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

C. Damesin[1], E. Ceschia[1], N. Le Goff[2], J-M. Ottorini[2] and E. Dufrêne[1]

[1]Université Paris XI, Laboratoire d'Ecologie, Systématique et Evolution, UPRESA n°8079, Bâtiment 362, F 91405 Orsay cedex, France; [2]UMR INRA-ENGREF 'Ressources Forêt-Bois', Équipe 'Croissance et Production', F 54280 Champenoux, France

Author for correspondence:
C. Damesin
Tel: +33 1 69 15 56 79
Fax: +33 1 69 15 72 38
Email: claire.damesin@eco.u-psud.fr

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Summary

• Stem and branch respiration of 30-yr-old *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 (R15) increased greatly during the growing season. On a volume basis, monthly means of R_{15} were higher for branches than for stems. For stems, Q_{10} was relatively constant throughout the year, with an annual average of 1.7. Estimated annual respiration was approx. 325 g C m^{-2} ground surface area yr^{-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: *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 *et al.*, 1996). Its importance relative to CO_2 assimilation could explain some variations in forest ecosystem production depending on climate (Ryan *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 *et al.*, 1991; Yoder *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 *et al.*, 1996; Ryan *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_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_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 (Möller *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 a 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).

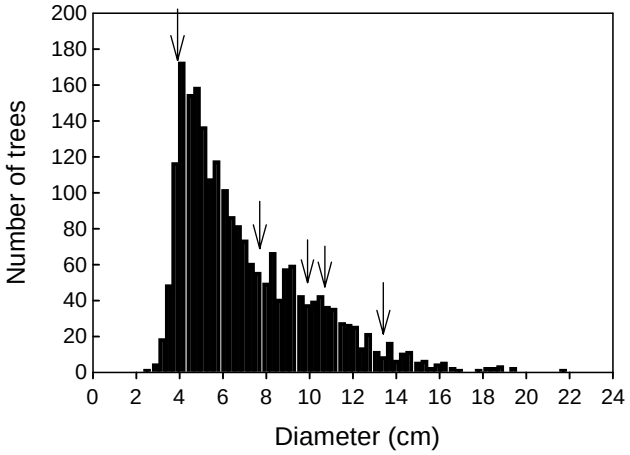

Fig. 1 Distribution of tree stem diameters at the experimental site (6300 m^2). All diameters were measured at 1.30 m height. The arrows on the histogram indicate the diameters of sample trees used for respiration measurements.

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, Teroson, Ludwigsburg, 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} m^3 min^{-1}) was maintained by the IRGA pump. The air in the chamber was homogenized by a fan. The CO_2 efflux measurement was stopped either when CO_2 variation reached 50 ppm or when measurement time reached 120 s. The rate of CO_2 evolution was verified as linear for the duration of the measurements. Between measurements, to avoid artificially high CO_2 concentrations, the chambers were opened by removable, 5-cm-diameter stoppers and the chamber fan speed was increased. The chamber air 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 cm^3, and chamber volumes with the stems inside ranged from 1092 to 2861 cm^3. 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 trees between monthly measurements; they were replaced on 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 CO_2 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 circumferences of stems enclosed by the chambers were measured manually each month. The total radial area increment of the part of the stem contained in the chamber was calculated for the year using the diameters measured between September 1997 and April 1997. Air temperature was recorded using a mercury thermometer positioned at 1.30 m height. Stem temperature was determined at 10 cm above the respiration chamber using thermistors (10 kΩ at 25°C; Bethaterm, Ireland) inserted 2 mm under the bark on the north-east aspect. Temperature was measured on five of the 15 trees measured for respiration (incorporating the five different diameter classes).

