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Environmental Effects on Spatial and Seasonal Variations of Stem Respiration in European Beech and Norway Spruce

Eric Ceschia

SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

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This thesis discusses the environmental and biological factors which control stem respiration processes in beech and Norway spruce trees. The results are based on field experiments in France in 1997–98 and in Sweden in 1999–2000. Effects of fertilisation and elevated atmospheric CO_2 concentration on stem growth and respiration were studied, as well as the causes of seasonal and spatial variation in stem respiration. Woody respiration varied with seasonal changes in temperature and secondary growth. Spatial variation in stem respiration was explained by temperature gradients and the uneven distribution of living cells within the stem, by differences in diameter increment along the axis and variations in tissue vitality. Sapflow had little effect on stem respiration at breast height. Higher respiration rates usually were found in the upper stem or in the crown. Neglect of spatial variation in stem respiration led to errors in estimating annual aboveground woody respiration (R_{AG}) of 30–110% and 30%, in beech and Norway spruce stands, respectively. R_{AG}, corrected for spatial variation in stem respiration, represented 30% of total annual respiration in the beech forest. R_{AG} was 245–289 g C m^{-2} a^{-1} in beech, 64 and 134 g C m^{-2} a^{-1} in unfertilised and fertilised stands of Norway spruce, respectively. Carbon use efficiency (CUE) was 0.58, 0.71, and 0.72 for beech trees, unfertilised and fertilised Norway spruce trees, respectively.

Stem respiration was separated into its components, maintenance and growth respiration. Growth respiration represented *ca.* 35% and 40% of total stem respiration. The wood construction cost (r_G) was on average 0.2 and 0.16 g C respired g^{-1} C fixed in the new wood of beech and spruce trees, respectively. For both beech and spruce, r_G was higher in the crown than at breast height, but the causes of this were not identified. Fertilisation tended to increase r_G in Norway spruce, but maintenance respiration was not affected. Elevated [CO_2] treatment had little effect on r_G in Norway spruce (+10% and 3.5% on unfertilised and fertilised plots, respectively) and none in beech. [CO_2] treatment had no effect on the phenology of wood growth or maintenance respiration when fertilisation was applied. On the unfertilised Norway spruce plot, however, maintenance respiration increased by a factor of 2.5, and [C] also increased in the newly formed ring. A change in the wood composition of trees grown in elevated [CO_2] without fertilisation, apparently caused the increase in r_G and in maintenance respiration rates. In the perspective of global warming, R_{AG} would increase by 25% and 14% in young beech and Norway spruce forests, respectively, and the combined effect of elevated atmospheric CO_2 and global warming would increase R_{AG} by a factor of 2.3 in Norway spruce stands.

Keywords: *Fagus sylvatica*, *Picea abies*, growth and maintenance respiration, wood construction cost, wood growth, Q_{10}, living cells, nitrogen concentration, fertilisation, global change, up-scaling.

Distribution: Swedish University of Agricultural Sciences
Department for Production Ecology
S-750 07 UPPSALA, Sweden.

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Eric Ceschia
Department for Production Ecology
Uppsala

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Abstract

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Contents

Appendix

Papers I-V

The present thesis is partly based on the following papers, which are referred to by their Roman numerals:

I Spatial and seasonal variations in stem respiration of beech trees (*Fagus sylvatica*). Eric Ceschia, Claire Damesin, Stephanie Lebaube, Jean-Yves Pontailler & Eric Dufrêne. *Tree Physiology* (Submitted).

II Effects of nutrition on spatial and seasonal variations in stem respiration of Norway spruce (*Picea abies*). Eric Ceschia & Sune Linder. *Tree Physiology* (Submitted).

III Stem and branch respiration of *Fagus sylvatica*: from tree measurements to estimations at the stand level. Claire Damesin, Eric Ceschia, Noël Le Goff, Jean-Marc Ottorini & Eric Dufrêne. *New Phytologist* (In Press).

IV The carbon balance of a young beech forest. André Granier, Eric Ceschia, Claire Damesin, Eric Dufrêne, Daniel Epron, Patrick Gross, Stéphanie Lebaube, Valérie Le Dantec, Noël Le Goff, Damien Lemoine, Eric Lucot, Jean-Marc Ottorini, Jean-Yves Pontailler & Bernard Saugier. 2000 *Functional Ecology* 14, 312-325.

V The effects of elevated [CO_2] on stem growth and respiration in beech and Norway spruce. Eric Ceschia, Göran Wallin, Franz-Werner Badeck, Bernard Saugier & Sune Linder (Manuscript to be submitted to *Trees*).

Papers III and IV were reproduced with the kind permission of New Phytologist and Functional Ecology, respectively.

Introduction

The global change perspective

Atmospheric CO_2 concentration, $[CO_2]$, has increased continuously since the beginning of the industrial revolution, mainly because of the burning of fossil fuel, and deforestation (Keeling, 1994). For more than 400,000 years, $[CO_2]$ has fluctuated between 180 and 280 µmol mol^{-1} (Petit *et al.*, 1999), but by 2000, it had reached 370 µmol mol^{-1} and is still increasing by *ca.* 1.5 µmol mol^{-1} a^{-1} (Keeling & Whorf, 1994). This increase, however, is not as large as was formerly expected. Every year, 23 Gt CO_2 are emitted into the atmosphere from the combustion of fossil fuels, while only 11 Gt accumulate in the atmosphere (IPCC, 2000). The missing 12 Gt is absorbed by the 'missing sink', thought to consist in part of the oceans (*ca.* 8.4 Gt a^{-1}), in part of terrestrial ecosystems (*ca.* 3.6 Gt a^{-1}). Terrestrial ecosystems, especially forest ecosystems, play a major part in the global carbon cycle, at the same time as they buffer the increase in atmospheric $[CO_2]$. It is therefore crucial to improve our understanding of the processes which control carbon cycling in forests, so that we can develop strategies allowing us to increase long-term carbon storage in forests. Such storage in biomass could decrease the rate of increase in atmospheric $[CO_2]$, and knowledge of the magnitude of this storage would help us plan reductions in our carbon emissions.

Forest ecosystems not only fix CO_2 *via* photosynthesis, but also respire like any other living organism, releasing CO_2 to the atmosphere. Respiration in forest ecosystems represents a large component of their annual carbon balance, since it returns to the atmosphere up to 60% of the carbon fixed by photosynthesis (Amthor, 1989; Ryan, 1991; Ryan *et al.*, 1994a). In some cases, the balance between carbon fixed by the ecosystem, and carbon respired, can be very narrow, and forest ecosystems may even act as a source of CO_2. Lindroth *et al.* (1998) and Valentini *et al.* (2000) showed that respiration is one of the key factors determining whether forest ecosystems will act as net sources or net sinks of carbon.

Sensitivity of respiration to temperature

Because of its abundance in the atmosphere, CO_2 is the main greenhouse gas (GHG; IPCC, 2000). Together with other GHGs, such as methane or ozone, its increase in the atmosphere is likely to cause a rise in the Earth's temperature through the absorbtion of more infra-red radiation emitted or re-emitted towards space by the Earth's surface. Wigley (1989) predicted a global warming of 1.5–4.5 °C in the 21st century, and Greco *et al.* (1994) predicted for the boreal region, for the period 1990–2050, a temperature increase of 2–3 °C in winter and 1–2 °C in summer, in consequence of the increase in GHGs.

It has long been known that respiration processes are sensitive to temperature changes. Arrhenius (1889) was the first to use an exponential function with a constant Q_{10} close to 2, which represents the rate of increase in respiration rate for an immediate increase in temperature by 10 °C (see Equation 1). Since then, many scientists have used this function to predict respiration rates from temperature changes. Global warming should therefore lead to an increase in the respiration of ecosystems, and would increase the risk that forest ecosystems would act as carbon sources. However, under natural conditions, respiration often acclimates to temperature increases (Paembonan *et al.*, 1991; Atkin *et al.*, 2000), but the range of acclimation, and its consistency among the various compartments of forest ecosystems, remain unclear.

Woody respiration

Since woody respiration represents between 17 and 67% of the annual respiration of a forest ecosystem, depending on tree species and age (Kinerson *et al.*, 1977; Ryan & Waring, 1992), interest in stem respiration studies has increased during recent decades. Although the biochemical pathways are similar, the total respiration of wood (R_T) is generally separated into two components (*e.g.* Amthor, 1984; Sprugel, 1990): growth respiration (R_G), which provides the energy needed to synthesise new tissues, and maintenance respiration (R_M), which maintains existing living cells. A simple model usually is used to calculate woody respiration separated into these two components (Amthor, 1989; Sprugel & Benecke, 1991). Maintenance respiration (R_M), can be estimated when R_T is measured outside the growing season, since R_T is equal to R_M during that period. Growth respiration is estimated by subtracting maintenance respiration from total respiration measured during the growing season, on the assumption that that R_M remains constant throughout the year (*i.e.* no acclimation occurs). A linear relationship between growth and growth respiration allows growth respiration to be modelled as a function of wood increment (Amthor, 1989; Sprugel & Benecke, 1991). The slope of this relationship represents the wood construction cost (r_G), also called the growth respiration coefficient.

Usually, R_G and R_M are estimated from measurements at breast height (1.3 m), but some studies have shown that R_T and R_M vary with stem and branch diameter or height (Möller *et al.*, 1954; Yoda *et al.*, 1965; Benecke & Nordmeyer, 1982; Lavigne, 1988; Matyssek & Schulze, 1988; Sprugel, 1990; Ryan *et al.*, 1996; Bosc, 1999, Cernusak & Marshall, 2000), or with the woody organ (stem or branch) considered (Möller *et al.*, 1954; Yoda *et al.*, 1965; Sprugel, 1990; Maier *et al.*, 1998; Bosc, 1999). The factors by which respiration varied within the tree differed greatly among the various studies, and depended on the units in which respiration was calculated. Möller *et al.* (1954) reported for *Fagus sylvatica* an almost 10-fold difference in respiration rates along the stem on a wood-volume base; Yoda *et al.* (1965) a 30-fold difference on a wood-mass base; Ryan *et al.* (1996) a 3- and 4.5-fold difference on a surface-area and volume base, respectively; and Sprugel (1990), a 10- to 40-fold difference on a surface-area

base for *Abies amabilis*. Therefore, failure to consider spatial variation in respiration rates when modelling stand-level woody respiration could cause serious errors (Stockfors, 2000).

Causes of seasonal and spatial variation in woody respiration

Seasonal variation in stem respiration rates has received much attention since the 1980s. The main causes of such variation were identified as seasonal changes in temperature and wood growth (Linder & Troeng, 1981; Kakubari, 1988; Ryan, 1990). The processes involved in spatial variation in R_T received little consideration. Several causes, however, may lie at the origin of these spatial variations. For example, differences in the amount of wood produced along the stem may induce differences in growth respiration, while the distribution of living cells within the stem will affect maintenance respiration rates (Stockfors & Linder, 1998; Stockfors, 2000). Malkina *et al.* (1985) and Lavigne (1988) supported the idea that variations in respiration rate could be caused by the transport and storage of carbohydrates in the stem and in the branches.

