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Original article

Spatial and seasonal variations in stem respiration of beech trees (*Fagus sylvatica*)

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Abstract – Stem respiration of adult beech (*Fagus sylvatica* L.) trees was measured in the field in eastern France at several levels in the crown and along the stem. Strong variations in respiration rates throughout the season and within the trees were mainly caused by gradients in stem temperature, growth rates and distribution of living cells. The higher respiration rates, were measured in the upper crown. During the non-growing season, maintenance respiration ranged between 7.2 and 528 µmol m^{-3} s^{-1} at breast height and in the upper crown, respectively. Q_{10} increased along the stem from 1.3 at breast height to 2.0 in the upper crown. There was a linear relationship between [N] and the percentage of living cells in the wood, but respiration increased strongly with [N]. Growth respiration accounted for 45–76% of annual stem respiration, and the growth respiration coefficient was close to 0.2 g C respired g^{-1} C fixed.

beech / stem and branch respiration / living cell / nitrogen concentration

Résumé – Variations spatiales et saisonnières de la respiration ligneuse chez le Hêtre (*Fagus sylvatica*). La respiration ligneuse a été mesurée de façon continue sur des Hêtres (*Fagus sylvatica* L.) adultes dans une forêt de l'est de la France, à trois niveaux dans la couronne de branches en 1997 et à deux voire trois niveaux le long du tronc en 1998. Les fortes variations du taux de respiration observées au cours de la saison et au sein de l'arbre étaient essentiellement causées par des gradients de température, de taux de croissance et de distribution des cellules vivantes. Les plus fortes valeurs de respiration correspondaient au sommet de la couronne. Pendant la période de non-croissance, la respiration d'entretien variait entre 7,2 et 528 µmol m^{-3} s^{-1} à 1,3 m et au sommet de la couronne, respectivement. Le Q_{10} augmentait aussi le long du tronc de 1,3 à 2,0 pour ces mêmes positions. Il existait une relation linéaire entre la concentration en azote, [N], dans le bois et le pourcentage de cellules vivantes. La respiration d'entretien augmentait fortement avec [N]. La respiration de croissance représentait 45 à 76 % de la respiration annuelle des troncs, et le coût de synthèse du bois était de 0,2 g C respiré g^{-1} C fixé dans le tissu.

hêtre / respiration ligneuse / cellule vivante / concentration en azote

1. INTRODUCTION

Interest in the carbon balance of forests has increased in recent decades. Autotrophic respiration is a major component in the annual carbon balance of forest ecosystems, and can consume up to 60% of gross carbon assimilation [38]. Woody-tissue respiration alone annually consumes ca. 11–33% of total net daytime carbon assimilation [37]. Moreover, since forest ecosystems are very finely balanced between being a carbon source or a carbon sink [26], it has become crucial to improve the accuracy of models used for estimating forest carbon budgets, and thus to improve our knowledge of stem respiration processes.

Although the biochemical pathways are similar, wood respiration is generally separated into two components e.g. [2, 41]: growth respiration, which provides the energy needed to synthesise new tissues, is a function of wood growth; and maintenance respiration, which maintains existing living

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cells, is usually a function of biomass [36], sapwood volume [19], surface area [46] or nitrogen content [28]. This separation in two components is necessary to understand how stand development, climate and management affect forest carbon cycling. A simple model can be used to calculate woody respiration separated into those two components on a short time scale or per annum [2, 42]. Thus estimates of the growth respiration coefficient (r_G) and biomass increments, of standing biomass and maintenance respiration rate (r_M), are required to estimate stem respiration at stand level. Usually, r_G and r_M are derived from measurements at breast height (1.3 m), but some studies have shown that respiration varies with stem and branch diameter or height [4, 5, 8, 18, 32, 40, 41, 49], or with the woody organ (stem or branch) considered [5, 28, 32, 41, 49].

The factor by which maintenance respiration varied between different locations in the trees differed greatly among the different studies, and depended on the units in which respiration was calculated. An almost 30-fold difference in respiration rates along the stem on a wood mass base was reported in Yoda et al. [49] for different tree species, a 3- and 4.5-fold on a surface-area base and volume base in Ryan et al. [40] for *Pinus radiata*, and a 10- to 40-fold on a surface-area base for *Abies amabilis* in Sprugel [41].

There may be several causes for a spatial variation in total stem respiration:

(1) Differences in wood composition [3] and in the amount of wood produced along the stem will give differences in growth respiration.

(2) The distribution of living cells within the stem can affect maintenance respiration rates [45, 46].

(3) The transport and storage of carbohydrates in the stem and in the branches can cause variations in respiration rates as it was shown by Malkina et al. [29] and Lavigne [18].

(4) Sapflow could transport part of the CO_2 respired by the stem [12, 23, 30, 33] and it could release it in the upper parts of the stem. However, Edwards and Wullschleger [11] and Ceschia [7] found little evidence of the effect of the sapflow on stem respiration.

(5) Temperature is also an important factor that influences the spatial variation of stem respiration. Stem temperature is usually higher in the upper parts of the canopy, since the stem is more exposed to sunlight and the temperature amplitude is greater. Because of the smaller diameter of the organs, the stem tissues also warm faster at the top than at the base of the stem. Indeed, Q_{10}, the factor expressing respiration increase for a temperature increase of 10 °C, can vary with height along the stem [8] or with the organ in question, stem or branch [28].

Very few models dealing with carbon budgets for an entire ecosystem, take into account spatial variations in stem respiration and few attempts have been made to test the impact of such variations on calculations of net carbon uptake at stand level [45]. More information is also needed to be able to choose the best unit to scale up stem or branch respiration to stand level, because this unit can have a large impact on the final results. Hitherto, the most common units have been surface area [18, 46] or sapwood volume [36], but sapwood fresh mass [49] or sapwood dry mass and nitrogen content [28, 37–40] have also been used to express maintenance respiration. Sprugel et al. [43] suggested that sapwood volume was a better calculation base, because respiration rates per unit volume are rather constant within coniferous species. Knowledge of the distribution of living cells in the stem would make it possible to choose the best unit (surface or volume) for expressing stem maintenance respiration, and it would minimize errors when scaling up local measurements to stand level [45].

Even if within-tree variability in respiration is large, it should be borne in mind that between-tree variability can be still larger, especially on a multi-aged forest. Indeed, temperature-corrected respiration, calculated on a surface-area base, was found to vary among trees by a factor 10 to 40 [41]. In Carey et al. [6], maintenance respiration, calculated on a sapwood volume base, decreased with diameter at breast height (DBH) and age; it was attributed to a decrease in the number of living cells or to diffusion problems in older trees.