Branch respiration Efflux of CO_2 from branches was measured on one tree. Its height and diameter at 1.30 m were 15.5 m and 10 cm, respectively. Measurements were made with permanent chambers sealed around branches at 0.25, 1.5 and 2.5 m from the top of the crown. These locations corresponded to three branch diameters: 0.25, 1.25, 2.50 cm. Each chamber was made of two halves of a closed glass cylinder. Like the stem chambers, they were sealed to the bark with rubber sealant and covered with aluminium foil. For the three chambers, measurements were performed automatically every 1.5 h from May to November 1997 using an IRGA (Li-6262, Li-Cor Inc., Lincoln, NB, USA) operating in an open system. Continuous air flow through the chambers was controlled with a mass-flow meter (Bronkhorst High-Tech, Veenendaal, The Netherlands) and maintained between 60 and 120 ml min^{-1} to prevent a CO_2 increase of > 50 ppm inside the chambers. The air passing through the various chambers was monitored using solenoid valves controlled by a data logger (CR10, Campbell Scientific, Logan, UT, USA) that also stored data every minute. The air temperature in the chambers was recorded automatically using thermistors. To avoid damage to the branches, branch temperature was not 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 CO_2 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. CO_2 efflux, R) were expressed in terms of Q_{10}, that is, the change in rate with a 10°C change in temperature as follows:

$$R = R_{Tb} Q_{10}^{(T-Tb)/10} \quad \text{Eqn 1}$$

(R_{Tb}, the basal respiration rate.) In our case, a basal temperature (Tb) of 15°C ($R_{Tb} = R_{15}$) was chosen. Respiration was either the total CO_2 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 R_{15} and Q_{10} values were calculated for the 24-h period using eqn 1. Data analyses were computed using

SASystem statistical software, version 6.10 (SAS, 1994). All nonlinear regressions were performed with the nonlinear procedure. Parameter estimates (Q_{10} and R_{15}) were accepted when $P < 0.05$. The effect of stem size was evaluated by ANOVA using the General Linear Models (GLM) procedure. When a factor was significant, means were compared with Tukey tests.

To separate maintenance and growth respiration, we defined the tree growth period as the time when radial growth occurred. We did not take into account cell wall thickening which may continue after radial growth has stopped (Sprugel & Benecke, 1990). In 1997, the circumferences at 1.30 m height of 541 trees of the experimental stand were measured every 15 d. The results showed that, regardless of the diameter class, radial growth started at the end of April and nearly ceased early in September (Lebaube *et al.*, 2000). Respiration measurements taken in the middle of April and at the end of September were considered to be out of the growth period. We determined Q_{10} and R_{15} monthly for growth respiration in May, June, July and August. We assumed that maintenance respiration and its response to temperature during the dormant season were representative also of the growing season, bearing in mind that a possible down-acclimation of maintenance respiration during the warmer period (Stockfors & Linder, 1998), and possible positive relationships between maintenance respiration and individual growth rate (Lavigne & Ryan, 1997), may not be accounted for. We calculated maintenance respiration using average Q_{10} and R_{15} values for the nongrowth period for each tree diameter class. For each measurement site on the sample trees during the growth period, 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 *F. sylvatica*) 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-order 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.