Negisi (1979) and Kakubari (1988) pointed out that sapflow could transport part of the CO_2 respired by the stem. Part of this CO_2 could be released in the upper parts of the stem, where the bark is thinner (Martin *et al.*, 1994) and where CO_2-saturated sapflow and higher stem temperature would facilitate CO_2 degassing. Moreover, Levy *et al.* (1999) showed that CO_2 in the sap, originating from the soil, could represent up to 12% of the CO_2 efflux measured on the stem during the peak of respiration. Edwards & Wullschleger (2000), in contrast, found little evidence of the effect of sapflow on measured stem respiration.

Finally, temperature is an important factor that influences spatial variation in 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, stem tissues also warm faster at the top than at the base of the stem. Stockfors (2000) showed that failure to consider temperature differences within the stem could produce errors representing about 58% of total annual stem respiration. Moreover, scaling of stem respiration from small chambers to the entire stand, usually also implies the assumption that the relationship between temperature and respiration is constant within the tree. However, Q_{10} can vary with the organ (stem or branch) considered (Maier *et al.*, 1998), partly as an effect of differences in organ diameter (Ryan, 1990).

Effects of atmospheric elevated [CO_2] on woody respiration

Since atmospheric [CO_2] is predicted to reach 700 μmol mol^{-1} by the end of the 21st century, if no reduction in anthropogenic carbon emissions occurs, it is important to know how plants will react to such a disturbance. Therefore, the effects of elevated [CO_2] concentration on plant respiration, and woody

respiration in particular, must be known. Unfortunately, only a few studies have addressed the effects of elevated [CO_2] on woody respiration, and they do not allow a consensus to be reached. Wullschleger *et al.* (1995), for *Quercus alba* trees, and Carey *et al.* (1996) for *Pinus ponderosa* trees grown in either ambient or ambient +350 µmol mol^{-1} CO_2, found evidence that stem respiration rates had increased in high [CO_2] conditions. Wullschleger *et al.* (1995) attributed this increase to an increase in wood growth. They found no [CO_2] effect, neither on maintenance respiration expressed per wood volume, nor on r_G. Carey *et al.* (1996) found no difference in growth rate or r_G between the two treatments, but they assumed an increase in maintenance respiration to be responsible for the increase in total stem respiration. They also found a [CO_2] effect on the coefficient of respiration response to changes in temperature for *Pinus ponderosa* trees, with higher values for the elevated treatment (Q_{10} was 2.20 and 1.67).

Dvorak & Oplustilova (1997) found lower total stem respiration rates and Q_{10} for branches in Norway spruce trees grown under elevated [CO_2]. Janous *et al.* (2000), in the same experiment, found that elevated [CO_2] prolonged the physiological activity of the stem at the end of the growing season, but that stem maintenance respiration was not affected.

Fertilisation effect on woody respiration

Fertilisation increases wood production (Bergh *et al.*, 1999), and can therefore be regarded as a means of fixing carbon in forest biomass in the short or medium term, in order to limit atmospheric [CO_2] increase. Both growth respiration and maintenance respiration could, however, increase with an increase in nitrogen availability. Indeed, if more biomass is produced, growth respiration will increase, and in consequence, maintenance respiration will also increase to supply energy to living cells in the newly formed tissue (Ryan *et al.*, 1996).

Nutrient availability also affects changes in carbon allocation pattern, photosynthesis and growth in response to elevated [CO_2] treatments (*e.g.* Mousseau, 1993; Mousseau *et al.*, 1996). Those effects will feed back to woody respiration. Moreover, nutrient availability could play a part in the response of growth respiration to an increase in [CO_2] concentration, if the nutrient balance in the newly formed tissue were affected. Indeed, Amthor (1989, 1991) suggested that changes in the biomass composition or nutrient sources could change r_G. In ambient atmosphere, Stockfors & Linder (1998) found no effect of nitrogen fertilisation on r_G for *Picea abies*, which indicates that the construction cost for new wood would not be affected by fertilisation alone.

Aims

Beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.) are two of the main hardwood and softwood tree species in Europe (Thomasius, 1992). Thus, the need for improving the modelling of carbon budgets for these tree

species is considerable. Therefore, the main aims of this thesis were (1) to study seasonal and spatial variations in woody respiration in beech and Norway spruce trees, (2) to identify and quantify the causes of those variations, (3) to quantify the effects of those variations when scaling up stem respiration to stand level, and (4) to study the effects of fertilisation and elevated [CO_2] on stem respiration, in order to develop new strategies that could help to limit an atmospheric [CO_2] increase.

Material and Methods

Experimental sites

Studies on beech

Beech (*Fagus sylvatica* L.) was studied in France, at Orsay University (Paper V), near Paris (48°N, 2°E) and at Hesse (Papers I, III and IV), eastern France (48°40'N, 7°04'E, altitude 305 m, area 7 km^2, slope < 2%). Hesse has a mean annual precipitation and a mean annual air temperature of 820 mm and 9.7 °C, respectively. The soil is a gleyic luvisol, according to the F.A.O. classification, and beech is the dominant tree species. In 1997, most of the trees were 25 to 35 years 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. All beech trees showed leaf emergence at the end of April, and the peak leaf-area index (LAI) was 5.6 in 1997.

At Orsay, beech seeds were sown in each of two open-sided chambers (OSCs) of 1.9 m^2 and a soil compartment of 0.9 m^3. Detailed descriptions of the chambers are presented in Epron *et al.* (1996) and Badeck *et al.* (1997). The soil was a mixture of one part sand-clay meadow soil and three parts sand (for further details, see Liozon *et al.*, 2000). After germination, in spring 1995, densities of 150 trees m^{-2} had been established.

Studies on Norway spruce

Woody-tissue respiration of Norway spruce (Papers II and V) was studied at the Flakaliden site in northern Sweden (64°07'N, 19°27'E, altitude 310 m a.s.l.). Mean annual precipitation is 580 mm; one-third of it as snow (Bergh *et al.*, 1999). The mean monthly temperatures vary from –8.7 °C in February to 14.4 °C in July, and the mean annual temperature is 2.3 °C. The growing season lasts about 120 days, and has a mean temperature of 11 °C. The soil is a sandy glacial till, with numerous blocks. Norway spruce (*Picea abies* (L.) Karst.) is the dominant tree species. The trees were planted in 1963 after clear-felling and soil scarification.

Nutrient treatments

At Orsay, solid fertiliser (Osmocote) was applied once to each growth chamber in spring 1995 (Paper V). In 1996 and 1997, varying amounts of nutrient solution, containing all macro-elements in appropriate proportions to N, were applied in step with the growth rate. The saplings were watered every 2–3 days with 12 to 24 litres of tapwater, to avoid a soil-water deficit. For further details, see Liozon *et al.* (2000).

At Flakaliden in 1987, a fertilisation experiment was started, comprising four different treatments and four replicates (Papers II and V): fertilisation with nutrient solution (IL), solid fertilisation (F), irrigation (I) and control (C). On the irrigated plots, water was provided to maintain water availability between field capacity and a maximum water deficit of 10 mm. For the IL treatment, the nutrient solution was injected into the irrigation system and supplied every second day during the growing season (June to August), to maintain an optimal concentration of nutrients in the needles. For further details regarding the experiment, see Linder (1995). In 1999, the control and irrigated treatments had an annual stem volume increment of 5.9 $m^3\ ha^{-1}\ a^{-1}$, while the fertilised treatments produced 16 $m^3\ ha^{-1}\ a^{-1}$ (J. Bergh pers. comm.).

Chamber treatments

At Orsay (Paper V), one chamber was held at ambient [CO_2] (chamber A1) and one at elevated (ambient +350 μmol mol^{-1}) [CO_2] (chamber E1). The chambers were ventilated, naturally illuminated and without temperature control. In 1997, the initial mean heights of the saplings grown in chambers A1 and E1 were 27.2 cm and 36.8 cm. At the end of the season, the final mean heights were 58.2 and 91.6 cm, respectively.

At Flakaliden, twelve whole-tree chambers (WTCs) were installed in March 1997, containing one tree each: six on a C plot and six on an IL plot (Paper V). Three WTCs on each plot were in ambient [CO_2] (CA and ILA), and three were in elevated [CO_2] (CE and ILE). The treatment with elevated [CO_2] commenced in March 1998, *i.e.* before photosynthesis begins at Flakaliden, and operated continuously until the end of the experiment in September 2000. The WTCs were constructed from aluminium frames covered with PVC plastic. The diameter of the chambers was 3.2 m and their height varied with the height of the trees, from 5.5 m to 10.5 m. Each WTC was equipped with an infrared CO_2 analyser (WMA-2, PP-systems, Hitchin, Herts, U.K.), which monitored chamber [CO_2]. As soon as this value fell below the target value (360 μmol mol^{-1} or 700 μmol mol^{-1}), pure CO_2 was injected into the air, which was re-circulated within the WTC. The temperature in the chambers was adjusted to track ambient air temperature, by circulating air over a heat exchanger (12,000 $m^3\ h^{-1}$), cooled by means of circulating glycol. A floor inside the chamber separated the aboveground parts of

the tree from the soil compartment, which means that the WTCs could be used to measure whole-tree gas exchange.

Stem and branch respiration

The main characteristics of the various experiments are summarised in Table 1. On most occasions, stem respiration was measured by means of an open gas exchange system. This consisted of a CO_2 infrared gas analyser (IRGA), a mass-flow meter and solenoid valves, controlled by a data logger, which directed the air passing continuously through permanent cuvettes towards the analyser. Air flows in the system were adjusted to prevent a $[CO_2]$ increase of more than 50 $\mu mol\ mol^{-1}$ inside the cuvettes. Flow meters before and after the cuvettes were used to verify their air-tightness. The cuvettes were in most cases constructed from two half-cylinders, 2.1 cm to 20 cm long, of transparent Acrylic resin or glass. At Flakaliden, however, the mid-stem and breast height cuvettes were half-cylinders of Plexiglas, covering an area of *ca.* 35 cm^2 and 70 cm^2 of the stem, respectively. All cuvettes were sealed to the stem or branch using PVC foam or rubber seal and a putty (Terostat-7, Teroson, Ludwigsburg, Germany), to allow the stems to grow. Before the cuvettes were installed, the stems were brushed to remove needles, loose bark, lichens, and algae from the cuvette area. The respiration cuvettes were covered with aluminium foil to prevent overheating, and photosynthesis by the bark. In large cylindrical cuvettes, a fan was used to mix the air (see Papers I to V for further details).