In the present paper, we measured stem respiration of a temperate deciduous species, *Fagus sylvatica* L. Measurements were performed almost continuously at three levels in the crown of one tree during the growing season of 1997. In 1998, measurements were performed continuously at two different positions along the stem on four dominant or co-dominant trees during the growing season and at a third level after the growing season. The aims were (1) to quantify the variability of different parameters (percentage of living cells and nitrogen concentration in the wood, stem temperature and growth) and their influence on stem respiration throughout the year, between trees and within trees; (2) to determine the relative importance of maintenance and growth respiration on an annual base and (3) to calculate the growth respiration coefficient.

2. MATERIALS AND METHODS

2.1. Site description

The study site is situated in the State forest of Hesse, eastern France (48° 40' N, 7° 04' E, elevation 305 m, area 0.63 ha, slope < 2%), and is one site within the Euroflux project (FR02). Mean annual precipitation and air temperature are 820 mm and 9.7 °C, respectively. The soil is a gleyic luvisol, according to the F.A.O. classification. Beech (*Fagus sylvatica* L.) is the dominant tree species and other species are *Betula pendula* Roth, *Carpinus betulus* L., *Fraxinus excelsior* L., *Larix decidua* Mill., *Prunus avium* L. and *Quercus petraea* (Matt.) Liebl. In 1997, most of the trees were 25 to 35-year-old and stand density was 4000 trees ha^{-1}, with a mean height of 13 m in 1997 and a diameter at breast height (DBH) of 72 mm. Leaf area index (LAI) was 5.6 in 1997 [14] and all beeches showed leaf emergence at the end of April.

2.2. Experimental set-up

Stem respiration measurements in Hesse started on one tree in 1997 (from May to December) and were extended to four trees in 1998 (from April to October). In the first year, three cuvettes were installed on the main stem at a high level in the crown of a beech tree. Its height and DBH were 15.5 m and 100 mm, respectively. Permanent cuvettes, made of two halves of a glass cylinder, were installed on the stem at 0.25 (upper crown), 1.5 (mid-crown) and 2.5 (low crown) m from the top of the tree. These positions corresponded to stem diameters of 2.5, 12.9 and 23.6 mm at the beginning of the season. The length of the cuvettes ranged from 2.1 (upper crown) to 4.5 cm (mid-crown and low crown).

In 1998, four dominant or co-dominant trees were selected among beech trees that were already equipped with sapflow sensors and band-dendrometers. Two cuvettes were installed on each tree: one at breast height (diameter ranged from 108 to 143 mm) and one at mid-stem (diameter ranged from 52 to 70 mm). This position usually corresponded to the base of the crown. The cuvettes were 22 cm long, made of two half-cylinders of transparent Acrylic resin and a fan was used to mix the air inside the chambers.

In 1998, after growth had ceased (day of year (DOY) 245, see below), stem respiration was also measured at 0.8 m from the top of the trees (upper stem) on which measurements were made at breast height and at mid-stem, but using the same glass cuvettes (4.5 cm long) as were used in the crown in 1997. The diameter of the organs ranged from 5.3 to 16.8 mm.

The cuvettes were sealed to the stem with large PVC soft foam and putty (Térostat-7, Téroson, Germany) that would allow the stem to grow. Stem respiration measurements were performed automatically using an infrared gas analyser (LI-6262, Li-COR, NE, U.S.A.) operating as an open system. CO_2 evolution in all cuvettes was measured in sequence every 90 minutes. The cuvettes were covered with aluminium foil to avoid CO_2 refixation by the bark. Airflow passing continuously through the cuvettes was adjusted to prevent a CO_2 increase of more than 50 μmol mol^{-1} inside the cuvettes. Airflow (ranging between 0.05 and 2 L min^{-1}) was measured with mass-flow meters (AMW-43600V and AMW-3300, Honeywell, IL, U.S.A.) before and after the cuvettes to check their air-tightness. The air passing through the various cuvettes was selected using solenoid valves controlled by a data logger (CR10X, Campbell Scientific, Logan, U.S.A.), and directed through the analyser.

All data from the IRGA and the mass flow meters were recorded and stored every minute by a data logger. Temperature measurements were averaged and stored every 30 minutes by the CR10X in 1997 and by a Deltalogger (Delta-T devices, Cambridge, U.K.) in 1998. The automatic gas-exchange system was installed between April and November 1998. Technical problems prevented the use of data between September and October 1998, for one cuvette installed at breast height outside the growing season and for one of the cuvettes installed at mid-stem.

In 1997, thermistors (10 kΩ at 25 °C, Betatherm, Ireland) were used to measure air temperature in the cuvettes, assuming that stem temperature tracked air temperature very closely. In 1998, thermistors were inserted 2 mm under the bark to measure stem temperature in the cuvette. The thermistors were installed at three levels in the tree in 1998: at breast height, at mid-stem and where some extra cuvettes were installed on the upper stem on DOY 245.

2.3. Diameter increment

In 1998, the diameter increment below the breast height and mid-stem cuvettes was recorded hourly with an automatic band-dendrometer (Megatron MM30, Allinges, France). In the crown, the stem diameter increment was recorded monthly both years, as the mean of two measurements at 90° to each other, made with a digital calliper (resolution 0.01 mm), immediately above and below each cuvette. Calculations of respiration on a stem volume or surface-area base were corrected throughout the year for stem diameter increment.

2.4. Data analysis

Stem respiration measurements were fitted to the temperature variations for each cuvette, using the following equation:

$$R = R_{15} Q_{10}^{((T-15)/10)} \quad (1)$$

where R is stem respiration measured, R_{15} is stem respiration estimated at 15 °C, Q_{10} is the relative increase in R for a temperature elevation of 10 °C in air or wood temperature in the cuvette, and T is air or wood temperature (°C) in the cuvette.

Statistical analyses were conducted with version 6.12 of the Statistical Analysis System (SAS). A non-linear model procedure PROC NLIN was used to estimate the parameters (R_{15} and Q_{10}) of the exponential equation. For each cuvette, daily R_{15} was averaged on three days (running mean) and Q_{10} was calculated on a one-day, three-day and seven-day base.

2.5. Estimation of the different components of stem respiration

Two methods were used to estimate the contributions of growth and maintenance to the total respiration.