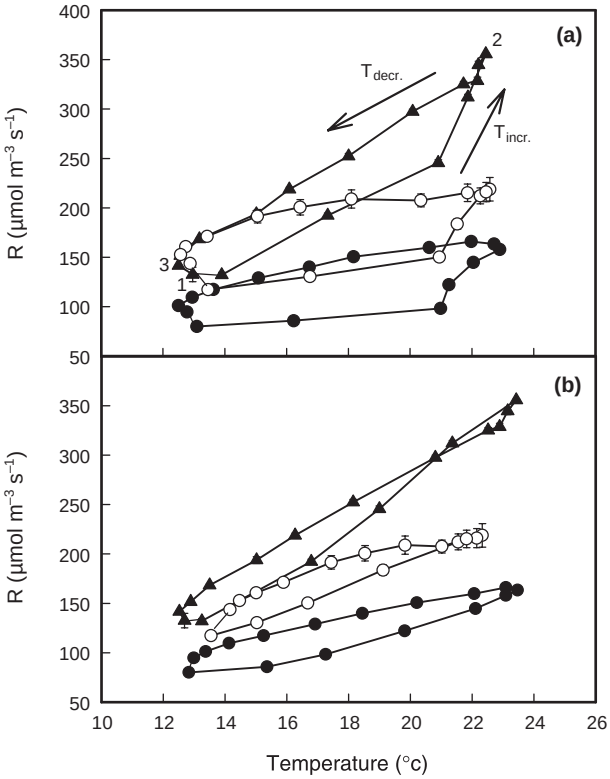

Fig. 2 Variation of stem respiration (R) at 1.30 m height in relation to air (a) or stem (b) temperature. Measurements were recorded over 24 h in July 1997 on three trees. Data obtained from two additional trees gave similar results but are omitted for clarity of the figure. Tree diameters were 4 cm (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.

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°C, respiration started to increase only after air temperature had reached its maximum (data not shown). Measurements recorded at 1.3 m height during 24 h in July showed the existence of a hysteresis between stem CO_2 efflux and air temperature (Fig. 2a). The hysteresis was clearly reduced but not suppressed when stem temperature instead of air temperature was considered (Fig. 2b). Allowing a time lag for respiration to respond to variations in air temperature cancelled the hysteresis effect, but the magnitude of this lag-time depended on the stem diameter.

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

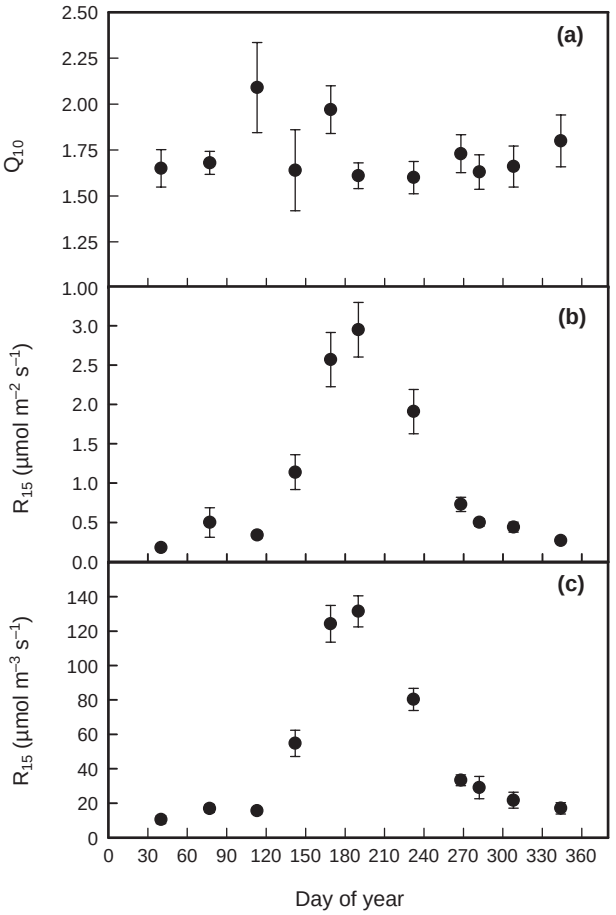

Fig. 3 Seasonal variations of (a) Q_{10}, the change in respiration with a 10°C change in air temperature (b) volume-based, and (c) area-based R_{15} (respiration normalized at 15°C) obtained from regression of measurements recorded on five to 15 stems at 1.30 m height (mean ± SE). Note: small error bars may be hidden by symbols for the means.

