( n = 105 \)). For most months, mean \( Q_{10} \) ranged from 1.6 to 1.8. The two highest values (2.1 and 2.0) occurred in April and June. When considering stem temperature rather than air temperature, annual mean \( Q_{10} \) was 1.8 (SD = 0.36, \( n = 126 \)). Contrary to \( Q_{10} \), volume-based and area-based \( R_{15} \) showed great seasonal variation (Fig. 3b,c). The lowest \( R_{15} \) values occurred during winter with a minimum in February (10.4 \( \mu mol \) m\(^{-3}\) s\(^{-1}\) or 0.2 \( \mu mol \) m\(^{-2}\) s\(^{-1}\)) and the highest values occurred in summer with a maximum in July (131.5 \( \mu mol \) m\(^{-3}\) s\(^{-1}\) or 3.0 \( \mu mol \) m\(^{-2}\) s\(^{-1}\)).

Regarding branch respiration, monthly \( Q_{10} \) means for the three diameters were generally higher than 2, with a maximum of 3.9 and no clear trend throughout the year (Fig. 4a). Monthly means for \( R_{15} \) were higher in spring and summer than in autumn (Fig. 4b,c). Volume-based \( R_{15} \) reached a maximum of 2436 \( \mu mol \) m\(^{-3}\) s\(^{-1}\) in June in the smallest diameter branch, and area-based \( R_{15} \) peaked at 3 \( \mu mol \) m\(^{-2}\) s\(^{-1}\) in June in the largest diameter branch. During winter, \( R_{15} \) values of branches (expressed on an area basis) were similar to those obtained for the stems.

**Stem diameter effect**

The effect of tree diameter was examined in terms of \( Q_{10} \) and \( R_{15} \) during and after the growing season. Annual means for \( Q_{10} \) (obtained with air temperature) showed no significant difference between growth and maintenance respiration, but they progressively decreased with increasing tree diameter (Fig. 5a,b). Only \( Q_{10} \) for the smallest trees was significantly different from the others. Using stem temperature rather than air temperature resulted in less of a diameter effect on \( Q_{10} \) (Fig. 5a,b). With increasing tree diameter, area-based \( R_{15} \) showed a gradual increase that was especially pronounced for...
the estimated growth respiration (Fig. 5c). For volume-based
R15, there was no difference between trees of different girth,
except that the smallest diameter trees had a significantly
higher maintenance respiration value compared to the others
(Fig. 5d).

The individual instantaneous growth respiration in July
and August, and the annual growth respiration were related
linearly to the total annual volume increment for the stem
sections in the chambers (Fig. 6a,b). The slope of the zero-
intercept regression (Fig. 6b) provides an estimation of the
construction cost of the stem organic matter equal to
0.01 mol CO2 per cm3 of stem produced. This value corre-
sponds to a cost of 0.38 g C of growth respiration to incorpo-
rate 1 g C into new stem tissue. We calculated this value for
dominant and codominant trees using 49% carbon content in
the organic matter (Matthews, 1993) and a mean green stem
wood specific gravity of 636 kg m–3.

Intra-tree variability
Figure 7 showed large variations in intratree area-based and
volume-based respiration, especially during the growing
season. In July and August, volume-based respiration in-
creased when diameter decreased, that is, with measure-
ments from the base to the top of the tree. Daily mean
respiration was 19 times higher at the top of the crown than
at the base of the stem in December and 42 times higher in
July. Area-based values did not show any clear trend between
daily mean respiration and diameter. During the summer,
maximum values were obtained in the crown for diameters of
2.5 and 3.8 cm (12.25 and 13 m in height). The daily mean
Fig. 7 Mean daily respiration (R) recorded at different heights on the stem and on branches of one 15.5 m tall beech tree, expressed on (a) a surface area, and (b) a volume basis. Measurements were recorded in July (open circles), August (closed circles), September (open squares) and December (closed squares). Mean diurnal temperatures in July (open circles), August (closed circles), September (open squares) and December (closed squares). Note: small error bars may be hidden by symbols for the means.

difference in air temperature between the top chamber and the chamber at 1.3 m height ranged from 0°C in December to 6°C in July.