Method 1, or mature-tissue method [2]: this method assumes that maintenance respiration (R_M) at a reference temperature and for a given volume or surface area of wood, is constant throughout the year. The averaged maintenance respiration corrected for a temperature of 15 °C (R_{M15}) was calculated for each cuvette from measurements made before and after the growing season. R_M was recalculated throughout the season using an averaged annual Q_{10} for each cuvette and the seasonal temperature variations. R_M was then subtracted from total respiration (R_T) during the growing season for each cuvette and measurement occasion: the difference representing growth respiration (R_G) was summed for the whole year. The slope of the relationship between R_G integrated over the year, and total stem growth in the cuvettes, is the growth respiration coefficient (r_G).

Method 2, or periodic-growth method: R_G was estimated daily by subtracting estimated R_M (see above) for each cuvette from R_T. A running mean over one week (3 days before and 3 days after the day of measurement) was then used to recalculate R_G and the stem growth rate in order to eliminate the diurnal variations in stem growth rate caused by water losses and recharge in the stem. The slope of the relationship between R_G and stem growth rate (corrected for time-lag to give the best fit) gave an estimate of r_G [1, 42]. Total respiration should not be used to calculate r_G since the part represented by maintenance respiration in R_T is changing with temperature throughout the season. This method provided a relationship between C fixed and C respired by growth respiration for each cuvette, while Method 1 gave a single relationship for all cuvettes.

For both methods, we used a wood density value of 636 kg m^{-3} [8], and we assumed that the carbon content of the woody tissues

was 0.49 g C / g dry wood [31]. In June 1997, after a strong storm the upper and lower cuvettes installed in the crown slightly moved from their original location on the stem. Therefore, those two cuvettes were disregarded when calculating the growth respiration coefficient.

2.6. Living cells and nitrogen content analysis

Since we couldn't take samples on the trees used for respiration measurement in 1998, five trees having DBH similar to those used for respiration measurements were chosen outside the experimental site (less than 50 m from the measured trees). In September, after growth had ceased and before leaf fall, two increment cores were taken at breast height from the five trees. The first core was dried at 70 °C for 48h, and milled before nitrogen analysis by means of a Carlo Erba Elemental Analyser NA 1500 [17].

The length of the second core was equal to half the DBH of the stem. The sample was immediately frozen in dry ice and kept at –80 °C. The frozen increment cores were sectioned in the xylem at 3 to 8 depths between 1 and 60 mm under the cambium by means of a microtome. To ensure that at least one cell layer was intact, sections were 70 µm thick. The sections were placed on a glass slide and stained with a Comassie blue solution for 3 minutes [44]. They were then rinsed, first with an identical solution, but without the stain, and finally with water [44]. The sections were mounted on slides in Canada balsam. The Comassie blue stained only the proteins of the cytoplasm and made it possible to determine which cells were living.

On the same date, several branches in the upper canopy were also sampled on the four trees for analysis of [N] and living cells. These branches were regarded as stems since for beech trees it is often difficult to distinguish the branches from the stem in this location and both are exposed to similar climatic conditions. The whole transverse-section of the branches was used for analysis of living cells. To estimate the amount of living cells in the periderm (including cambium, phloem, parenchyma and collenchyma) at breast height, the amount of living cells per volume of periderm for the branches was multiplied by the volume of the periderm at breast height. It was not possible to measure directly the amount of living cells in the periderm at breast height since the cells were damaged by the core sampler. The percentage area of live cells in each section was determined by means of a computer image-analysis system (Image Tool, University of Texas Health Science, San Antonio, TX, U.S.A.). To calculate the total surface area of living cells at breast height, the various sections in the xylem and the percentage of living cells in the periderm were integrated over the cross-sectional area of the stem.

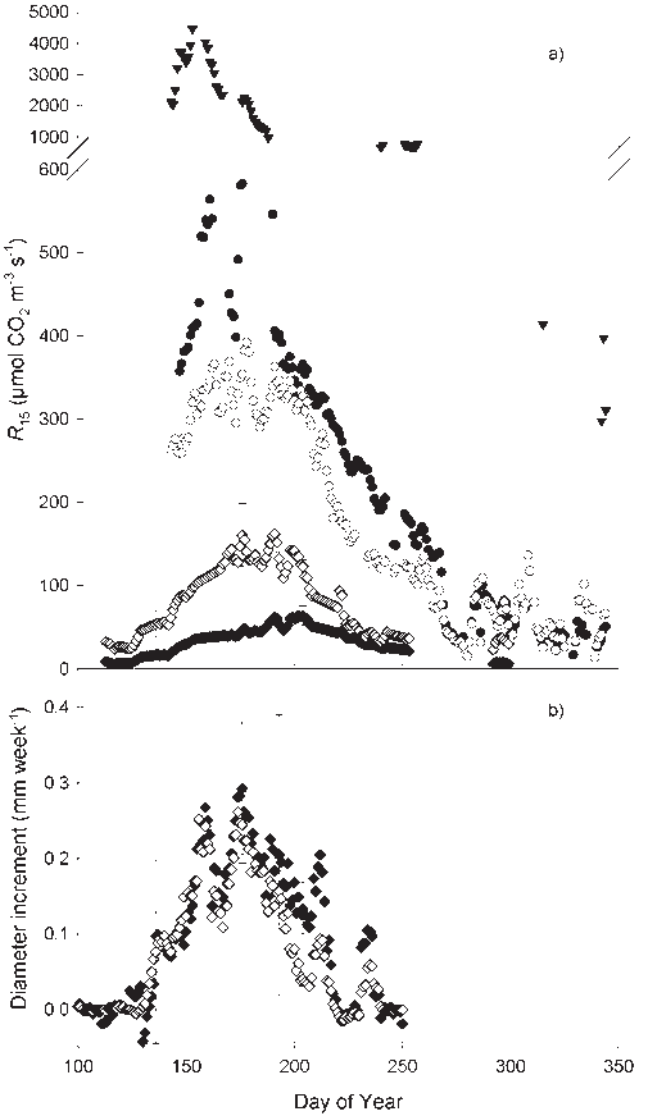

Figure 1. Seasonal and spatial variation in (a) stem respiration normalised to 15 °C (R_{15}) and calculated on a volume basis at breast height (◆, three to four cuvettes per point) and in the middle of the stem (◇, three cuvettes per point) in 1998 and at the base (●), middle (○) and top (▼) of the crown in 1997 of dominant 25-year-old beech trees at Hesse; (b) averaged stem diameter increment at breast height (◆) and in the middle of the stem (◇) in 1998. The error bars represent the standard errors of the mean for the 1998 measurements and are presented for each of the four dates for which the standard errors were maximum for either the respiration rates or the diameter increments at breast height or in the middle of the stem. For further details, see text.