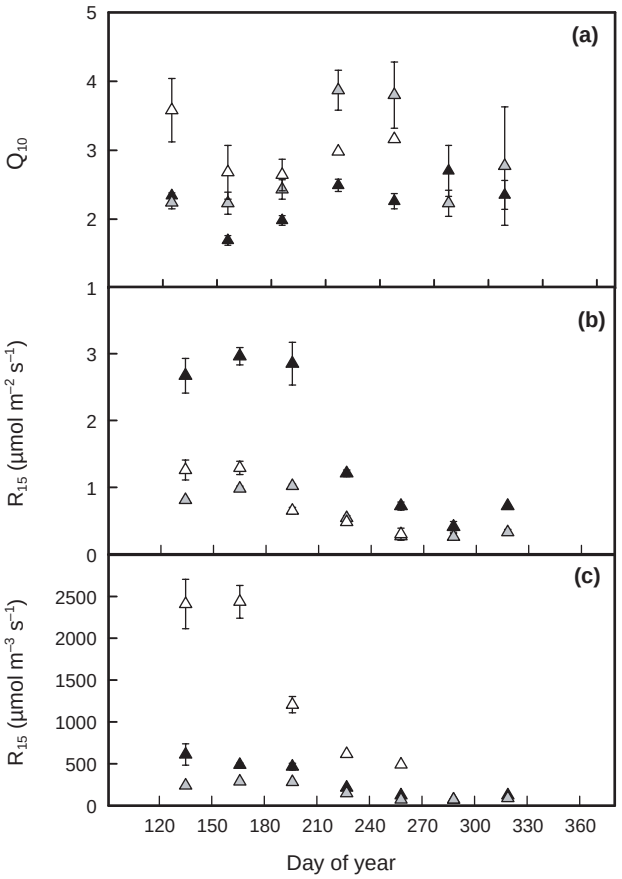

Fig. 4 Seasonal variations (mean ± SE) of (a) Q_{10}, the change in respiration with a 10°C change in air temperature (b) volume-based, and (c) area-based R_{15} (respiration normalized at 15°C) obtained from measurements recorded on three branches at different heights in the crown. The branch diameters were: 0.25 cm (open triangles), 1.25 cm (grey triangles), and 2.5 cm (black triangles). Note: small error bars may be hidden by symbols for the means.

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 μmol m^{-3} s^{-1} or 0.2 μmol m^{-2} s^{-1}) and the highest values occurred in summer with a maximum in July (131.5 μmol m^{-3} s^{-1} or 3.0 μmol 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 μmol m^{-3} s^{-1} in June in the smallest diameter branch, and area-based R_{15} peaked at 3 μmol 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