Table 1. *Principal characteristics of the experiments concerning stem respiration in this thesis*

Site	Species	Year	Treatments	Cuvette locations	Gas exchange systems
Orsay	beech	1997	$[CO_2]$ (ambient and elevated)	base and top	open
Hesse	beech	1997	none	breast height and top	closed and open
Hesse	beech	1998	none	breast height, middle and top	open
Flakaliden	spruce	1999	fertilisation (C and IL)	breast height, middle and top	open
Flakaliden	spruce	2000	fertilisation + $[CO_2]$	breast height	open

Stem, branch or air temperature in the cuvettes was measured by means of thermistors or thermocouples protected from light. When air temperature was measured, it was assumed that there was no time-lag between variations in air temperature and respiration, because of the small diameter of the organs studied. Stem or branch temperatures were measured 2–3 mm under the bark below each cuvette. All data were recorded and stored, with various time steps, by a data logger (for further details, see Papers I to V).

In 1997, stem respiration at Hesse was measured by mean of a closed gas exchange system and temporary clamp-on cuvettes. The respiration measurements were stopped either when the [CO_2] increase had reached 50 µmol mol^{-1} or when the time measurement reached 120 s.

Total stem respiration (R_T) was considered as the sum of maintenance respiration (R_M) and growth respiration (R_G) during the growing season. During the periods preceding growth respiration and after it ceased, R_T could be considered equal to R_M. Growth respiration corresponded to diameter growth, usually with a delay period of 15 to 30 days.

Orsay (Paper V)

In April 1997, three saplings were selected in each growth chamber for measurement of stem respiration. The criterion for selection was that a respiration cuvette could be fixed to the base of the stem, *i.e.* the lowest branch must be at least 6–7 cm above the ground. The saplings used for stem respiration measurements had, at the beginning of 1997, a mean height of 79 cm for saplings in ambient conditions, and 88 cm for saplings in elevated [CO_2]. From April to October 1997, stem respiration was measured daily at the base and at the top of the selected saplings. The respiration cuvettes at the base of the saplings were 4.6 cm long. Those at the top were only 2.1 cm long, because of shorter internodes. Each cuvette was measured for 30 minutes every second hour.

Hesse (Papers I, III and IV)

In 1997, stem respiration was essentially measured at two positions: at breast height and in the crown. Stem in the upper part of the crown was regarded as branches and *vice versa*, since in beech it is often difficult to distinguish branches from stem.

Stem respiration at breast height

Measurements were conducted on 15 different trees each month, except January 1998, from March 1997 to February 1998. The 15 trees were pooled into five classes of diameter at breast height (DBH), which corresponded to internal chamber diameters of 40, 75, 100, 110 and 135 mm. Sample trees covered the range of diameter and social status present on the site. The three smallest trees (belonging to the 40 mm class) were 9 m tall. The height of the other trees ranged from 12 m to 15 m. The trees of the two smallest DBH classes were suppressed, whereas the others were co-dominant or dominant. The measurements were performed monthly during 2–3 days. Three measurements were recorded every second hour from predawn to sunset. When replicates differed by more than 10%, additional replicates were taken. Respiration was monitored throughout a 24-hour period in July, to assess the change in respiration with temperature during day and night.

Respiration in the crown

Respiration in the crown was measured on one tree, with a diameter at 1.30 m of 100 mm, and a height of 15.5 m, respectively. Measurements were made using permanent glass chambers sealed to the stem at 0.25, 1.5 and 2.5 m from the top of the crown. These positions corresponded to the branch diameters 2.5, 12.9, and 23.6 mm. From May to November 1997, the three chambers were automatically recorded every 90 min.

In April 1998, four dominant or co-dominant trees, already equipped with Granier sapflow sensors and automatic band-dendrometers, were selected among the beech trees. Two 20-cm long cylinder cuvettes were installed on each tree: one at breast height (diameter ranged from 108 to 143 mm) and one at mid-stem (diameters ranging from 52 to 70 mm). This position usually corresponded to the base of the crown. [CO_2] evolution in all cuvettes was measured in sequence every 90 minutes by means of an automatic, open gas-exchange system, until November 1998. After growth had ceased (DOY 245), stem respiration was also measured 0.8 m from the top of the trees. The diameter of the stems ranged from 5.3 to 16.8 mm. Stem temperature had been measured since April at the three levels in the tree.

Flakaliden

The 1999 experiment (Paper II)

During the summer of 1998, an automatic system was installed at Flakaliden to measure stem respiration on eight trees; four on a C plot and four on an IL plot. Stem respiration was measured continuously, between January and December 1999, on five trees: one tree in each treatment was measured continuously, and three trees in each treatment were measured for seven days every second week. Respiration was measured at three different levels along the stem: at breast height, in the middle of the stem and at the top of the stem. The diameter of the stem where the middle cuvette was installed was the average between the stem diameter of the upper and lower levels. The upper cuvette was installed on a current or one-year-old shoot. The time interval between two measurements on the same cuvette was two hours. From June to October 1999, six cylindrical cuvettes were also installed at three levels, on the branches close to the stem respiration cuvettes in one of the four trees from the C plot.

In October 1999, two trees from the C plot were harvested to measure stem (10 and 13 samples) and branch respiration (20 samples each, 14 first-order and 6 second-order branches) on detached samples in the laboratory, C and N content in the wood, and percentage of living cells (see below). The segments of stem and branches were approximately 20 cm long. Needles, loose bark, lichens and algae were removed from the surface of the segments, and their length, diameter at both ends, fresh mass, age and position on the tree were recorded. The stem and branch segments included those that had been enclosed in the permanent cuvettes during the season of 1999. The cut ends of the samples were covered with

beeswax to prevent CO_2 leakage from the sections, and the segment was placed at 10 °C for 1–3 h, depending on the diameter of the segment. After acclimation, the sample was placed in a Plexiglas cuvette immersed in a water bath at 10 °C. A fan mixed the air in one of the two cuvettes used for the larger samples. Stem respiration was measured in a closed system with an IRGA (LI-6200, Li-COR, Inc., Nebraska, U.S.A.). Before each measurement, fresh ambient air (350–400 μmol mol^{-1}) was flushed into the cuvette. The respiration rate of each segment was calculated on a volume basis.

At the beginning of the experiment at Flakaliden, stem diameters on the control plot ranged from 73 to 86 mm at breast height, 47 to 49 mm in the middle, and 11.2 to 15.7 mm at the top of the trees. For the IL plot, the stem diameter ranged from 111 to 126 mm at breast height, 64 to 71.5 mm in the middle, and 11.8 to 22.9 mm at the top of the trees. The average height of the trees on the C and IL plot was 510 and 728 cm in the end of 1998 and 530 and 754 cm in the end of 1999, respectively.

The 2000 experiment (Paper V)

During the summer of 2000, stem respiration was measured at breast height on twelve Norway spruce trees enclosed in the whole-tree chambers. The stem respiration measurements were made continuously between mid-June and the end of August on the C plot, and from the beginning of July to the end of August on the IL plot. The measurements were made on the north-facing side of the stem, by means of half-cylinder cuvettes, and an open gas exchange system operating in differential mode (for further details, see Wallin *et al.* 2001). The time interval between measurements on each cuvette was 30 minutes. Stem temperature measurements were recorded every 45 minutes by a SIOX module (S12, Telefrang AB, Göteborg, Sweden) and stored on a computer. During two short periods in August, two trees on each plot (one at ambient and one at elevated [CO_2]) were placed at normal temperature +10 °C. During those periods, the measurements from those chambers were disregarded.

Diameter increments

On organs less than 25 mm in diameter (branches and higher levels on the stem), diameters immediately above and below the cuvettes were recorded weekly (Orsay and stems at Flakaliden) or monthly (Hesse and branches at Flakaliden), as the mean of two measurements at 90° to each other, made with a digital calliper (resolution 0.01 mm). At Hesse in 1997 (Paper III), DBH was measured monthly by means of a diameter tape immediately above and below the cuvettes. In 1998 at Hesse and for both years at Flakaliden, automatic band-dendrometers (Megatron MM30, Allinges, F- 4200, France at Hesse and ELPA-93, University of Oulu, Finland at Flakaliden) were installed at the base and in the middle of each tree just above the cuvette. Diameter increments were measured every third

minute and averaged over 30-minute intervals. Calculations of respiration, on a stem volume or surface-area basis, were corrected for stem diameter increment.

Data analysis

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

$$R = R_{TREF} * Q_{10}^{((T-T_{REF})/10)} \quad (1)$$

where R is stem respiration measured, (μmol CO_2 m^{-3} stem s^{-1} or in μmol CO_2 m^{-2} stem s^{-1}), R_{TREF} is stem respiration normalised to a reference temperature (15 °C for beech or 10 °C for Norway spruce), Q_{10} is the relative increase in R for a temperature increase of 10 °C, T is air or stem temperature in the cuvette at the moment of measurement, and *TREF* is the reference temperature, °C.

Statistical analyses were conducted with the Statistical Analysis System version 6.12 statistical package (SAS). A non-linear model procedure, PROC NLIN, was used to estimate the parameters (R_{15}, R_{10} and Q_{10}) of the exponential equation. R_{15}, R_{10} and Q_{10} were fitted daily, or on a three-, five-, or even seven-day basis, to the temperature variations for each cuvette (see Papers I to V for details).

Estimate of the components of stem respiration

Two methods were used to estimate the contributions of growth and maintenance respiration to total respiration (Papers I, II, III and V).

Method 1

The mature-tissue method (Amthor, 1989) 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, normalised to a temperature of 10 °C or 15 °C (R_{M10} or R_{M15}) was calculated for each cuvette from measurements made before and after the growing season. R_M was recalculated throughout the season by means of 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 entire year. The slope of the relationship between R_G integrated over the year, and total stem growth in the cuvette, is the wood construction cost (r_G).

Method 2

The periodic-growth method, whereby R_G was estimated daily by subtracting estimated R_M for each cuvette from R_T. To eliminate diurnal variations in stem growth rate, caused by water losses and water recharge in the stem, a running mean over one week (3 days before and 3 days after the day of measurement) was used to recalculate stem growth rate and R_G. The slope of the relationship between R_G and stem growth rate (corrected for time-lag) gave an estimate of r_G (Amthor, 1989; Sprugel & Benecke, 1991). 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, appropriate wood basic density and carbon-content values were used (see Papers I, II, III and V).

Analysis of living cells

Since samples could not be taken on the trees used for respiration measurements at Hesse (Paper I), five trees having DBH similar to those used for respiration measurements were chosen outside the experimental area (less than 50 m from the measured trees). In September, after growth had ceased and before leaf fall, two increment cores (5 mm in diameter) were taken at breast height from the five trees. The first core, used for [N] analysis, was 50 mm long and the second core was equal to half the DBH of the stem. The sample was frozen in dry ice and sectioned in the xylem in the laboratory at 3 to 8 depths (usually 1, 5, 10, 20, 30, 40, 50 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, stained with a Comassie blue solution, rinsed and mounted on slides in Canada balsam (see Stockfors (1997) for further details). 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. 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 in the periderm 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, Texas, U.S.A.). Since the branches were sampled in the upper part of the crown, they were regarded as stems.

At Flakaliden, 2–3 cm thick disks from stem and branches were sampled on the two trees harvested in October 1999 for maintenance respiration measurements. Only a sub-sample of five stem samples instead of the 13 used for stem

respiration measurements was analysed on one of the two trees, because the method was very time-consuming. Transverse sections were made in the frozen stem and branches, and living cells were stained as described above. The percentages of living cells in the periderm and xylem were determined, as well as their respective thickness. The percentage of living cells was then integrated over the whole section.