3. RESULTS

3.1. Stem growth

Stem diameter increment in the crown started at the end of April in 1997 [22] and ceased approximately on 20 August (DOY 232). In 1998, growth started ca. DOY 130, and ceased at the end of August (ca. DOY 240), both in the middle and at the base of the stem (*figure 1b*). Growth, which was very well synchronised along the stem during this period, peaked for the first time in early June (DOY 157), decreased until DOY 167 (corresponding to a cool period), and peaked a second time on DOY 175. Thereafter, it slowly decreased until the end of August, even if minor peaks occurred on DOY 212 and 236. The diameter increment was on average 3.9 mm (SE = 0.4) at breast height, 4.9 mm (SE = 0.6) in the mid-stem cuvettes and 4.4 mm (SE = 0.6) in the upper stem cuvettes corresponding to annual relative diameter growth of 3.1, 8.1 and 33.5%, respectively.

3.2. Stem temperature

Stem temperature at breast height and for the upper stem location ranged from –13 and –12.8 °C, respectively, in November 1998, to 29.7 and 38.3 °C in August 1998. The largest difference in temperature between the two levels was recorded in January, and reached 15.7 °C. On a diurnal and monthly average, temperature usually increased with height along the stem. On a monthly base, the difference in temperature between the cuvettes installed on the upper stem and at breast height was always positive (between 0.2 °C in March and 1.5 °C in June), except in April, when the difference was close to –0.2 °C.

3.3. Stem respiration

The peak of respiration, corrected for temperature, occurred in the middle of the growing season (*figure 1a*). In 1997, respiration increased first for the upper crown cuvette, but was rather well synchronised for the mid-crown and lower crown positions and growth respiration ceased for all cuvettes around DOY 270. In 1998, respiration increased suddenly on DOY 126, both at breast height and at mid-stem. This increase occurred four days before measurable growth started (*figures 1a* and *1b*). The peaks of respiration in the mid-stem cuvette occurred on DOY 176 and 191, while at breast height they occurred on DOY 191 and 204. Growth and respiration were not synchronised, and the peak of respiration at breast height occurred ca. 27 days after the first stem growth peak compared with only 18 days for the mid-stem cuvette.

Respiration estimated at 15 ºC (R_{15}), calculated on a volume base, generally increased with height on the stem or decreased with increasing diameter. However, the lower crown cuvette installed in 1997 had a slightly higher respiration rate than the mid-crown cuvette on many occasions (*figure 1a*). The respiration rate in the upper crown cuvette was far higher than in the lower crown and mid-crown cuvettes throughout the season. In 1998 (*figure 1a*), the maximum values averaged for the breast height and mid-stem cuvettes were 65.4 (*SE* = 11.0) and 181 µmol m^{-3} s^{-1} (*SE* = 33) respectively, whereas in 1997, the maximum value for the upper crown cuvette was above 4469 µmol m^{-3} s^{-1} (see *table I*). During the non-growing season, the trend of increase in respiration rates with increasing height or decreasing diameter remained, but the respiration rate at breast height, specifically, increased with increasing diameter (see *figure 2a* and *table I*). The values of R_{M15} before and after growth in 1998 were very similar, 7.0 (*SE* = 0.9) and 7.1 (*SE* = 1.6) µmol m^{-3} s^{-1}, respectively, at breast height and 26.9 (*SE* = 3.0) and 32.6 (*SE* = 2.5) µmol m^{-3} s^{-1} in the mid-stem cuvette. The variation in R_{15} between trees in 1998 was relatively small compared with variation within trees. At breast height and at mid-stem, on a volume basis, the larger factors of variation during the season between trees were 2.4 and 3.6, respectively.

Table I. Spatial variation in stem respiration and Q_{10} in the cuvettes during the season 1998 at breast height, mid-stem and for the upper stem of dominant beech trees and at three positions within the crown (low, mid-crown and upper crown) during the season of 1997. The maximum annual values of stem respiration (R_{15MAX}) and the averaged maintenance respiration before and after growth, normalized to 15 ºC (R_{M15}), were calculated on a volume (µmol m^{-3} s^{-1}) or surface (µmol m^{-2} s^{-1}) of stem base. Values in parenthesis are standard errors of the means.

Cuvette positions	Year	Diameter (mm)	Height (m)	R_{15MAX} (µmol m^{-3} s^{-1})	R_{M15} (µmol m^{-3} s^{-1})	R_{15MAX} (µmol m^{-2} s^{-1})	R_{M15} (µmol m^{-2} s^{-1})	Q_{10}
Breast height 1	1998	128	1.8	95.2	7.35 (0.34)	3.14	0.239 (0.010)	1.18 (0.03)
Breast height 2	1998	108	1.4	46.0	–	1.27	–	1.38 (0.046)
Breast height 3	1998	115	1.7	52.3	5.09 (0.11)	1.55	0.149 (0.003)	1.44 (0.05)
Breast height 4	1998	143	1.6	68.2	9.12 (0.49)	2.50	0.330 (0.018)	1.33 (0.05)
Mean Breast height	1998	124 (8)	1.6 (0.1)	65.4 (11.0)	7.18 (1.16)	2.12 (0.43)	0.239 (0.052)	1.33 (0.11)
Mid-stem 1	1998	60.8	11.0	141	30.2 (1.7)	2.25	0.479 (0.030)	1.28 (0.04)
Mid-stem 2	1998	51.6	10.4	248	33.5 (1.0)	3.35	0.449 (0.013)	1.47 (0.08)
Mid-stem 3	1998	56.5	11.6	156	27.5 (0.8)	2.36	0.406 (0.014)	1.52 (0.06)
Mean Mid-stem	1998	56.3 (0.3)	11.0 (0.3)	181 (33)	30.4 (1.8)	2.65 (0.35)	0.445 (0.021)	1.42 (0.11)
Upper stem 1	1998	13.6	15.0	–	547*	–	2.30*	1.99*
Upper stem 2	1998	15.4	13.2	–	147*	–	0.56*	2.11*
Upper stem 3	1998	15.2	14.7	–	236*	–	0.90*	2.25*
Upper stem 4	1998	16.8	14.2	–	89.4*	–	0.30*	1.79*
Mean Upper stem	1998	15.2 (0.7)	14.3 (0.3)	–	255 (102)	–	1.02 (0.44)	2.04 (0.08)
Low crown	1997	23.6	13	583	48.0 (3.2)	3.67	0.287 (0.019)	1.79 (0.03)
Mid-crown	1997	12.9	14	392	60.4 (3.6)	1.33	0.225 (0.013)	1.87 (0.05)
Upper crown	1997	2.5	15.3	4469	528 (56)	2.32	0.441 (0.039)	1.85 (0.07)

* Based on measurements made on DOY 245 only.