Allometric relationships

**Branch level** The branch profile equations for first- (eqn 2) and second-order (eqn 3) branches fit the following models

\[ dL/dL = 0.000542 + 0.008295/\ell \]  
(MSE = 0.0703, \( r^2 = 0.88 \))  
Eqn 2

\[ dL/dL = 0.002024 + 0.006147/\ell \]  
(MSE = 0.1093, \( r^2 = 0.64 \))  
Eqn 3

where \( d \) is the cross-sectional diameter at a given point on the branch (cm), \( L \) the distance from the given point to the branch apex (cm), and \( L \) is the length of the branch (cm). The variables \( d \) and \( L \) were divided by \( L \) to homogenize the variance of data when fitting the equations.

The surface \( (S) \) and volume \( (V) \) of the part of the branch from the given point to the apex are described by the following equations derived from eqns 2 and 3:

\[ S = \pi \left( \alpha L + \beta l^2 \right) \]  
Eqn 4

\[ V = \frac{\pi}{12} \left( \alpha L + \beta \right)^3 - \left( \alpha L \right)^3 \]  
Eqn 5

The parameters \( \alpha \) and \( \beta \) are the intercept and the slope, respectively, of eqns 2 or 3. To estimate \( S \) and \( V \) from branch cross-sectional diameter \( (d) \), \( L \) can be replaced in eqns 4 and 5 by one of the following relations:

\[ l = L - 113.282(d_0 - d) \]  
Eqn 6

\[ l = L - 127.942(d_0 - d) \]  
Eqn 7

where \( d_0 \) is the basal diameter of the branch (\( L \) and \( d \) are in cm).

These equations were obtained by fitting the data to the following linear model, forced through the origin to ensure that \( l = L \) when \( d = d_0 \), \( L = l = k(d_0 - d) \). The model coefficients are significantly different from 0 \( (P < 0.0001) \).

The lengths, \( L \) (m), of first- and second-order branches were related to \( d_0 \) (cm) with eqns 8 and 9, respectively:

\[ L = 1.09481d_0 \]  
(MSE = 0.448, \( P < 0.0001 \))  
Eqn 8

\[ L = -0.0966 + 1.2694d_0 \]  
(MSE = 0.140, \( r^2 = 0.89 \), \( P < 0.0001 \))  
Eqn 9

Following the methods explained earlier and using eqns 4 to 7 and 9, the total area (and volume) of each size class of branches was estimated and related to the basal diameter (or length) of the first-order branches (Table 1). The total volume of the size class of branches of diameter > 2.0 cm was calculated as the difference between the total volume of the first-order branches (with their ramifications) and the sum of the volumes of the diameter classes ≤ 2.0 cm (see Table 1).

**Tree level** Using the branch volume and area equations developed above, and eqn 8 to estimate the length of branches from the inventory of branch basal diameters, the total area and total volume of the branches in each diameter class were calculated for each of the 23 sample trees. Stem area and volume equations, as well as area and volume equations for branches of each class, were then obtained using a nonlinear, least-squares regression analysis (Tables 2 and 3) with the following model:

\[ y = a \log_2 (1 + e^{(\alpha + \beta)}) \]  
Eqn 10
branches. The regression model was: \( y = a + bx \)

### Table 1
Parameters and statistics of the regressions between area or volume of the three size classes of first-order branches, including their ramifications, and basal diameter \( d \) or length \( L \) of the first-order branches. Size classes are based on the cross-sectional diameter \( d \) of the branches. The regression model was: \( y = a + bx \)