Wood analysis

For the beech saplings at Orsay (Paper V), the samples were taken inside the respiration cuvettes. Those samples were separated into two sub-samples; the first was used for mineral nutrient analysis and the second for wood basic density analysis. Some extra samples were taken for mineral nutrient analysis from an ambient (A2) and elevated (E2) chamber (for further details see Liozon *et al.*, 2000). For the Norway spruce trees, 2–3 cm thick disks were sampled directly above or in the cuvettes. In 1999 (Paper II), the disks were sampled on the stem and branches of the two control trees harvested in October for respiration measurements. In 2000 (Paper V), the disks were sampled at breast height only, and the annual rings corresponding to the period 1996-2000 were analysed.

The stem and branch samples were weighed before and after being dried at 70 °C during two days, thereafter ground for [C] and [N] analysis. Mineral nutrients were analysed by means of an elemental combustion analyser (Carlo Erba, NA 1500, Carlo Erba Strumentazione, Milan, Italy), using a modified version of the method described by Kirsten & Hesselius (1983).

Sapflow measurements

To study the effects of sapflow on the measured rates of stem respiration, sapflow sensors (Granier, 1985) were installed at Hesse in 1998 on the trees used for stem respiration measurements, and at Flakaliden in 1999. At Hesse, the sapflow effect was studied between days 187 and 225. At Flakaliden, the sapflow sensors were installed approximately 30 cm below the cuvettes, under the living crown. The relationship between sapflow and stem respiration was studied during two weeks in September 1999.

Respiration at 15 °C and Q_{10} were estimated daily using the non-linear procedure in SAS and equation (1), after correction for the time-lag between respiration and temperature. The difference between a respiration measurement and the corresponding estimated respiration calculated from equation (1) and stem temperature (time-lag corrected), was the residual. These residuals were then plotted against sapflow, to analyse the effect of sapflow on the residual distribution.

Internal CO_2 concentration in the stem

The $[CO_2]$ in the stem of Norway spruce was measured by a technique similar to the one described by Levy *et al.* (1999). In September 1999, one cuvette was installed on each of the four trees on the IL plot. These cuvettes were identical to those used for stem respiration measurements, except that there was no airflow through them. They were installed 5–50 cm below the stem respiration cuvettes. A tap, which could be opened to remove air samples with a syringe, was fitted on one of the two outlets of the cuvette. A balloon fitted on the second outlet formed an impermeable lung outside the chamber, that allowed atmospheric pressure to be maintained in the cuvette even after several samples had been taken. The cuvettes were carefully sealed on the surface of the stem, and kept until the partial pressure of CO_2 (pCO_2) inside the cuvette had stabilised. They were shaded with aluminium foil to prevent bark refixation of CO_2.

During the first week, samples (2.5 to 5 cm^3) were taken once a day at about 17:00h, and a final sample was taken after 11 days. The samples were injected into an IRGA (ADC-225-MK3, ADC, Hoddesdon, U.K.) operating in close mode. A balloon fitted to the tube, close to the sample injection point, formed an impermeable lung that allowed atmospheric pressure to be maintained in the system. Before each measurement, ambient air was flushed through the system. The exact volume of the system was determined by adding 5 cm^3 of a $[CO_2]$ calibrated gas to the system. After a stabilisation period, 5 cm^3 of the new $[CO_2]$ gas was removed. The initial volume of the system was calculated as:

$$V_{system} = \left[\frac{\left(pCO_{2(sample)} - pCO_{2(initial)} \right) V_{sample}}{\Delta pCO_2} \right] - V_{sample} \qquad (2)$$

where V_{SYSTEM} is the volume of the closed system, V_{SAMPLE} the volume of the sample injected in the system (cm^3), $pCO_{2(SAMPLE)}$ and $pCO_{2(INITIAL)}$ the pCO_2 of the sample gas and of the initial gas in the closed system, and ΔpCO_2 is the difference in pCO_2 in the closed system before and after injection of the gas sample.

Scaling up stem respiration to an annual and stand level

Hesse (Paper III)

Allometric relationships

For trunks, a sample of 23 trees, representing the population of trees in the experimental stand at Hesse, were felled in the vicinity of the experimental stand and measured for dimensional and biomass data. Each stem, including all fork arms, was cut into logs shorter than 1.2 m, and the basal diameter of each primary branch was measured. To estimate the total volume and surface area under the

bark of the stem, a 10 cm long stem sample was cut at the base of each log and processed at the laboratory.

For branches, three trees with different crown status (two co-dominant and one suppressed) were selected, to establish relationships between the total area and volume of various branch fractions and the basal diameter of the first-order branches. On the basis of observed branch diameter distributions, and considering the branch diameters used for respiration measurements, it was decided to distinguish the following classes (branch fractions) of cross-sectional diameter (d) for the branches: $d \leq 5$ mm, 5 mm $< d \leq 20$ mm, $d > 20$ mm (for further details, see Paper III).

The allometric relationships obtained at organ level (trunk and branch) were used to estimate volume and area at an individual level by means of the inventory of branches, and at stand level by means of tree density and tree diameter at 1.3 m, for all trees on the site. The allometric relationships used in Paper IV to describe stem and branch biomass were much simpler, since they were derived from DBH only and branches were not separated into several diameter classes.

Scaling stem respiration to an annual and stand level

Total stem respiration throughout the year was estimated by using monthly-derived Q_{10} and R_{15} values, half-hourly air temperature data, and areas or volumes concerning four compartments: stems and the three diameter-classes of branch. For the stems, Q_{10} and R_{15}, obtained by averaging the values for each trunk diameter class, were used. Since no measurements were made in January, monthly Q_{10} and R_{15} derived from averaged December and February values, were used.

For the crown, Q_{10} and R_{15} values, derived from the three chambers installed in the crown, were used. Results from chambers corresponding to the smallest diameter (diameter ≤ 2.5 mm) were applied to the thin branch category ($d \leq 5$ mm). For larger branches, results from the chambers corresponding to diameters of 12.5 and 25 mm, respectively, were applied to branch classes of $5 < d \leq 20$ mm and > 20 mm. For December, January and February, Q_{10} and R_{15} values, derived from the averaged values over September, October and November, were used. All calculations were made on a volume or a surface area basis.

In 1997, the estimated wood construction cost was less accurate than that in 1998, since stem respiration was not recorded continuously. Therefore, annual growth respiration values calculated in Paper III were estimated by using the construction cost calculated in 1998. Carbon-use efficiency (CUE)—the ratio of C fixed in the new wood / (C fixed in the new wood + C respired)—was calculated for Hesse in 1997, for an annual stem wood production of 12.0 $m^3\ ha^{-1}\ a^{-1}$ (Le Goff, pers. comm.).

Flakaliden

Respiration of stems and branches in 1999, was calculated for the C and IL plots, for average trees for each plot and stand densities of 2560 and 2330 trees ha^{-1}, respectively. Average heights and DBH were 670 (C) and 890 (IL) cm and 84 (C) and 134 (IL) mm, respectively (J. Bergh pers comm.). Allometric relationships (J.G.K. Flower-Ellis pers. comm) were used to describe the changes in diameter along the stem as a function of total tree height (Equation 3 and 4 for C and IL trees, respectively).

$$D = 105.9 - (96.7 * \frac{H}{H_{TOT}}) \qquad (3)$$

and

$$D = 155.1 - (149.9 * \frac{H}{H_{TOT}}) \qquad (4)$$

where D is stem diameter in mm at height H, cm, and H_{TOT} the total height of the tree.

Maintenance respiration was integrated along the stem using the relationships described by Equations 3 or 4 and the relationship between maintenance respiration at 10 °C and stem diameter (Paper II). Live-branch dry mass of first- and second-order branches was calculated from a live-branch to stem mass quotient (0.33 for both the C and IL plots) and a first- to second-order mass quotient (2.25 for both the C and IL plots) derived from trees harvested at Flakaliden in 1997 (J.G.K. Flower-Ellis pers. comm). Different average maintenance respiration rates at 10 °C (Paper II) were used for first- and second-order branches. The respiration rate per unit volume of branches was converted to respiration per unit biomass, after measuring branch-wood density (branch-wood basic density, 587 kg m^{-3}, R_{M10}, 0.079 and 0.142 μmol kg^{-1} DM s^{-1} for first- and second-order branches, respectively). An average Q_{10} of 2.25 for branches, and 2.08 (C) and 2.03 (IL) for the stems, was used in combination with measured temperature data (frequency 10 minutes), to calculate the annual maintenance respiration of the mean C and IL trees.

Annual growth respiration was estimated for stems from the wood construction cost obtained for the C and IL trees (Paper II; r_G was 0.16 and 0.18, respectively), and annual stem-wood production in 1999 of 5.9 (C) and 16 (IL) m^3 ha^{-1} a^{-1} (J. Bergh pers comm.). The annual wood production of branches was estimated from the branch-to-stem mass ratio and from annual increment in stem biomass.

Simulating the impact of global change on woody respiration

To simulate the effects of global warming on stem and branch respiration, two different climate scenarios were used for Hesse and Flakaliden (see Table 2). For Hesse, the Hadley Centre model scenario (Rummukainen *et al.* 2001, 1% pa

increase in $[CO_2]$, with sulphate aerosols taken into account) was used for the period 2070–2100, which would correspond to an atmospheric $[CO_2]$ of 700 μmol mol^{-1}. At Flakaliden, a SWECLIM (1998) scenario, corresponding to an atmospheric $[CO_2]$ of 700 μmol mol^{-1}, was used. In combination with global warming, the effect of an increase in atmospheric $[CO_2]$ was tested for Flakaliden but not for Hesse, because atmospheric $[CO_2]$ had no effect on maintenance respiration, and because the effects on growth respiration were uncertain.

Table 2. *Increases in monthly mean temperatures compared to the actual values at Hesse and Flakaliden using, respectively, the Hadley Centre model for the period 2070–2100 and the SWECLIM model for the year 2100, corresponding to an atmospheric $[CO_2]$ of 700 μmol mol^{-1}.*

Month	Hesse	Flakaliden
January	3.57	5.3
February	3.91	4.7
March	2.78	3.8
April	2.04	3.2
May	2.24	3.1
June	1.76	2.9
July	3.26	2.8
August	4.07	2.8
September	3.91	3.5
October	2.72	4.5
November	3.4	5.1
December	3.44	5.6

Statistical analysis

Statistical analyses were conducted with versions 6.10 and 6.12 of the Statistical Analysis System (SAS, 1994, 1996). In Paper III, the effect of trunk size was tested by analysis of variance (ANOVA) using the General Linear Models procedure. Means were compared with Tukey tests, and considered as significantly different when $P < 0.05$. The GLM procedure was used to test the differences in slopes and intercepts between treatments, and for the relationships between growth and growth respiration (Papers I, II and V).