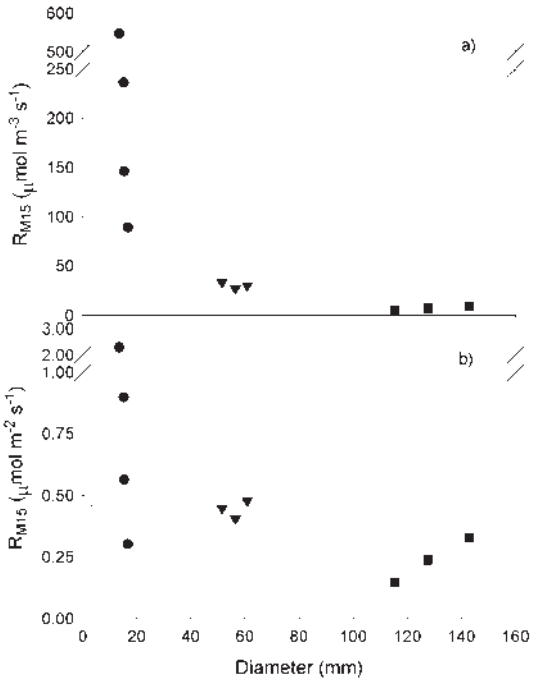

Figure 2. Spatial variation in annual mean of maintenance respiration estimated at 15 °C (R_{M15}) calculated on a volume (a) or a surface-area base (b) as a function of stem diameter at Hesse in 1997 (○) and 1998 (●) at the top of the crown; in the middle of the stem (▼) and at breast height (■). One cuvette per point.

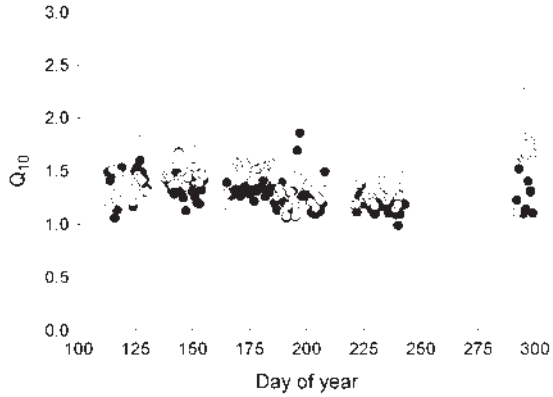

Figure 3. Seasonal variation in averaged Q_{10} of dominant or co-dominant 25-year-old beech trees at Hesse in 1998: at breast height (●, three to four cuvettes per point) and at mid-stem (○, three cuvettes per point). The error bars represent the maximum standard errors for both locations.

On a surface area base, the differences in R_{15} between the different levels along the stem were smaller than on a volume base. There was less consistency in the variation of R_{15} and R_{M15} along the stem in 1997 and 1998 than on a volume base (*figure 2b*) since the respiration rate did not necessarily increase with height or decrease with diameter. Therefore, maintenance respiration is more difficult to predict on a surface area base. At breast height, the factor of variation between the trees was 39% higher when respiration was calculated on a surface base than when it was calculated on a volume base.

3.4. Q_{10} calculations

As a rule, Q_{10} tended to increase with the number of days used to calculate it. In 1998, on a one-day, three-day and seven-day calculation base, the averaged Q_{10} was 1.29 (SE = 0.06), 1.33 (SE = 0.05) and 1.35 (SE = 0.06), respectively, for cuvettes installed at breast height. Q_{10} can be underestimated when calculated with a short time-step and calculations over a long period can also induce problems, if calculations are applied to different physiological status of the wood. A three-day period was found to be a good compromise. When calculated with day-time values only, but for a three days period, Q_{10} was 1.43 instead of 1.33. The hysteresis commonly observed when respiration is plotted against temperature tends to overestimate Q_{10} when it is calculated on a diurnal base only. Introduction of a time-lag correction into the calculations increased the estimate of Q_{10}. However, as the time-lag between respiration and temperature varied inconsistently from 0 to 12 hours, and because this lag was not predictable, our Q_{10} estimates are presented without a correction for time-lag. There was no significant temperature-dependence of the Q_{10} at the top of the trees since the slope of the linear relationship between Q_{10} and stem temperature was very small and not significant (data not shown).

Through the season, Q_{10} values ranged from 1.0 to 1.85 at breast height and from 1.08 to 2.25 at mid-stem. No clear seasonal variations were observed and most of the time Q_{10} was higher at mid-stem than at breast height (*figure 3*). The annual averaged Q_{10} from 1998 and 1997 for each position shows that Q_{10} increased with height or decreased with increasing diameter (*table I*). The diameters, heights, peaks of respiration rates, estimated at 15 °C, and maintenance respiration rates estimated at 15 °C, for the different cuvette positions in 1997 and 1998 are also given in *table I*.

3.5. The growth and maintenance components of stem respiration

Method 1: The relationships between total growth respiration and the amount of wood produced in six cuvettes during 1998 and in the mid-crown cuvette during 1997, are shown in *figure 4*. The linear relationship (r^2 = 0.89, n = 7) shows that the growth respiration coefficient was rather constant along the stem. For 1 g of carbon fixed in the new tissue, 0.23 g of carbon was respired.

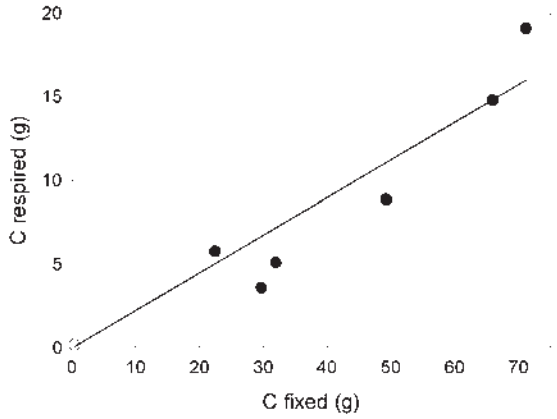

Figure 4. Relationship obtained by Method 1 between carbon fixed in the newly-formed tissue and carbon respired by growth respiration in the lower and middle cuvettes in 1998 (●) and the middle cuvette in the crown in 1997 (○). One cuvette per point; the solid line represents the regression $Y = 0.23 \times X$ (the intercept was set to 0), $r^2 = 0.89$.