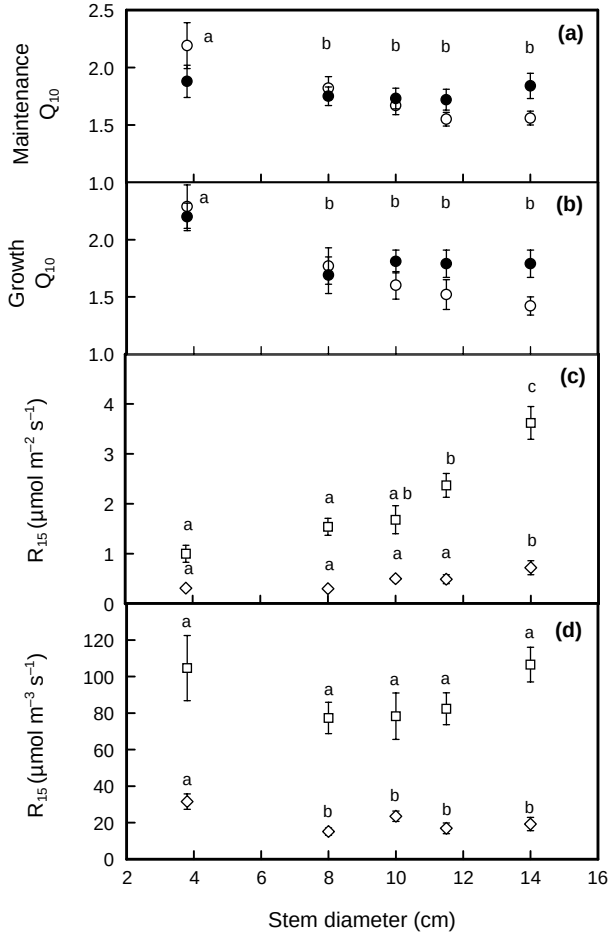

Fig. 5 Q_{10} estimated from air (open circles) or stem (closed circles) temperature for (a) maintenance and (b) growth respiration; and, R_{15} calculated from air temperature measurements on (c) a surface-area basis, or (d) a volume basis for maintenance (open diamonds) and growth (open squares) respiration relative to stem diameter at 1.30 m height. Maintenance and growth Q_{10} and R_{15} are the means of values obtained during the nongrowth and growth periods, respectively. Estimated R_{15} from stem temperature is not shown because it did not differ significantly from that estimated with air temperature. Each point is the mean (± SE) of three sample trees. Points with different superscripts correspond to significantly different means ($P < 0.05$). In (a) and (b), only the superscripts for Q_{10} adjusted with air temperature (open circles) are shown. Note: small error bars may be hidden by symbols for the means.

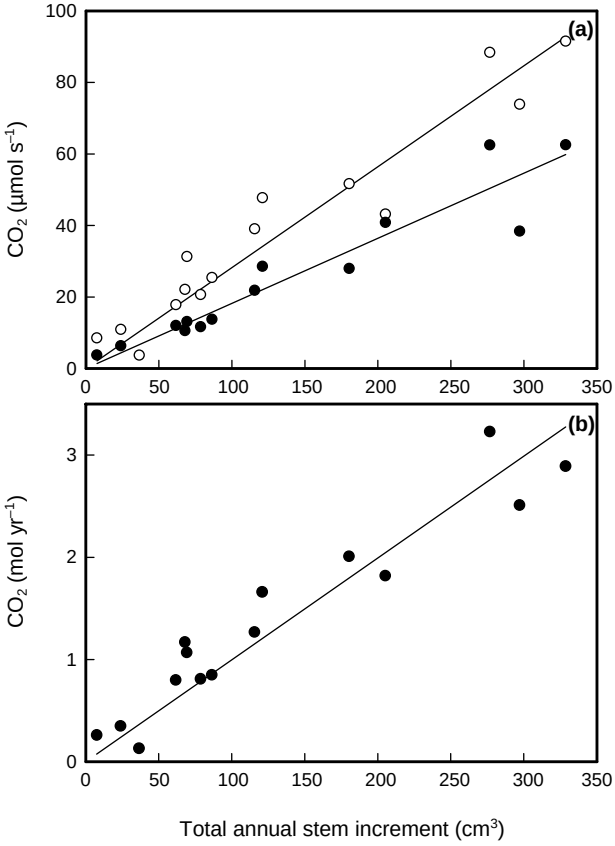

Fig. 6 (a) Maximal diurnal instantaneous growth respiration during July (open circles) and August (closed circles), and (b) total annual growth respiration, compared with annual production of stem volume. Each point represents a tree. In (a) $y = 0.28x$ (MSE = 64.65, $P < 0.0001$) for July (open circles); and $y = 0.18x$ (MSE = 38.81, $P < 0.0001$) for August (closed circles). In (b) $y = 0.01x$ (MSE = 0.101, $P < 0.0001$).

the estimated growth respiration (Fig. 5c). For volume-based R_{15}, 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 CO_2 per cm^3 of stem produced. This value corresponds to a cost of 0.38 g C of growth respiration to incorporate 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 increased when diameter decreased, that is, with measurements 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