<table>
<thead>
<tr>
<th>Branch size class</th>
<th>Independent variable ( x ) (cm)</th>
<th>Regression model</th>
<th>( p )</th>
<th>( a )</th>
<th>( b )</th>
<th>( r^2 )</th>
<th>MSE(^a)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area (cm(^2))</td>
<td>( d )</td>
<td>Linear</td>
<td>1.6</td>
<td>–607.86</td>
<td>710.66</td>
<td>0.95</td>
<td>438.9</td>
</tr>
<tr>
<td>0.5 &lt; ( d ) ≤ 2.0</td>
<td>( d )</td>
<td>Linear</td>
<td>1.4</td>
<td>–564.62</td>
<td>581.40</td>
<td>0.90</td>
<td>384.1</td>
</tr>
<tr>
<td>Total</td>
<td>Nonlinear</td>
<td>1.14</td>
<td>0</td>
<td>923.97</td>
<td>–</td>
<td>231.1</td>
<td></td>
</tr>
<tr>
<td>Volume (m(^3))</td>
<td>( d )</td>
<td>Nonlinear</td>
<td>2.07</td>
<td>0</td>
<td>1.34 \times 10^{-3}</td>
<td>–</td>
<td>34.15</td>
</tr>
<tr>
<td>0.5 &lt; ( d ) ≤ 2.0</td>
<td>( L )</td>
<td>Nonlinear</td>
<td>2.02</td>
<td>0</td>
<td>4.00 \times 10^{-3}</td>
<td>–</td>
<td>62.64</td>
</tr>
<tr>
<td>Total</td>
<td>Nonlinear</td>
<td>2.86</td>
<td>0</td>
<td>7.47 \times 10^{-3}</td>
<td>–</td>
<td>142.2</td>
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</tr>
</tbody>
</table>

\(^a\)\( r^2 \), coefficient of determination. \(^a\)MSE = residual mean square error

### Table 2
Parameters and statistics of the equations to predict branch areas and volumes at the tree level, \( y = u \log_e (1 + e^{sx+w}) \)

<table>
<thead>
<tr>
<th>Branch size class</th>
<th>Independent variable ( x ) (cm)</th>
<th>( u )</th>
<th>( v )</th>
<th>( w )</th>
<th>MSE(^a)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area (m(^2))</td>
<td>Tree diameter</td>
<td>0.699</td>
<td>0.93</td>
<td>–5.656</td>
<td>0.698</td>
</tr>
<tr>
<td>0.5 &lt; ( d ) ≤ 2.0</td>
<td>Tree diameter</td>
<td>0.363</td>
<td>1.04</td>
<td>–5.363</td>
<td>0.444</td>
</tr>
<tr>
<td>( d ) &gt; 2.0</td>
<td>Tree diameter</td>
<td>0.195</td>
<td>1.19</td>
<td>–9.393</td>
<td>0.076</td>
</tr>
<tr>
<td>Volume (m(^3))</td>
<td>Tree diameter</td>
<td>6.53 \times 10^{-4}</td>
<td>0.6945</td>
<td>–5.976</td>
<td>3.8 \times 10^{-4}</td>
</tr>
<tr>
<td>0.5 &lt; ( d ) ≤ 2.0</td>
<td>Tree diameter</td>
<td>1.57 \times 10^{-3}</td>
<td>0.7084</td>
<td>–5.862</td>
<td>9.5 \times 10^{-4}</td>
</tr>
<tr>
<td>( d ) &gt; 2.0</td>
<td>Tree diameter</td>
<td>1.65 \times 10^{-3}</td>
<td>0.9897</td>
<td>–9.874</td>
<td>5.3 \times 10^{-4}</td>
</tr>
</tbody>
</table>

\(^a\)MSE, residual mean square error

### Table 3
Parameters and statistics of the equations to predict the stem area and volume of each sample tree, \( y = u \log_e (1 + e^{sx+w}) \)

<table>
<thead>
<tr>
<th>Predicted variable</th>
<th>Independent variable ( x ) (cm)</th>
<th>( u )</th>
<th>( v )</th>
<th>( w )</th>
<th>MSE(^a)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area (m(^2))</td>
<td>Tree diameter</td>
<td>0.662</td>
<td>0.711</td>
<td>–2.866</td>
<td>0.270</td>
</tr>
<tr>
<td>Volume (m(^3))</td>
<td>Tree diameter</td>
<td>0.045</td>
<td>0.441</td>
<td>–7.714</td>
<td>0.004</td>
</tr>
</tbody>
</table>

\(^a\)MSE, residual mean square error

\( y \), either the surface area or the volume of stem or branches; and \( x \), the tree diameter at 1.30 m.) This model combined an initial nonlinear component with a subsequent linear component to better adapt to the behaviour of the data (Chambers & Hastie, 1992).