Results and Discussion

Temperature and woody respiration

Temperature gradients within stands

Stem temperature, both at Hesse and Flakaliden, and its range of variation, generally increased with height along the stem (Papers I and II). At Hesse, the

maximum difference in temperature recorded 2 mm under the bark was 15.7 °C between breast height and the top of the stem in January 1998. At Flakaliden, gradients in temperature were up to 12 °C between the top of the stem and the breast height locations. On a monthly time-base, however, differences in temperature between those two locations were much smaller, but almost always positive (between –0.2 °C and 1.5 °C at Hesse and 0 °C to 1.9 °C at Flakaliden).

Stem temperature also varied within the stem. At breast height, differences up to 5 °C were measured between the core and 2 mm beneath the bark of a 11.5 cm diameter beech stem (Paper III). Derby & Gates (1966) found temperature gradients at breast height of up to 12 °C within the stem of a *Populus tremuloides* tree, and Stockfors (2000) found temperature differences up to 21.5 °C within the entire stem of Norway spruce trees at Flakaliden. Edwards & Hanson (1996) showed that north-facing sapwood temperature is usually lower than the mean stem temperature. Therefore, mean stem temperature and temperature gradients along the stem were probably underestimated, since all our measurements were made on the north-facing side of the stem. For the branches, differences in temperature usually ranged between 0 and 8 °C, and branches exposed to sunlight usually had higher temperatures (Paper II).

Gradients in temperature could explain up to 68.5% and 45% of spatial variation in stem respiration for beech at Hesse in 1998 and Norway spruce at Flakaliden in 1999, during the non-growing season. Stockfors (2000) showed that failure to consider temperature differences within the stem could produce errors representing about 58% of total annual stem respiration in a young Norway spruce stand.

Respiration response to temperature changes

Delay in respiration response to changes in temperature

Stem respiration usually increased exponentially with temperature, even if breast-height measurement at Hesse showed hysteresis between stem respiration and stem temperature changes in beech (see Paper III). Such hysteresis was also observed by Lavigne *et al.* (1996). The hysteresis was cancelled or greatly reduced when a time-lag for respiration to variations in temperature was considered. The magnitude of this time-lag depended on stem diameter (Paper III), and varied inconsistently throughout the season, from 0 to 12 hours (Paper I). The introduction of a time-lag correction into the calculations clearly increased the estimated Q_{10}. For one of the cuvettes installed at breast height in 1998, the lag correction changed the Q_{10} value from 1.24 to 1.5 (Paper I).

For Norway spruce, the hysteresis was much smaller than for beech, and the introduction of a time-lag correction into the calculation had a negligible effect or no effect on Q_{10} (Paper II). Stockfors & Linder (1998), for Norway spruce, found a seasonal trend in the time-lag between respiration and stem temperature changes; this time-lag varied between *ca.* 10 and 130 minutes. The time-lag could

be caused by a delay in warming-up the internal parts of the stem, compared to the superficial parts. Indeed, the efflux of CO_2 measured at the surface of the stem is the result of the integration of several tissues which have different temperatures and which respire at different rates. The larger the diameter, the longer it will take to reach an homogeneous temperature. Consequently, the time-lag between changes in temperature and changes in respiration, increases with the diameter of the stem (Lavigne *et al.*, 1996; Bosc 1999). Negisi (1979) and Martin *et al.* (1994) also suggested that the midday depression in respiration rates, at the origin of the hysteresis, could be caused by CO_2 transport in the sapflow.

Since the time-lag varied inconsistently and could not be predicted for beech, and because a time-lag correction had very little effect for Norway spruce, the measurements were not corrected for time-lag in the present study. Consequently, Q_{10} values for beech at breast height (mean Q_{10} = 1.33 in Paper I and 1.8 in Paper III), were low compared with some other values in the literature. Lavigne & Ryan (1997) found Q_{10} values between 1.0 and 1.7 for old *Populus tremuloides* trees. In the same study, they found values between 1.5 and 1.8 in *Pinus banksiana* and *Picea mariana* trees. Other studies report Q_{10} values of 1.2 to 3 for *Pinus banksiana* (Lavigne, 1996), 1.5 to 3.2 for *Chamaecyparis obtusa* (Paembonan *et al.*, 1991) and 1.9 to 2.6 for *Picea abies* (Stockfors & Linder, 1998). The values of 1.89 to 2.00 and 1.67 to 1.90 at breast height for Norway spruce on the C and IL plots (Papers II and V), respectively, were consistent with other Q_{10} values found in the literature.

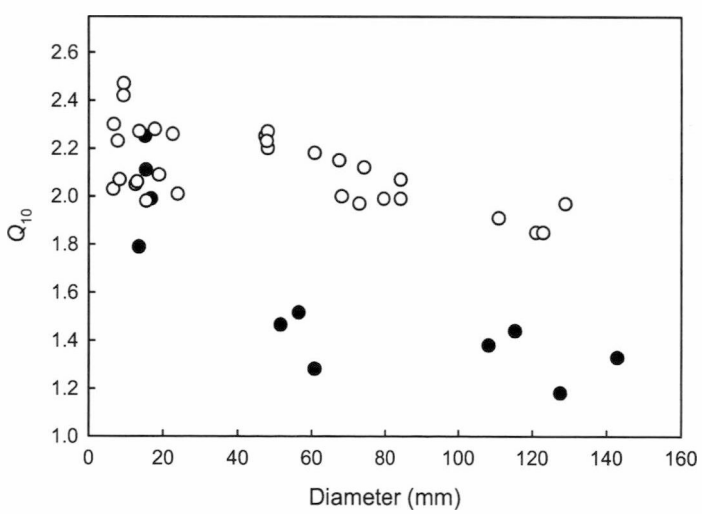


Figure 1. Variation in Q_{10} with stem or branch diameter for beech trees (●) at Hesse in 1998 and Norway spruce trees (o) at Flakaliden in 1999. For further details, see text.

Q_{10} spatial and seasonal variations

Q_{10} varied within the trees, from 1.18 (Paper I) and 1.67 (Paper V) at breast height to 2.25 (Paper I) and 2.38 (Paper II) in the crown of beech and Norway spruce, respectively. For beech, Q_{10} clearly increased with height or decreased with increasing diameter. But for Norway spruce, the relation between diameter or height and Q_{10} was not as clear (Figure 1). Maier *et al.* (1998) found differences in Q_{10} between branches and stems. The response of respiration to changes in temperature was often faster for smaller-diameter organs, because they have less temperature inertia. The thicker bark and periderm could also slow down the diffusion of CO_2 through the stem, and partly be responsible for this observation (Eklund & Lavigne, 1995).

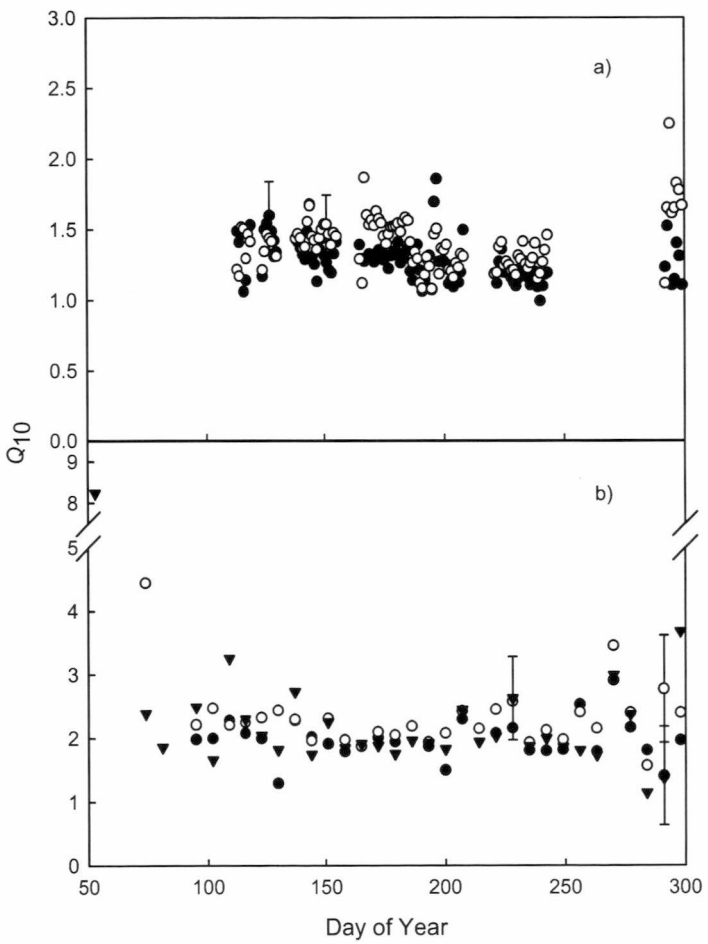


Figure 2. Seasonal variation in (a) averaged Q_{10} of dominant or co-dominant 25-year-old beech trees at Hesse in 1998, at breast height (●, three to four cuvettes per point) and at mid-stem (o, three cuvettes per point). (b) in averaged Q_{10} on four 40-year-old Norway spruce trees at Flakaliden in 1999 on the C plot at breast height (●), mid stem (o) and at the top of the stem (▼). The error bars represent the maximum standard errors for each location. For further details, see text.

For beech, no clear seasonal trend in Q_{10} variation was observed (Figure 2a), and for Norway spruce, Q_{10} was quite stable around 2.0 throughout the growing season (Figure 2b). However, during very cold periods before and after the growing season, Q_{10} values for Norway spruce could exceed 20, especially when temperatures were becoming positive after a long freezing period. Those rapid increases in respiration with temperature could be associated with frost damage recovery, or with the freezing and thawing of water in the stem (Linder & Troeng, 1980). Stockfors & Linder (1998) for *Picea abies* and Paembonan *et al.* (1991) for *Chamaecyparis obtusa*, observed a clear seasonal variation of Q_{10}, with higher respiration rates during the winter for *Picea abies*. However, Linder & Troeng (1980, 1981) did not find such variation in *Pinus sylvestris*. In contrast to some other studies (Lloyd & Taylor, 1994; Tjoelker *et al.*, 2001), no Q_{10} temperature-dependence was found for beech (Paper I) or Norway spruce when only frost-free periods were considered. These results indicate that an acclimation of Q_{10} to global warming is unlikely to happen for woody tissue of beech and Norway spruce.

Seasonal and spatial variations in respiration rates

Seasonal variations

Higher respiration rates occurred in the middle of the growing seasons, corresponding to higher temperatures and higher dates of stem diameter increment (Figures 3 and 4). At Flakaliden, 90% of the annual respiration occurred between April and May, and 50% in June-July (see Paper II). Stem respiration, even normalised to 10 °C or 15 °C (R_{15} at Hesse and R_{10} at Flakaliden), varied very rapidly, and continuous measurements were needed to match changes in diameter increment and variations in respiration rate (Papers I, II and V). The variation in respiration rates, however, was not synchronised with stem diameter increment, and the time-lag between them varied throughout the season from –4 to 30 days for beech (Paper I & V) and from 10 to 30 days for Norway spruce (Papers II and V). Stockfors & Linder (1998) observed a similar time-lag for Norway spruce, probably caused by the delay between diameter increase, and the increase in dry matter following secondary and tertiary wall thickening and lignification (Žumer, 1969).