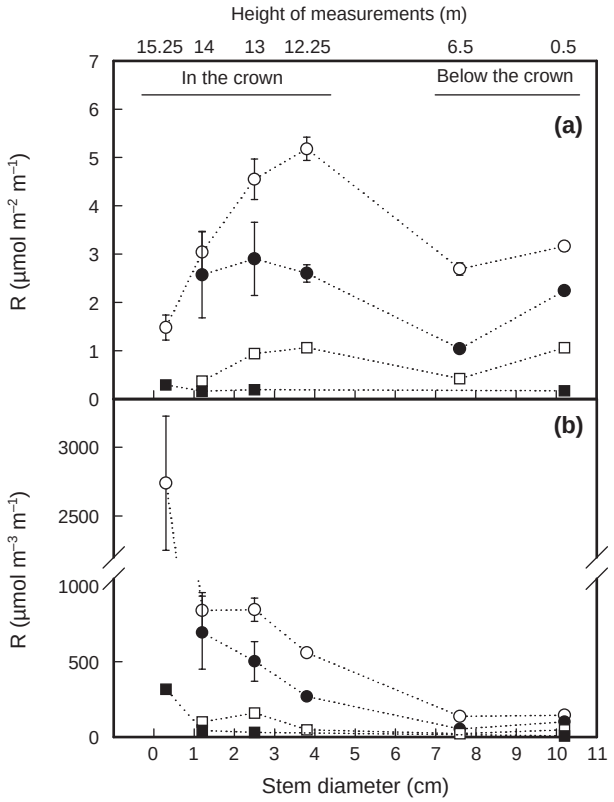

Fig. 7 Mean daily respiration (R) recorded at different heights on the stem and on branches of one 15.5 m tall beech tree, expressed on (a) a surface area, and (b) a volume basis. Measurements were recorded in July (open circles), August (closed circles), September (open squares) and December (closed squares). Mean diurnal temperatures at 1.30 m height were 20, 22, 15.5, 10.5°C in July, August, September and December, respectively. 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

$$[d/L = 0.000542 + 0.008295\, l/L^{-1}] \quad (\mathrm{MSE} = 0.0703,\ r^2 = 0.88) \qquad \text{Eqn 2}$$

$$[d/L = 0.002024 + 0.006147\, l/L^{-1}] \quad (\mathrm{MSE} = 0.1093,\ r^2 = 0.64) \qquad \text{Eqn 3}$$

(d, 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, 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:

$$S = \pi\left(\alpha lL + \beta\frac{l^2}{2}\right) \qquad \text{Eqn 4}$$

$$V = \frac{\pi}{12}\frac{1}{b}\left[(\alpha L + \beta l)^3 - (\alpha L)^3\right] \qquad \text{Eqn 5}$$

(the units of S, cm^2; V, cm^3; and l and L, cm.) The parameters α and β 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:

$$l = L - 113.282(d_0 - d) \text{ for first-order branches} \qquad \text{Eqn 6}$$

$$l = L - 127.942(d_0 - d) \text{ for second-order branches} \qquad \text{Eqn 7}$$

(d_0, the basal diameter of the branch (l, 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 $d = d_0$: $L - l = \lambda(d_0 - d)$. 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:

$$L = 1.09481 d_0 \quad (\mathrm{Mse} = 0.448,\ P < 0.0001) \qquad \text{Eqn 8}$$

$$L = -0.0966 + 1.2694 d_0 \quad (\mathrm{MSE} = 0.140,\ r^2 = 0.89,\ P < 0.0001) \qquad \text{Eqn 9}$$

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, then were obtained using a nonlinear, least-squares regression analysis (Tables 2 and 3) with the following model:

$$y = u\,\mathrm{Log}_e(1 + e^{(vx+w)}) \qquad \text{Eqn 10}$$

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_0) 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: $y = a + bx^p$

Branch size class	Independent variable x (cm)	Regression model	p	a	b	r^{2a}	MSE[b]
Area (cm^2)							
$d \leq 0.5$	d_0	Linear	1.6	−607.86	710.66	0.95	438.9
$0.5 < d \leq 2.0$	d_0	Linear	1.4	−564.62	581.40	0.90	384.1
$d > 2.0$	d_0^{-2}	Nonlinear	1.14	0	923.97	–	231.1
Volume (cm^3)							
$d \leq 0.5$	L	Nonlinear	2.07	0	1.34×10^{-3}	–	34.15
$0.5 < d \leq 2.0$	L	Nonlinear	2.03	0	4.00×10^{-3}	–	62.64
Total	L	Nonlinear	2.86	0	7.47×10^{-5}	–	142.2