### Table 4
Areas and volumes in March 1997 of the different tree compartments at the stand level. The branches were sorted into three size classes based on their cross-sectional diameter, \( d \)

<table>
<thead>
<tr>
<th>Tree compartment</th>
<th>Area (m(^2) ha(^{-1}))</th>
<th>Volume (m(^3) ha(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branches</td>
<td>4733.5</td>
<td>3.20</td>
</tr>
<tr>
<td>0.5 &lt; ( d ) ≤ 2.0 cm</td>
<td>2897.4</td>
<td>8.02</td>
</tr>
<tr>
<td>( d ) &gt; 2.0 cm</td>
<td>427.7</td>
<td>2.64</td>
</tr>
<tr>
<td>Total</td>
<td>8018.6</td>
<td>13.86</td>
</tr>
<tr>
<td>Trunks</td>
<td>7021.5</td>
<td>111.86</td>
</tr>
</tbody>
</table>

Annual totals at the stand level

The relations established at the tree level were used, together with the diameter inventory of all trees in the experimental stand (0.63 ha), to estimate the area and volume of the stems and the branch size classes at the stand level. Table 4 shows the area and volume per hectare of the different tree compartments before the growing season in 1997 which were considered in scaling-up the respiration measurements. Branches accounted for 11% and 53% of the total stem and branch volume and area, respectively.

Estimates of annual stand-level stem and branch respiration are shown in Table 5. Area-based estimates gave slightly higher values than volume-based estimates. Total respiration was 14.9% higher when calculated on an area basis compared to a volume basis. Growth respiration, calculated on a volume basis, accounted for approx. 50% of the total annual respiration (54% for stems and 51% for branches). Total respiration was half stem-respiration and half branch-respiration.
Discussion

Response of stem respiration to temperature: seasonal and stem diameter effect

The hysteresis we observed between respiration and air temperature indicated that it is preferable to record measurements over a daily period during which temperature both increases and decreases. Even when we used the stem temperature, a small hysteresis remained because our measurements probably were not representative of the temperature of the whole sapwood. In fact, wood temperature could differ substantially from air temperature, and it could also vary within the stem (Derby & Gates, 1966; Ryan, 1990; Stockfors, 2000). At 1.3 m height, we measured differences up to 5°C between the core and 2 mm beneath the bark of an 11.5-cm diameter tree. The Q10 values that we found for F. sylvatica stems were within the range of reported values for different conifer and broadleaved species during dormant and growth seasons (see Table 6). Generally, Q10 values were close to 2. Some lower and higher values (<1.5, >2.4) have been found for various Pinus species. Contrary to our results for stems, some authors have reported pronounced seasonal variation of Q10. Clear differences between two dates within a year were found by Carey et al. (1997) for Pinus ponderosa (Q10 about 1.6 in September and 2.4 in July), and by Stockfors & Linder (1998) for Picea abies (1.92 in August and 2.55 in June). With measurements throughout the year, Paembonan et al. (1991), on Chamaecyparis obtusa and Lavigne (1995), on Pinus banksiana found Q10 values between c. 1.5 and 3. Nevertheless, the seasonal dynamics of Q10 and R15 that we observed are in accordance with Linder & Troeng (1981) who showed a stable Q10 throughout the year and large variations of the basal respiration on Pinus sylvestris.

In our study, we observed a decrease in the Q10 of the stem with increasing stem diameter and higher values for branches. This result can be explained by the greater temperature inertia of large bodies relative to air temperature fluctuations (that is, small stems gain and lose heat faster that large ones). This was confirmed by the greater stability of Q10 values for different stem diameters when calculated with stem temperature rather than air temperature. In studying the relationship between mean air temperature and respiratory fluxes on a seasonal scale in a beech forest, Valentini et al. (1996) found a Q10 intermediate (2.17) between our stem and branch values.

Maintenance and growth respiration

In other studies, stem maintenance respiration measured in chambers (µmol s⁻¹) has been found to be linearly related to the volume of sapwood enclosed in the chambers (for conifers see Sprugel, 1990; Ryan et al., 1995, for tropical broadleaved species see Ryan et al., 1994a). In the present experiment with F. sylvatica, all wood was live sapwood. Consequently, we expected a fairly stable volume-based maintenance respiration, regardless of the stem diameter. The results generally supported this hypothesis. However, on a volume basis, the maintenance R15 was higher for the smallest suppressed trees compared to the other sample trees. One explanation for this result is that the proportion of phloem, wherein approx. 70% of the cells are living (E. Ceschia, unpublished), to xylem is larger in the smallest trees than in the larger ones. This explanation is also valid for the branches. Other parameters, such as tissue nitrogen content, which have been shown to strongly affect stem maintenance respiration (Maiter et al., 1998) could also explain these results.