Surprisingly, respiration in mid-stem and at the base was not synchronised for beech and for spruce on the C plot (Figure 3a), whereas growth was (Figure 3b). The lag between growth and respiration was larger at the stem base in beech, perhaps because more wall thickening is needed there to support the structure of the tree. A second hypothesis is that assimilates from the leaves and the crown, initially were allocated to nearby woody organs for wall-thickening; after those sinks had been filled, the assimilates were used for wall-thickening in lower positions. This hypothesis, however, did not fit well for Norway spruce on the C plot, since the peak in respiration in the middle of the tree occurred after the peak for the higher and lower locations (Figure 4).

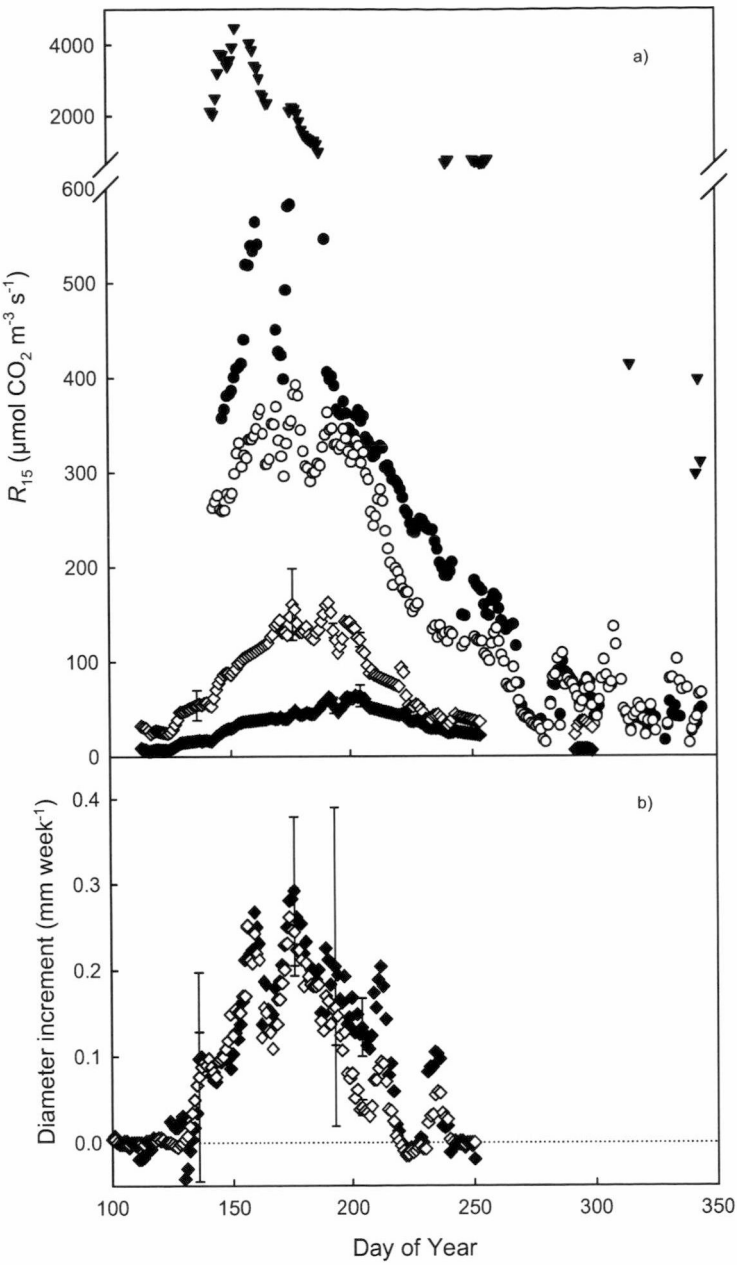


Figure 3. Seasonal and spatial variation in (a) stem respiration normalised to 15 °C (R_{15}) and calculated on a volume basis at breast height (◆, three to four cuvettes per point) and in the middle of the stem (◇, three cuvettes per point) in 1998 and at the base (●), middle (o) and top (▼) of the crown in 1997 of dominant 25-year-old beech trees at Hesse, (b) averaged stem diameter increment at breast height (◆) and mid-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. (Day 100 = April 10, Day 250 = September 7). For further details, see text.

Spatial variation in respiration rates

After the effects of temperature gradients on respiration were removed by estimating respiration rates at a constant reference temperature, strong differences in respiration rates remained within the trees (Figures 3a, 4a and 4b). When respiration rates were calculated on a volume basis, R_{15} and R_{10} generally increased with height on the stem or decreased with increasing stem diameter. The maximum factors of variation in R_{15} and R_{10}, between cuvettes installed at breast height and at the top of the stem, were 68, 72 and 90 at Hesse in 1998 and for the C and IL plots at Flakaliden, respectively. Branch respiration rates on the C plot at Flakaliden were highest, on average, for the middle branches, while the lower branches had the lowest respiration rates throughout the season. The difference in respiration rates between individual branches reached 9-fold during the growing season. Other studies have shown strong variation in respiration rates within trees (Möller *et al.*, 1954; Yoda *et al.*, 1965; Sprugel, 1990; Ryan *et al.*, 1996; Maier *et al.*, 1998). Respiration rates in the crown of beech trees were higher than those in a study performed by Möller *et al.* (1954) on beech trees. However, Yoda *et al.* (1965) found maintenance respiration rates of broadleaved trees similar to those in the present study. Respiration rates in the crown of Norway spruce were consistent with those reported by Maier *et al.* (1998) and Sprugel (1990).

The differences in R_{15} or R_{10} between the different levels along the stem or within the crown were smaller on a surface-area base than on a volume base. For beech, there was no consistent respiration pattern within the crown, since the respiration rate did not necessarily increase with height or decrease with diameter (see Papers I and III). At Flakaliden, the factors of variation in respiration rates along the stem were up to 2.7 and 2.1 on the C and IL plots, respectively (Paper II). The respiration rate increased, in most cases, with height or decreased with increasing diameter along the stem. For trees grown on the C plot, the peak respiration rates were 1.13, 2.65, and 2.93 μmol m^{-2} s^{-1} at the base, middle and top of the stem, respectively (see Paper II for further details). Our measurements in the crown of spruce, were similar to those reported for conifers by Ryan *et al.* (1996).

The effect of relative diameter increment

Diameter increment partly explained the spatial variation in respiration rates during the growing season (Papers I and II). At Hesse in 1998, diameter increments were on average 3.9 mm within the lower cuvettes, 4.9 mm in the middle cuvettes, and 4.4 mm at the top of the tree. This corresponded to an annual relative diameter growth of 3.1, 8.1, and 33.5%, respectively. At Flakaliden in 1999, the relative diameter increment along the stem ranged from 3.3% at breast height, to 59.3% at the top of the tree. For Norway spruce branches, relative diameter increment ranged from 3.2% to 16.2% from the base to the top of the crown.

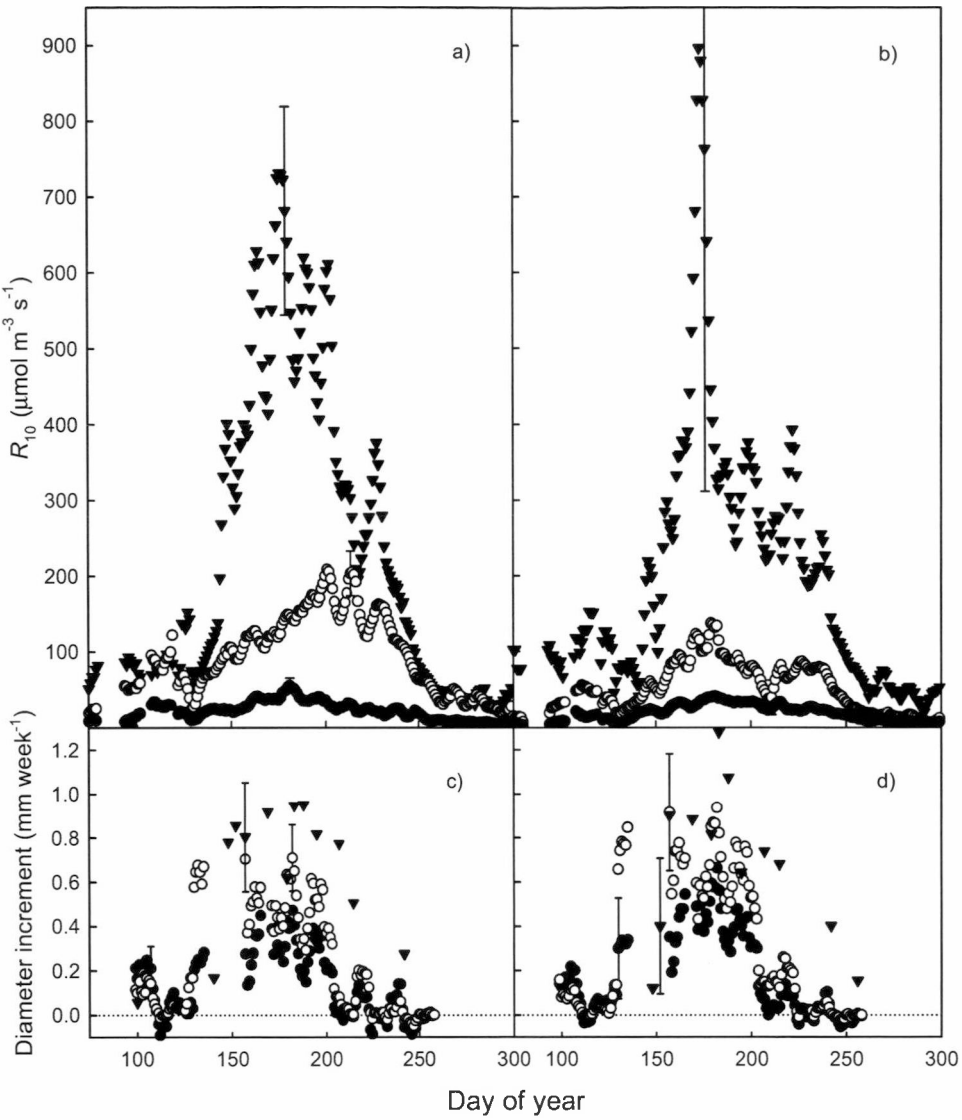


Figure 4. Seasonal and spatial variation in stem respiration normalised to 10 °C (R_{10}) and calculated on a wood volume basis for three positions along the stem of four 36-year-old Norway spruce trees at Flakaliden in 1999 on a C plot (a) and on a IL plot. (b) top of the stem (▼), middle of the stem (o) and breast height (●). Averaged diameter increment for the same three stem locations on the C plot (c) and IL plot (d). Four cuvettes per point. The error bars represent the maximum standard errors of the mean for the 1999 measurements.