[a]r^2, coefficient of determination. [b]MSE = residual mean square error

Table 2 Parameters and statistics of the equations to predict branch areas and volumes at the tree level. Data from 23 trees were fitted to the model, $y = u\ \mathrm{Log}_e(1 + e^{(vx+w)})$

Branch size class	Independent variable x (cm)	u	v	w	MSE[a]
Area (m^2)					
$d = 0.5$	Tree diameter	0.699	0.93	–5.565	0.698
$0.5 < d \leq 2.0$	Tree diameter	0.363	1.04	–5.363	0.444
$d > 2.0$	Tree diameter	0.195	1.19	–9.393	0.076
Volume (m^3)					
$d \leq 0.5$	Tree diameter	6.53×10^{-4}	0.6945	–5.976	3.8×10^{-4}
$0.5 < d \leq 2.0$	Tree diameter	1.57×10^{-3}	0.7084	–5.862	9.5×10^{-4}
$d > 2.0$	Tree diameter	1.65×10^{-3}	0.9897	–9.874	5.3×10^{-4}

[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. Data from 23 trees were fitted to the model, $y = u\ \mathrm{Log}_e(1 + e^{(vx+w)})$

Predicted variable	Independent variable x (cm)	u	v	w	MSE[a]
Area (m^2)	Tree diameter	0.662	0.711	–2.866	0.270
Volume (m^3)	Tree diameter	0.045	0.441	–7.714	0.004

[a]MSE, residual mean square error.

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

Tree compartment	Area (m^2 ha^{-1})	Volume (m^3 ha^{-1})
Branches		
$d = 0.5$ cm	4733.5	3.20
$0.5 < d = 2.0$ cm	2857.4	8.02
$d > 2.0$ cm	427.7	2.64
Total	8018.6	13.86
Trunks	7021.5	111.86

(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).

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.

	Stems		Branches (≤ 0.5 cm)		Branches (0.5–2 cm)		Branches (> 2 cm)		Total	
	Rm	Rg	Rm	Rg	Rm	Rg	Rm	Rg	Rm	Rg
From volume-based Q_{10} and R_{15}	75	90	53	49	18	21	8	12	154	172
From area-based Q_{10} and R_{15}	95	130	55	35	25	26	8	11	182	201

Table 5 Annual estimates of maintenance, R_m, and growth respiration, R_g, 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 Q_{10} and R_{15} derived from measurements at 1.30 m on the stems, and on the branches

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 Q_{10} 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, Q_{10} 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 Q_{10}. Clear differences between two dates within a year were found by Carey *et al.* (1997) for *Pinus ponderosa* (Q_{10} 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 (1996), on *Pinus banksiana* found Q_{10} values between *c.* 1.5 and 3. Nevertheless, the seasonal dynamics of Q_{10} and R_{15} that we observed are in accordance with Linder & Troeng (1981) who showed a stable Q_{10} throughout the year and large variations of the basal respiration on *Pinus sylvestris*.

In our study, we observed a decrease in the Q_{10} 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 Q_{10} 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 Q_{10} 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 R_{15} 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 (Maier *et al.*, 1998) could also explain these results.

Considering growth respiration, the variability of R_{15} in relation to stem diameter depends largely on the unit of measure used. The great increase of area-based R_{15} with stem size (in contrast to volume-based R_{15} 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 R_{15} measured in branches during the growth season showed large differences between diameters and was much greater than the stem R_{15}.