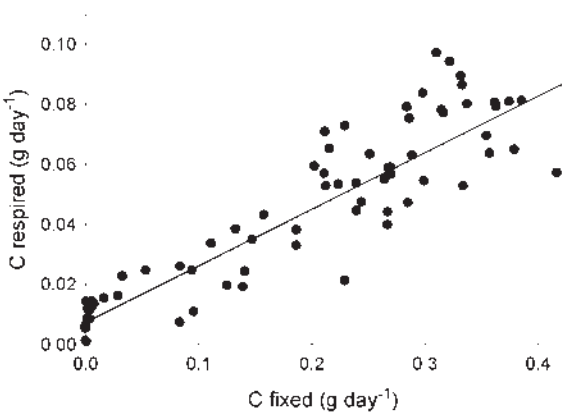

Figure 5. Relationship obtained by Method 2 between carbon fixed in the newly-formed tissue and carbon respired by growth respiration in one of the middle cuvettes in 1998. The solid line represents the regression $Y = 0.19 \times X + 0.008$, $r^2 = 0.85$.

The use of the mature-tissue method indicated that in 1998, 66.6% (*SE* = 1.3) of total stem respiration at breast height was growth respiration, compared with 44.6% (*SE* = 4.5) at mid-stem (*table II*), in spite of a higher annual relative diameter growth than at breast height (8.1%, *SE* = 0.5 and 3.1%, *SE* = 0.2, respectively). The relative growth for the upper stem was ca. 33.5% (*SE* = 3.8) in 1998. On average for 1997 and 1998, the percentage of total respiration represented by growth respiration (R_G%) was 56.5% (*SE* = 4.8).

Method 2: The use of the periodic-growth method indicated that on average for 1 g of carbon fixed in new tissues, 0.20 g (*SE* = 0.04) of carbon was respired (*figure 5*). The r^2 of the relationship between carbon fixed and carbon respired by growth respiration, ranged between 0.57 and 0.85 ($P = 0.05$). Growth respiration was estimated to be on average 64.9% (*SE* = 7.8) of the total annual respiration in the cuvettes (*table II*).

Both methods gave on average similar estimates of the growth respiration coefficient, but the contribution of growth respiration to total respiration differed. For Method 2 the averages were calculated on mid-stem and breast height cuvettes, whereas the averages for r_G and R_G%, respectively, were 0.13 and 53.9% at breast height and 0.27 and 75.9% at mid-stem. Both r_G and R_G% had higher values at mid-stem than at breast height according to Method 2, but the difference was significant for r_G only (*t*-test, $P = 0.019$).

3.6. Live cells and nitrogen analysis

In the xylem, all of the living cells were found in the rays and down to the centre of the stem. The percentage of living cells was rather stable in the xylem from the surface to the centre of the stem (mean = 20.6, *SE* = 0.43). The total percentage of living cells at breast height was very close to the

Table II. Spatial variation in total annual respiration (R_T) and wood production in each cuvette and comparison between Methods 1 and 2 for the percentage that represents growth respiration (R_G%) in R_T and comparison of the growth respiration coefficient (r_G). The r^2 of the relationship between C respired and C fixed for Method 2 is also presented for each cuvette. Values in parenthesis are standard errors of the means.

Cuvette positions	Wood production (10^3 mm^3)	R_T (mol)	Method 1		Method 2		
			r_G	R_G%	r_G	r^2	R_G%
Breast height 1	207	644		66.7	0.12	0.70	64.8
Breast height 3	155	438		69.2	0.18	0.67	63.1
Breast height 4	224	691		63.9	0.10	0.85	33.8
Mean Breast height	195 (21)	591 (63)		66.6 (1.3)	0.13 (0.02)	0.74 (0.05)	53.9 (10.1)
Mid-stem 1	164	128	0.23	33.7	0.31	0.67	92.8
Mid-stem 2	71	188		51.2	0.30	0.57	72.7
Mid-stem 3	101	146		49.1	0.19	0.85	62.1
Mean Mid-stem	112 (48)	154 (15)		44.6 (4.5)	0.27 (0.04)	0.69 (0.07)	75.9 (9.0)
Mid-crown	1.4	4		61.9	–	–	–

total percentage of living cells in the xylem (*figures 6a* and *6b*), which demonstrates that the number of living cells in the periderm is negligible in this location. The integration of the sections at several depths over the entire stem section showed that the mean percentage of living cells was close to 20.6% (*SE* = 0.88), but decreased with DBH (*figure 6b*).

In the crown, the percentage of living cells in the xylem decreased strongly with increase of stem diameter (*figure 6a*), from 48% to 21% at 1.8 mm and 8.2 mm diameter, respectively. The total percentage of living cells also decreased with increase of stem diameter, from 60.3% to 32.7% for stem diameters of 2.2 and 11 mm, respectively (*figure 6b*). Moreover, the proportion of xylem tissue compared to the other tissues strongly increased with stem diameter (*figure 7*). Pith thickness was constant and the percentage of living cells in the pith was on average 45% lower than the percentage of living cells in the xylem at the same diameter (data not shown). The percentage of living cells in the periderm was rather constant, averaging 55.6% (*SE* = 0.90).

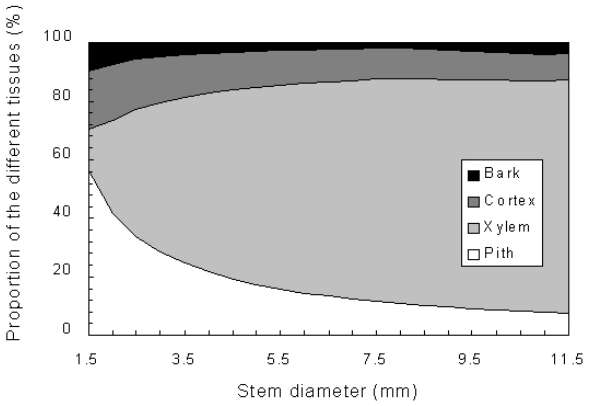

Figure 7. Representation of the relative proportion of different tissues in the stem within the crown, as a function of their diameter for 25-year-old beech trees at Hesse in 1998.