Spatial variation in maintenance respiration

Even after growth had ceased, spatial variation in stem respiration rates remained. On a volume basis, R_{M15} and R_{M10} varied from 5.1 to 2008 µmol m^{-3} s^{-1} (Papers I, III, IV & V) and from 4.9 to 223 µmol m^{-3} s^{-1} (Papers II & V) for beech and Norway spruce, respectively. Higher R_M values were found for the upper parts of

the stem, and R_M decreased strongly with stem diameter for both beech and Norway spruce (Figure 5). Since larger stem diameters usually corresponded to older stems, our observations are in agreement with Carey *et al.* (1997), who showed that R_M decreased with DBH and age. On a surface-area base, there was less consistency in the variation of R_{M15} and R_{M10} along the stem than there was on a volume base for beech (Papers I & III) and Norway spruce (Papers II).

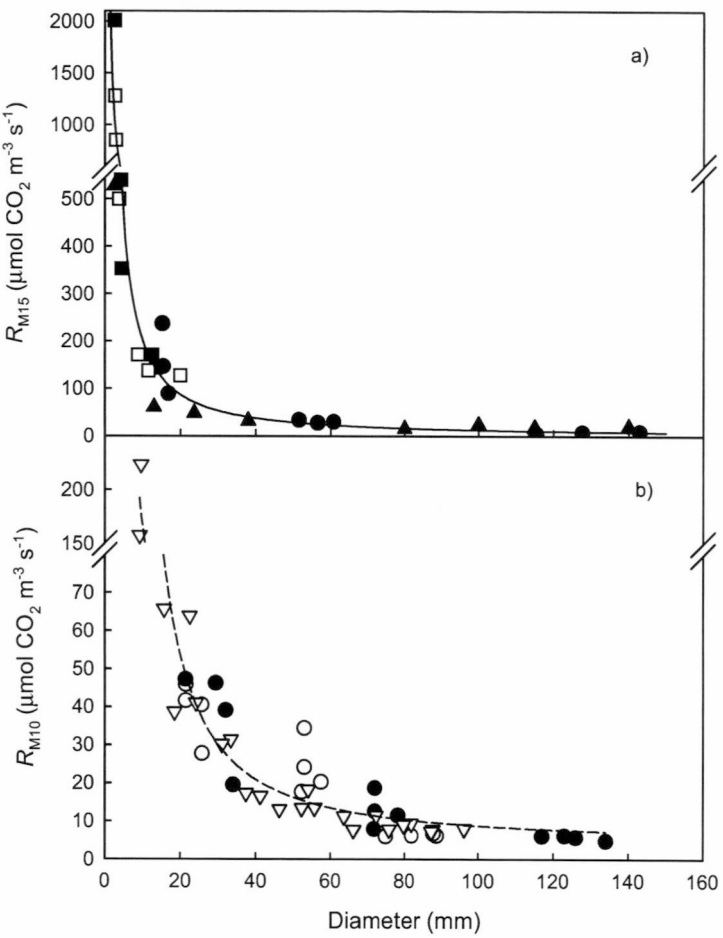


Figure 5. Spatial variation in annual mean of maintenance respiration calculated on a volume base normalised to 15 °C (R_{M15}) for beech (a) and normalised to 10 °C (R_{M10}) for Norway spruce, (b) as a function of stem diameter: (a) at Orsay in 1997 on ambient (■) and elevated trees (□), at Hesse in 1997 (▲) and 1998 (●), (b) at Flakaliden in 1999 on the stem of standing trees from the C plot (○) and IL plot (●), on sectioned stem samples measured in the laboratory for two C plot trees (▽). One cuvette per point. The solid line represents the regression including all the points for beech ($Y = 2810 / (X + 0.0075)$, $r^2 = 0.71$) and the dashed line represents the regression including all the stem cuvettes for Norway spruce ($Y = 3.81 + 363.9 / X + 12686 / X^2$, $r^2 = 0.92$).

For Norway spruce, branch maintenance respiration was poorly related to branch diameter (Figure 6). First-order branches respired less than second-order branches (46.6 µmol m^{-3} s^{-1}, *SE* = 3.9 and 83.3 µmol m^{-3} s^{-1}, *SE* = 11.4, respectively) but the difference was not significant ($P = 0.14$). Considering age and diameter together would explain almost 50% of variability in branch respiration:

$$R_{M10} = \left(\frac{11916}{D + 0.858 * A + 38.5} \right) - 1 \qquad r^2 = 0.49 \qquad (5)$$

where D is branch diameter in mm and A is the age of the organ in years.

Bosc (1999) found that a combined effect of age and tissue vitality explained the differences in maintenance respiration rates within the tree. Yoda *et al.* (1965) also showed that large branches (more than 10 mm in diameter) respire less than the main stem, when a similar diameter of those organs is considered. They suggested that the age of the organs was a factor of variation in respiration rates.

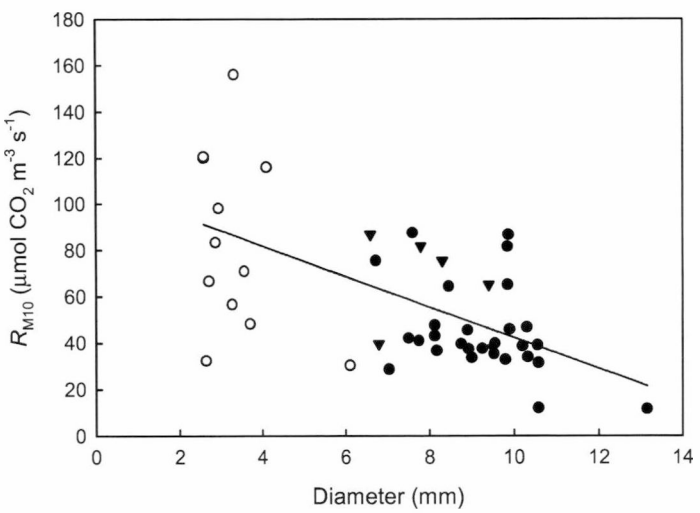


Figure 6. Effect of branch diameter and order on branch maintenance respiration (R_{M10}) for Norway spruce trees at Flakaliden in 1999; first (●) and second (o) order branches, sectioned samples measured in the laboratory, and first order branches measured *in situ* (▼). The solid line represents the regression including all points ($Y = -6.58 * X + 108.2$, $r^2 = 0.37$).

Distribution of living cells in woody organs

A main cause of spatial variation in R_M, is the change in percentage of living cells with stem or branch diameter. The periderm had a higher proportion of living cells than other tissues (mainly xylem and pith). It was 55.6% (*SE* = 0.9) and 39.0% (*SE* = 1.0) for beech and Norway spruce, respectively. The proportion of the periderm compared to the other tissues decreased when the diameter of the

organ increased, *i.e.* the total amount of living cells decreased when diameter increased (Figure 7a & 7b). Moreover, the percentage of living cells in the xylem also decreased with increasing diameter (Figure 7c & 7d). For beech, all of the living xylem cells were found in the rays down to the centre of the stem, and the percentage of living cells was rather constant toward the centre of the organ (see Paper I). In contrast, for Norway spruce, the percentage of living cells strongly decreased toward the centre of the organ (data not shown), until it reached zero in the heartwood, as was previously shown by Stockfors & Linder (1998). At breast height, they found that 80% of the living cells occurred in the first 4 mm beneath the bark. In contrast, Ryan (1990) found that more than 80% of the living cells were situated in the xylem at breast height in *Pinus contortata* and *Picea engelmanii,* while for beech, in the present study, it was close to 97%.

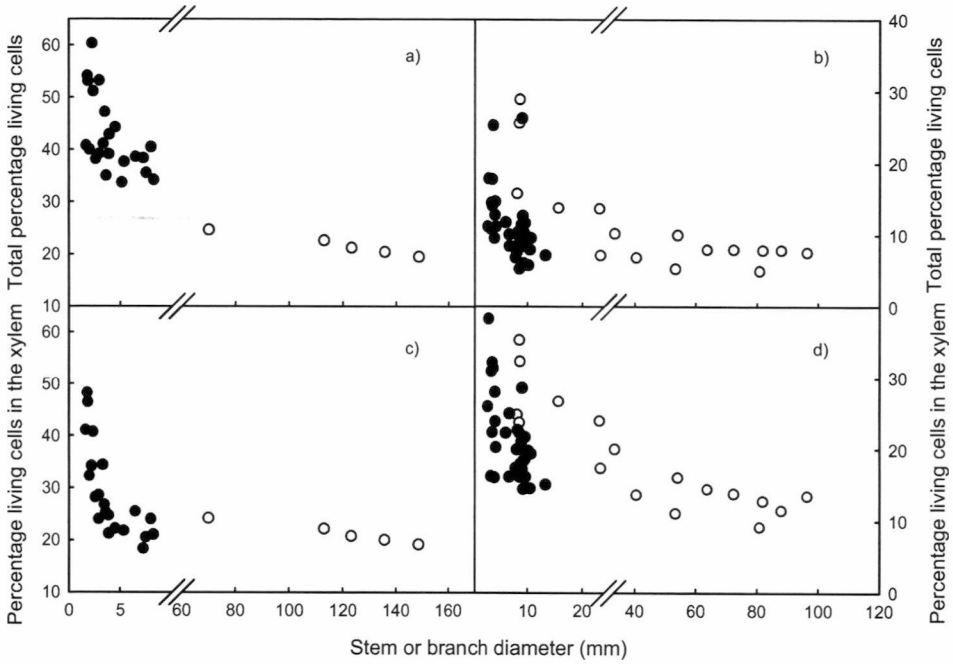


Figure 7. Percentage of living cells in the stem (o) and branches (●) over the entire section for 25-year-old beech trees at Hesse in 1998, (a), for 40-year-old Norway spruce trees at Flakaliden in 1999, (b), in the xylem for beech, (c), Norway spruce, (d), as a function of stem diameter. For further details, see text.

The percentage of living cells in the woody organs was much higher for beech than for most of the other species studied, and the size and number or rays were much larger for beech than for Norway spruce. At breast height, the percentage of living cells in the sapwood was 5.0% for *Pinus contortata*, 5.7% for *Picea engelmanii* (Ryan, 1990) and only 0.1–0.5% for Norway spruce (Stockfors & Linder, 1998), compared with *ca.* 22% for beech. Our results for Norway spruce were higher than those obtained by Stockfors & Linder (1998), possibly because transverse sections were used instead of longitudinal sections. Consequently, several cell layers were present in the transverse sections of the xylem rays, and

the percentage of living cells in the xylem may therefore have been overestimated.

The difference in distribution of living cells within the stem between species, may explain why some authors found that respiration was better correlated with wood surface (Stockfors & Linder, 1998) or with stem volume (Ryan, 1990). For beech, in this study, volume was the most appropriate base for calculation of stem respiration rates, since a large part of the living cells was situated in the xylem. For older trees, however, surface area might be the most appropriate unit, for organs in which heartwood represents a large proportion of its cross-section. For Norway spruce, while measurements at breast height indicated that surface area was the best unit for calculating stem respiration, this was no longer true when respiration was integrated along the stem. This was due to an increase in the proportion of living cells in the xylem at higher stem locations.