Considering growth respiration, the variability of R15 in relation to stem diameter depends largely on the unit of measurement. The great increase of area-based R15 with stem size (in contrast to volume-based R15 which remained constant) can be explained by a higher rate of increase in biomass of large trees for a given stem surface area. The use of the volume unit seems to be more accurate for scaling-up stem respiration to the stand level. However, the volume-based R15 measured in branches during the growth season showed large differences between diameters and was much greater than the stem R15.

Stem construction cost

The highest rates of respiration during the growth period could not be explained solely by the summer increase in air

| Table 5 Annual estimates of maintenance, Rm, and growth respiration, Rg, at the stand level for stems, three diameter classes of branches, and the total (stems + all branch classes). Units are g C m⁻² ground surface area year⁻¹. Estimates were calculated using monthly volume- or area-based Q10 and R15 derived from measurements at 1.20 m on the stems, and on the branches |
|-------------|-------------|-------------|-------------|-------------|
| Stems       | Branches (≤ 0.5 cm) | Branches (0.5–2 cm) | Branches (> 2 cm) |
|  | Rm | Rg | Rm | Rg | Rm | Rg | Rm | Rg |
| From volume-based Q10 and R15 | 75 | 90 | 53 | 49 | 18 | 21 | 8 | 12 | 154 | 172 |
| From area-based Q10 and R15 | 95 | 130 | 55 | 35 | 25 | 26 | 8 | 11 | 182 | 201 |
Table 6  Stem respiration $Q_{10}$ for various tree species. The parameters reported were calculated with either air or stem temperature (and occasionally with a time-lag adjustment) during either the dormant or the growth season. The diameter of trees (generally at 1.30 m height) and sources of the data are specified.

<table>
<thead>
<tr>
<th>Species</th>
<th>Air or stem temperature</th>
<th>$Q_{10}$</th>
<th>Period</th>
<th>Diameter (cm)</th>
<th>Location</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies amabilis</td>
<td>Air</td>
<td>2.0</td>
<td>Growing</td>
<td>3-9.5</td>
<td>Washington</td>
<td>Sprugel (1990)</td>
</tr>
<tr>
<td>Abies balsamea</td>
<td>Air or stem</td>
<td>2.1, 2.3</td>
<td>Dormant</td>
<td>2.6-12.3</td>
<td>Canada (4 stands)</td>
<td>Lavigne et al. (1996)</td>
</tr>
<tr>
<td>Acer rubrum</td>
<td>Air</td>
<td>1.7</td>
<td>Growing</td>
<td>21-52</td>
<td>Tennessee</td>
<td>Edwards &amp; Hanson (1996)</td>
</tr>
<tr>
<td>Chamaecyparis obtusa</td>
<td>Air</td>
<td>2.8-3.2</td>
<td>Growing</td>
<td>7.4-8.5</td>
<td>Northern Sweden</td>
<td>Stockfors &amp; Linder (1998)</td>
</tr>
<tr>
<td>Pinus ponderosa</td>
<td>Air or stem</td>
<td>1.7-2.2</td>
<td>Dormant</td>
<td>7.4-11.6</td>
<td>Montana</td>
<td>Ryan et al. (1994b)</td>
</tr>
<tr>
<td>Pinus contorta</td>
<td>Air</td>
<td>2.0</td>
<td>Dormant</td>
<td>4-40</td>
<td>Colorado</td>
<td>Ryan (1990)</td>
</tr>
<tr>
<td>Pinus elliottii</td>
<td>Air or stem</td>
<td>1.9</td>
<td>Growing</td>
<td>17.3</td>
<td>Florida</td>
<td>Ryan et al. (1995)</td>
</tr>
<tr>
<td>Pinus engelmannii</td>
<td>Air or stem</td>
<td>2.84</td>
<td>Dormant</td>
<td>17.3</td>
<td>Florida</td>
<td>Ryan (1990)</td>
</tr>
<tr>
<td>Pinus ponderosa</td>
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<td>2.4</td>
<td>Growing</td>
<td>5 at collar</td>
<td>California</td>
<td>Carey et al. (1996)</td>
</tr>
<tr>
<td>Pinus resimosa</td>
<td>Air</td>
<td>1.6-1.9</td>
<td>Dormant</td>
<td>10-77</td>
<td>California</td>
<td>Carey et al. (1997)</td>
</tr>
<tr>
<td>Pinus sylvestris</td>
<td>Air or stem</td>
<td>1.3</td>
<td>Dormant</td>
<td>15.5</td>
<td>Wisconsin</td>
<td>Ryan et al. (1995)</td>
</tr>
<tr>
<td>Quercus alba</td>
<td>Air</td>
<td>1.5</td>
<td>Growing</td>
<td>20-65</td>
<td>Tennessee</td>
<td>Edwards &amp; Hanson (1996)</td>
</tr>
<tr>
<td>Quercus prinus</td>
<td>Air</td>
<td>2.2</td>
<td>Growing</td>
<td>Mean = 27</td>
<td>Costa Rica</td>
<td>Ryan et al. (1994a)</td>
</tr>
<tr>
<td>Tsuga heterophylla</td>
<td>Air or stem</td>
<td>1.8</td>
<td>Dormant</td>
<td>29.1</td>
<td>Oregon</td>
<td>Ryan et al. (1995)</td>
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</table>