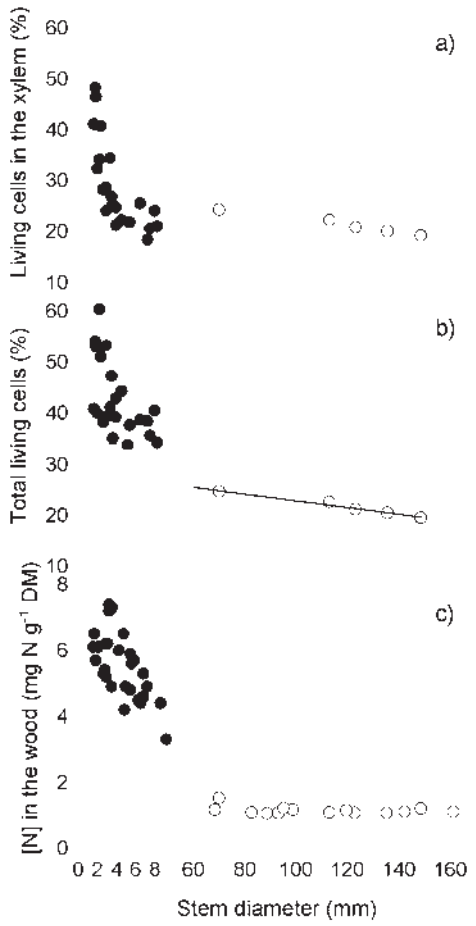

Figure 6. Percentage of living cells in the xylem (a), over the entire section (b) and nitrogen concentration in the wood (c) as a function of stem diameter for 25-year-old beech trees at Hesse in 1998; in the crown (●) and at breast height (○). The solid line represents the regression for the breast height samples, $Y = -0.066 \times X + 24.5$, $r^2 = 0.97$.

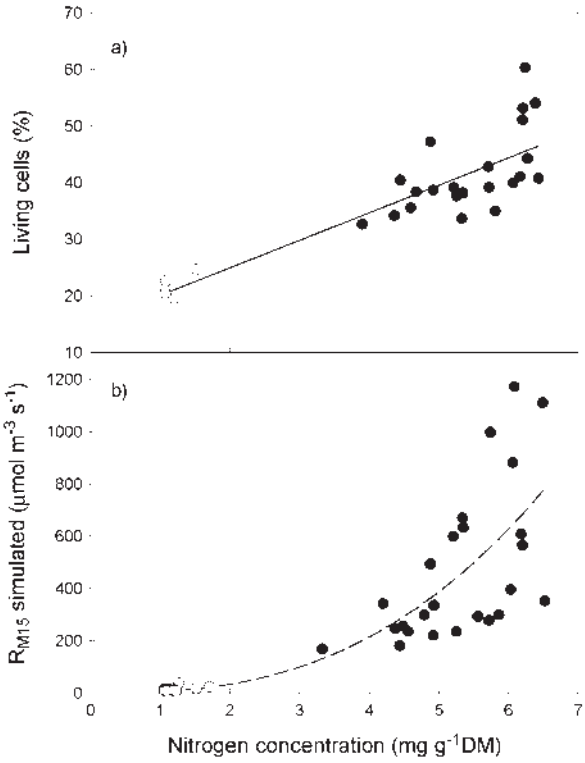

Figure 8. Percentage of living cells in the stem and simulated R_{M15} as a function of nitrogen concentration in the stem in the crown (●) and at breast height (○) for 25-year-old beech trees at Hesse in 1998. The solid line represents the regression for the percentage of living cells ($Y = 4.86 \times X + 15.3$, $r^2 = 0.74$). The dashed line represents the regression for the simulated R_{M15} ($Y = -88.9 + 62.0 \times e^{(0.41 \times X)}$, $r^2 = 0.68$).

Corresponding to the decrease in living cells, the nitrogen concentration decreased strongly with stem diameter in the crown, from 7.5 mg N g^{-1} DM to 3.3 mg N g^{-1} DM for organs with diameters close to 2 and 9 mm, respectively (*figure 6c*). At breast height, there were very little changes in [N] with changes in stem diameter and nitrogen concentration was close to 1 mg N g^{-1}. There was a linear relationship between the total percentage of living cells in the stem and [N] ($Y = 4.86 \times [N] + 15.3$, $n = 20$ and $r^2 = 0.74$), but the relationship between simulated respiration (calculated from the relationship shown in *figure 2a*) on a volume base and nitrogen concentration was not linear (*figure 8*). The model $Y = -88.9 + 62.0 \times e^{(0.41 \times [N])}$ was the best fit to the respiration data ($n = 41$ and $r^2 = 0.68$), suggesting that respiration increases non-linearly with the volume of living cells.

4. DISCUSSION

4.1. Seasonal variations in respiration

Total stem respiration varied throughout the year with maximum rates during summer and minimum rates during winter. These variations, corrected to 15 ºC, were related to variations in diameter increment, but were not synchronised. The time-lag between respiration and growth was not constant, which implies that daily measurements are needed to match the changes in growth and respiration through the season. This is necessary for estimating the growth respiration coefficient by the periodic-growth method. In Stockfors and Linder [46], it was noted that the lag between growth and respiration peaks varied between 10 and 20 days for *Picea abies*. A possible explanation for this phenomenon is the lag between diameter growth and increase in dry matter caused by a delay in wall thickening and lignification [50]. Surprisingly, respiration at mid-stem and breast height was not synchronised, whereas growth was. The lag between growth and respiration was greater at breast height, perhaps because more wall thickening is needed at breast height to support the entire structure of the tree. A second hypothesis is that allocation of assimilates translocated from the leaves in the crown went as a first priority to closer woody organs for wall thickening.

4.2. Spatial variations in respiration

In accordance to previous studies [28, 32, 40, 41, 49], stem respiration varied strongly within a tree in Hesse. The factor of variation for respiration was higher when calculated on a volume base than on a surface-area base. The stem respiration rates measured at breast height were similar to those reported in similar studies for conifers [21, 38] and broadleaved trees [10, 15, 16]. Our measurements in the crown showed respiration rates higher than those in Möller et al. [32] on beech trees, but Yoda et al. [49] on broadleaved trees found maintenance respiration rates similar to those in our study. On a surface-area base, our measurements in the crown are also similar to those reported on conifers [28, 40].

A principal factor responsible for the spatial variation of woody total respiration was the difference in temperature between the organs. Considering R_{M15} and Q_{10} values at breast height and for the upper stem location, the differences in temperature would explain at most 68.5% of the spatial variation in measured respiration rates during the non growing period. Stockfors [45] showed that failure to consider temperature differences within the stem could produce errors representing about 58% of total annual stem respiration.

Even after total respiration was corrected for temperature differences, respiration calculated on a volume base at the top of the tree was greater than that at breast height. This is partly caused by the higher relative growth of the stem in its upper parts during the growing season. The measurements of spatial variability in R_{M15} during the non-growing periods showed that R_M also increased with height along the stem. The main reasons are that periderm had a higher percentage of living cells than other tissues and that the proportion of the periderm compared to the other tissues decreased when the diameter of the organ increased. Moreover, the proportion of living cells in the xylem and in the pith also decreased with increasing diameter. In consequence, the total amount of cells per unit surface or volume of stem decreased with increasing diameter, corresponding to a decrease in the maintenance respiration rate. Since larger diameters usually corresponded to older stems, our observations are globally in agreement with Carey et al. [6], who showed that R_M decreased with DBH and age.