Stem construction cost

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

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

Species	Air or stem temperature	Q_{10}	Period	Diameter (cm)	Location	Reference
Abies amabilis[a]	Air	2.0	Growing	3–9.5 at 18 cm	Washington	Sprugel (1990)
Abies balsamea	Stem	2, 2.1, 2.3, 2.5	Dormant	2.6–12.3	Canada (4 stands)	Lavigne *et al*. (1996)
Acer rubrum	Air	1.7	Dormant	21–52	Tennessee	Edwards & Hanson (1996)
Chamaecyparis obtusa	Air	*c*. 2.8–3.2	Dormant	–	Nagoya University	Paembonan *et al*. (1991)
Chamaecyparis obtusa	Air	*c*. 1.5–2.2	Growing	–	Nagoya University	Paembonan *et al*. (1991)
Picea abies	Stem + lag time	*c*. 2.2	Dormant	6.5–10.8	Northern Sweden	Stockfors & Linder (1998)
Picea abies	Stem + lag time	1.9, 2.6	Growing	6.5–10.8	Northern Sweden	Stockfors & Linder (1998)
Picea mariana	Stem + lag time	1.5–1.8	Growing	7.4–8.5	Canada (2 sites)	Lavigne & Ryan (1997)
Picea mariana	Stem + lag time	2.2	Dormant	7.4	Canada	Lavigne & Ryan (1997)
Pinus banksiana	Stem + lag time	*c*. 1.7–2.7	Dormant	–	Canada	Lavigne (1996)
Pinus banksiana	Stem + lag time	*c*. 1.2–3	Growing	–	Canada	Lavigne (1996)
Pinus cembra	–	2.2	Growing	27	–	Havranek (1981); Ryan *et al*. (1994b)
Pinus cembra	–	1.8	Dormant	27	–	Havranek (1981); Ryan *et al*. (1994b)
Pinus contorta	Stem	2.04	Dormant + growing	4–40	Colorado	Ryan (1990)
Pinus elliottii	Stem + lag time	1.9	Dormant	17.3	Florida	Ryan *et al*. (1995)
Pinus engelmannii	Stem	2.84	Dormant + growing	4–40	Colorado	Ryan (1990)
Pinus ponderosa	Stem + lag time	1.4	Dormant	17.2	Montana	Ryan *et al*. (1995)
Pinus ponderosa	Stem	1.7	Growing	5 at collar	California	Carey *et al*. (1996)
Pinus ponderosa	Air	2.4, 2.3	Growing	10–77	California (2 sites)	Carey *et al*. (1997)
Pinus ponderosa	Air	1.6, 1.9	Dormant	10–77	California (2 sites)	Carey *et al*. (1997)
Pinus resinosa	Stem + lag time	1.3	Dormant	15.5	Wisconsin	Ryan *et al*. (1995)
Pinus sylvestris	Air All the year	*c*. 2 + growing	Dormant	–	Central Sweden	Linder & Troeng (1981)
Pinus taeda	Air	2.9	–	17	North Carolina	Kinerson (1975)
Populus tremuloides	Stem + lag time	1.2–1.3	Growing	20.5–11.6	Canada (2 sites)	Lavigne & Ryan (1997)
Populus tremuloides	Stem + lag time	1	Dormant	20.5	Canada	Lavigne & Ryan (1997)
Prunus persica[a]	Air	1.5, 2.0	Growing	–	University of California	Grossman & Dejong (1994)
Quercus alba *Quercus prinus*	Air	2.4	Dormant	20–65	Tennessee	Edwards & Hanson (1996)
Simarouba amara	Air	2.2	Growing	Mean = 27	Costa Rica	Ryan *et al*. (1994a)
Tsuga heterophylla	Stem + lag time	1.8	Dormant	29.1	Oregon	Ryan *et al*. (1995)

[a]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*; Matyssek & Schulze, 1988 for *Larix* sp.; Grossman & Dejong, 1994 for *Prunus persica*; 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 *Sequoia 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 *Picea 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* (0.11–0.16 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 Stockfors & 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 values were close to those found by 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}). Our range of values is higher than the values found by Edwards & Hanson (1996) in a mixed oak and red maple stand (149–204 g C m^{-2} yr^{-1}) and by Ryan *et al.* (1995) for conifer stands in different climates (52–162 g C m^{-2} yr^{-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 methods 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 approx. 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 main objective of many 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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