*Measurements done on branch rather than stem.

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</table>

*Measurements done on branch rather than stem.

Temperature. Many studies have shown the same result (see Linder & Troeng, 1981 for Pinus sylvestris; Zabuga & Zabuga, 1985 for Pinus sylvestris; Marynska & Schulze, 1988 for Larix sp.; Grossman & Dejong, 1994 for Pinus ponderosa; Yokota et al., 1994 for Chamaecyparis obtusa), Anekonda et al. (1994) found correlations between respiration rates and different growth rate parameters such as height, basal diameter and stem volume (for young Sequioia sempervirens). During summer months, Zabuga & Zabuga (1985) found, for Pinus sylvestris, a positive correlation between the mean daily respiration rate and the radial growth rate averaged over 10 d. On another scale of integration, Ryan (1990) showed that instantaneous stem growth respiration was linearly related to annual dry matter production for Pinus contorta and Pinus engelmannii. In our study, we found a linear relationship between the annual growth respiration and the annual stem increment, which allowed us to calculate a stem construction cost. This construction cost (0.38 g C g⁻¹ C) is consistent with the values already in the literature which show a large interspecies variability (see for example, Lavigne & Ryan (1997), their range for boreal tree species is from 0.25 to 0.76 g C g⁻¹ C). These values are much higher than estimates obtained by Stockfors & Linder (1998) for Picea abies (0.11–0.18 g C g⁻¹ C), or than results obtained from a calorimetric method for Pinus ponderosa (0.16–0.18 g C g⁻¹ C; Carey et al., 1996, 1997). We tested another method of calculating the construction cost by dividing our estimates of stem growth respiration by an estimate of the total stem biomass.
increment during 1997 (data not shown): we found a slightly lower value of 0.29 instead of 0.38 g C g\(^{-1}\) C.

Intra-tree variability

Several authors have found small variations in respiration along the stem. During the dormant season, Ryan et al. (1996) found that respiration per unit area did not vary consistently with height on stems of Pinus radiata. With Abies amabilis, Sprugel (1990) found little variation in respiration per unit area between two different heights on the same stem during the growing season. On the contrary, we recorded (as in Möller et al., 1954; Yoda et al., 1965) large intratree variations of both area- and volume-based respiration, especially in summer. Differences in temperature with height (the maximum observed was 6°C in July when air temperature was 20°C at 1.30 m) could not explain why respiration doubled (and more) with increased height on the stem. From our data we cannot reach any firm conclusions on the real cause(s) of high levels of respiration in the crown in summer (differences in wood increment or in bark CO\(_2\) diffusion are two possibilities). More investigation is needed to explain the vertical variations of respiration and to take this into account in scaling-up respiration to the stand level.

Scaling-up to the stand level

Having documented the temporal (seasonal) and spatial (stem and branch) variations in the response of respiration to temperature, the final objective of this study was to estimate the annual amount of carbon released at the stand level. Since, in our case, neither the volume-based nor the area-based R\(_{15}\) was constant between stems and in the branches (especially for growth respiration), a simple scaling rule from the tree to the stand level cannot be derived. Consequently, we tested two units (volume and area) to scale-up to the stand. We obtained similar results regardless of the unit used (slightly higher results using area-based parameters).