The percentage of living cells in the organs was much higher for beech than for most of the other species studied. At breast height, the percentage of living cells in the sapwood was 5.0% for *Pinus contorta*, 5.7% for *Picea engelmanii* [36] and only 0.1–0.5% for *Picea abies* [46] compared with about 22% for beech. Such a difference is explained by the much bigger size and number or rays for beech compared to the conifers mentioned above. This is confirmed by our own observations of the living tissues in *Picea abies* [7].

The distribution of the living cells in the stem was also quite different from that found for *Picea abies* [7, 46]. In *Picea abies*, 80% of the living cells were situated in the first 4 mm beneath the bark at breast height, and the percentage of live cells decreased towards the centre of the stem [46]. For *Pinus contorta* and *Picea engelmanii* more than 80% of the living cells were also situated in the sapwood [36]. The difference in distribution of the living cells within the stem in different species could explain why some authors have found that respiration was better correlated with wood surface [46] or with volume [36]. For the beech trees we studied, volume seems to be the most appropriate base for calculation of stem maintenance respiration rates since an important proportion of the living cells are situated in the xylem.

As in our study, Bosc [5] found that in maritime pine (*Pinus pinaster* Ait.), maintenance respiration increases strongly with [N]. For beech, maintenance respiration increased according to an exponential relationship with [N]. Since the relationship between [N] and the percentage of living cells was linear for beech, respiration also increased in an exponential relationship with the percentage of living cells. For the smaller and younger organs, respiration increased strongly, indicating that the living cells in these young organs are probably more physiologically active than those in the older ones. Bosc [5] showed that the combined effect of age and tissue vitality could explain part of the differences in maintenance respiration rates within the tree.

Nevertheless, branches and stems in the crown have a much higher respiration rate on a volume or mass base than does the stem at breast height [32, 49]. This fact is critical, since the proportion of organs in the crown (stem and branches) compared to the total amount of wood is large in beech trees (11% in volume and 53% in area in [8]). Further investigations concerning the variation in respiration rates within the crown, especially for branches in the lower part of the canopy, would be needed in order to assess the relationships between R_M, diameter and age of the organs.

4.3. Estimation of Q_{10}

Our value of Q_{10} without correction for the time-lag at breast height (Q_{10} = 1.33 on average) is low compared with most other values found in the literature, even if Lavigne and Ryan [20] found Q_{10} values between 1.0 and 1.7 for old aspen trees. Other studies report Q_{10} values of 1.2 to 3 for *Pinus banksiana* [19], 1.5 to 3.2 for *Chamaecyparis obtusa* [34] and 1.9 to 2.6 for *Picea abies* [46].

Q_{10} also varied within the trees, from 1.18 at breast height to 2.25 in the crown. The response of respiration to changes in temperature was faster for smaller-diameter organs. The thicker bark and periderm could slow down the diffusion of CO_2 through the stem and partly be responsible for this observation [13]. However, the slower response of respiration to changes in temperature measured 2 mm under the bark, is also probably caused by the delay in warming of the internal parts of the stem compared to the superficial parts. Stockfors [45] and Derby and Gates [9] have observed gradients in temperature within the stem, of up to 21 °C. The greater the diameter, the longer it will take to reach a homogeneous temperature, and in consequence, the time-lag between changes in temperature and changes in respiration increases with the diameter of the stem [5, 21].

In contrast to some other studies [27, 47], no Q_{10} temperature-dependence was found and no clear seasonal pattern in Q_{10} was observed. Stockfors and Linder [46] for *Picea abies* and Paembonan et al. [34] for *Chamaecyparis obtusa*, observed a clear seasonal variation of Q_{10}, but Linder and Troeng [24, 25] did not find such variations in *Pinus sylvestris*.

4.4. Separation of the total respiration into its components

Continuous respiration measurements improve the accuracy of the estimated components of stem respiration, since respiration rates vary relatively fast. However, both methods used to separate total respiration into its components lead to rather similar results concerning the growth respiration coefficient (r_G = 0.23 by Method 1 and 0.20 by Method 2), but not for the percentage of growth respiration over total respiration (56.5% by Method 1 and 64.9 by Method 2). These percentages are similar to those found by Ryan [36] and Stockfors and Linder [46] in conifers (R_G% ranged between 40 and 60% of the total annual respiration). R_G% was, however, higher at mid-stem than at breast height by Method 2 (75.9% and 53.9% respectively), but lower by Method 1 (44.6 and 66.6% respectively).

Our mean values of r_G are rather consistent with similar studies and are close to the theoretical value of 0.25 found by Penning de Vries [35], but the r_G values obtained at breast height by Method 2 are among the smallest reported. Lavigne and Ryan [20] estimated that the growth respiration coefficient in *Pinus banksiana* and *Picea mariana* was between 0.24 and 0.39 and Wullschleger et al. [48] estimated r_G to be 0.21 to 0.25 for *Quercus alba* saplings. Stockfors and Linder [46] found r_G values between 0.11 and 0.2, depending on the methods used, but with the lower values for the mature-tissue method. They suggested that the use of the mature-tissue method can pose problems, since R_M is assumed to be constant through the year, whereas some studies have shown that R_M can acclimate to changes in temperature [25, 34] or varies with [N] in the wood [28]. Moreover, similar regressions as those obtained by Method 2 were made by using total respiration instead of growth respiration (which is the result of the subtraction of maintenance respiration from total respiration) and the slopes were similar to those obtained by Method 2. This result indicates that Method 2 is not sensitive to errors in estimates of maintenance respiration.

5. CONCLUSION

Annual growth respiration accounted for about 60% of total respiration with a growth respiration coefficient close to 0.2. The distribution of the living cells in the stem tends to show that for young beech trees, volume is a better base for calculating stem maintenance respiration than is surface area.

Respiration rates varied within the tree by a factor up to 68-fold when calculated on a volume base. Most forest carbon-cycle models that estimate stem respiration at stand level assume that respiration rates, temperature and Q_{10} are constant within the tree. Such assumptions can induce large errors of estimation for woody respiration at the tree and stand level, if those parameters vary within the tree, as in our study. More information is also needed concerning variations in

branch respiration rates and bark CO_2 refixation, in order to improve the stand-level calculations for respiration of woody organs.

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