Nevertheless, if we applied parameters (Q\(_{10}\) and R\(_{15}\)) obtained from stems to both stems and branches, we obtained total respiration values of 198 (volume-basis) and 511 (area-basis) g C m\(^{-2}\) ground surface area, rather than the values 325 (volume-basis) and 383 (area-basis) g C m\(^{-2}\) ground surface area obtained previously by applying the stem and branch Q\(_{10}\) and R\(_{15}\) values to the respective compartments. Based on these calculations, the common practice of considering only stem respiration characteristics appears to be a significant source of error in scaling-up to the stand level. This simplified approach underestimates the annual total respiration value by 39% if volume units are used, and overestimates it by 33% if area units are used.

Thus, the experimental protocol may have great implications for modelling and scaling-up respiration and the protocol should include measurements on stems and branches to properly scale-up respiration from local measurements to the stand level.

Ecosystem-level considerations

Our calculations showed that branch respiration is a nonnegligible component of the total stand-level stem and branch respiration (approx. 50%). The proportion we attributed to maintenance respiration, relative to the total annual respiration, was approx. 50% which is close to values obtained by Stocker & Linder (1998) for stems of Picea abies. Indeed, in the literature, the proportion that represents maintenance respiration varies largely. Published estimates range from 22.5% for Pinus taeda (Ryan & Waring, 1992) to 85% for Pinus ponderosa (Carey et al., 1997). If we consider our range of estimates (between 325 and 383 g C m\(^{-2}\) yr\(^{-1}\)) for aerial stem and branch respiration of the stand in 1997, our results are close to those of Ryan et al. (1994a) in two tropical forests in Costa Rica (220–350 g C m\(^{-2}\) s\(^{-1}\)) and by Lavigne et al. (1996) for Abies balsamea (120–424 g C m\(^{-2}\) s\(^{-1}\)). Some higher values are mentioned in the literature, such as 544 g C m\(^{-2}\) yr\(^{-1}\) for a beech forest in Italy (Valentini et al., 1996), 910 g C m\(^{-2}\) yr\(^{-1}\) and 1314 g C m\(^{-2}\) yr\(^{-1}\) for a rain forest (Withmore (1984) and Müller & Nielson (1965), respectively, cited in Ryan et al. (1994b)), and 1251 g C m\(^{-2}\) yr\(^{-1}\) for a Pinus taeda plantation (Kinerson, 1975). Stand respiration values are very different among these studies and interspecies comparisons are difficult because climate, tree density, age and scaling-up differ.

The stem and branch respiration we calculated represents about 1/3 of the total carbon loss by ecosystem respiration (soil and above-ground respiration) estimated at the same site from eddy correlation measurements (988 g C m\(^{-2}\) yr\(^{-1}\); Granier et al., 2000). This is close to the proportion obtained across European forests where stem and branch respiration has been found to represent an average of 37% of the total annual ecosystem respiration (Janssens et al., 2001). At Hesse Forest, the amount of stem and branch respiration is similar to root respiration, which was estimated at 398 g C m\(^{-2}\) plot area yr\(^{-1}\) (Epron et al., 1999); and it is higher than heterotrophic respiration (Granier et al., 2000). Total stem and branch respiration is a major CO\(_2\) efflux from the Hesse forest: it accounted for 26% of the gross primary production (the total C assimilated by the system) which was estimated to be 1245 g C m\(^{-2}\) yr\(^{-1}\) (Granier et al., 2000).

In conclusion, our study confirmed that stem and branch respiration is a major component of the carbon balance of deciduous temperate forests. Consequently, it needs to be quantified properly to accurately predict carbon sequestration by forests, which is currently a major objective of functional ecosystem studies. As branch respiration accounted for 50% of the total annual respiration, both stem and branch components should be considered in estimating the respiratory...
component at the stand level. More information is now needed, especially concerning branch respiration characteristics and vertical stem respiration profiles, to improve our ability to scale-up to the stand level. The differences in respiration rates that we observed between measured branches indicate that difficulties probably will be encountered when considering the intracrown variability of growth respiration from quantitative and seasonal dynamic points of view.

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References