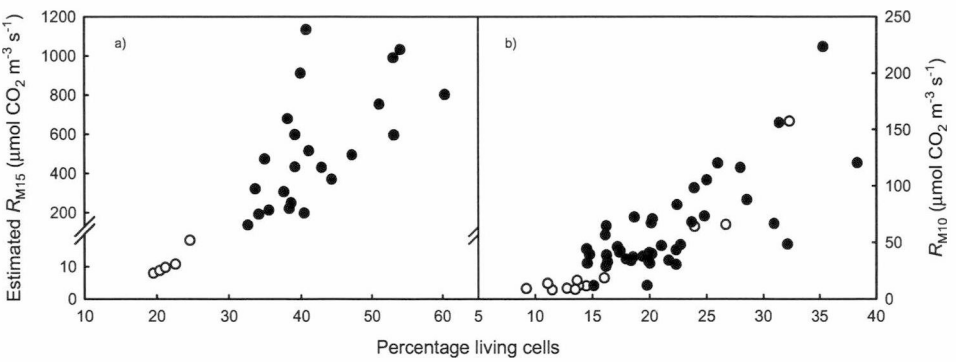
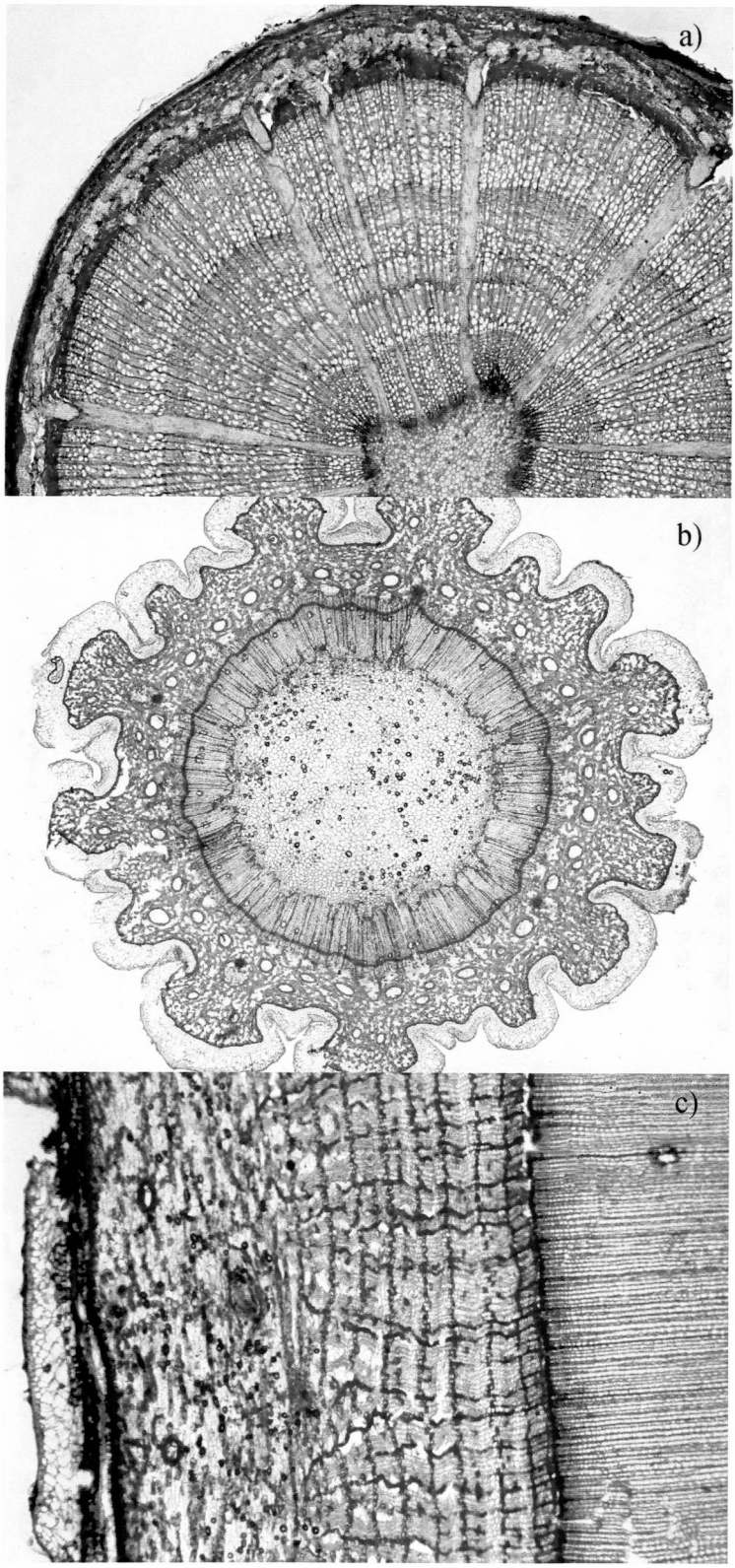


Figure 8. Variation in maintenance respiration normalised to 15 °C (R_{M15}) for beech at Hesse in 1998, (a), and normalised to 10 °C (R_{M10}) for Norway spruce at Flakaliden in 1999, (b), as a function of stem (o) or branch (●) percentage of living cells. For further details, see text.

For both beech and Norway spruce stems, respiration increased with the percentage of living cells (Figure 8). Respiration increased strongly for the smaller and younger organs, indicating that these living cells were more physiologically active than those in the older organs. The relationship between respiration and living cells was weaker for branches, indicating that one or several other important factors influenced maintenance respiration of branches.

For similar amounts of living cells, Norway spruce respired more than beech. When a stem diameter of 10 cm is considered, the ratio between respiration and the percentage of living cells was 0.66 and 1.09 for beech and Norway spruce, respectively. Thus beech was more efficient than Norway spruce when maintenance respiration was considered at a cellular level.

Plate 1: (Opposite page) Transverse sections a) of a 4-year-old beech branch at Hesse, b) in a one-year-old stem and c) in the outer part of a 10-year-old stem of a Norway spruce tree on the control plot at Flakaliden. The living cells are stained in blue.


a)
b)
c)

Maintenance respiration and nitrogen concentration

For beech, nitrogen concentration decreased strongly with the diameter of the organs, from 7.5 mg N g^{-1} DM to about 1 mg N g^{-1} DM at Hesse in 1998 and from 20.3 mg N g^{-1} DM to 5.7 mg N g^{-1} DM at Orsay, in 1997 (see Papers I & V). This corresponded with a decrease in living cells with increasing organ diameter. There was a linear relationship at Hesse between the total percentage of living cells in the stem and [N] (Y = 4.86 * [N] + 15.3, n = 20 and r^2 = 0.74), but the relationship between estimated respiration on a volume base and nitrogen concentration was not linear (Figure 9a). As in the present study, Bosc (1999) found that maintenance respiration of Maritime pine increased strongly with [N], but according to a power-type relationship.

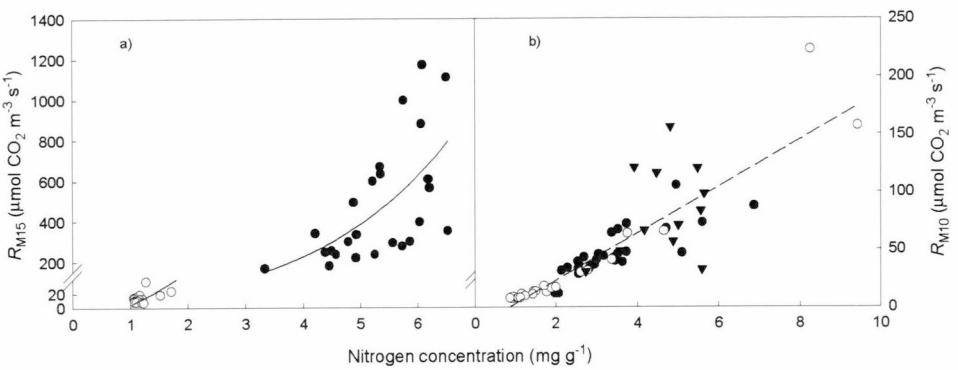


Figure 9. Variation in maintenance respiration normalised to 15 °C (R_{M15}) for beech at Hesse in 1998 (a) and normalised to 10 °C (R_{M10}) for Norway spruce at Flakaliden in 1999, (b) as a function of stem (O) or first order branch (●) or second order branch (▼) nitrogen concentration. The solid line represents the regression for beech (Y = –88.9 + 62.0 * $e^{(0.41 * X)}$, r^2 = 0.68) and the dashed line represents the regression for Norway spruce (Y = 20.3 * X – 17.7, r^2 = 0.73). The regressions were calculated for stems and branch samples together. For further details, see text.

For Norway spruce, a linear relationship was found between R_{M10} calculated on a volume basis, and stem or branch nitrogen content or concentration (Paper II & Figure 9b). The slopes of the two regressions were significantly different (P = 0.025). The intercepts were significantly different (P < 0.01) when nitrogen was expressed as kg N m^{-3} stem or branch (Paper II). Maier *et al.* (1998) also showed that R_M was a linear function of nitrogen content in the wood of *Pinus taeda,* and that the slope of the relationship between maintenance respiration and nitrogen content differed for stems and branches. These results indicate that Norway spruce branches had a higher wood density than the stem. When R_{M10} was expressed as a function of nitrogen concentration, a single relationship could be used for both stems and branches (Figure 9b). However, respiration for the second order branches was poorly related to [N]. Those results suggest that the relationship between nitrogen and maintenance respiration differs between the

species, and that nitrogen content or concentration are good predictors of maintenance respiration.

Table 3. *Comparison of two methods of calculation for the percentage that represents annual growth respiration in the total annual wood respiration (R_G%) and the wood construction cost (r_G) at Hesse (beech trees) and Flakaliden (Norway spruce trees) during the seasons 1997-2000 at different positions along the stem. The numbers in parentheses are the standard errors of the means*

Site	Year	Treatment	Position	Mature-tissue method			Periodic-growth method		
				R_G%	r_G	r^2	R_G%	r_G	r^2
Hesse	1997	none	Top	61.9			/	/	/
	1998		B.H.	66.6 (1.3)	0.23	0.89	53.9 (10.1)	0.13 (0.02)	0.67-0.85
			Middle	44.6 (4.5)			75.9 (9.0)	0.27 (0.04)	0.57-0.85
		C	B.H.	70.2 (1.2)			30.9 (7.8)	0.12 (0.02)	0.69-0.75
			Middle	72.4 (3.1)	0.13	0.35	40.5 (11.5)	0.20 (0.03)	0.75-0.89
			Top	79.4 (2.9)			39.0 (7.0)	0.15 (0.03)	0.56-0.70
	1999		B.H.	66.5 (1.8)			34.6 (7.4)	0.16 (0.01)	0.68-0.77
		IL	Middle	74.8 (3.4)	0.12	0.40	33.9 (8.8)	0.17 (0.01)	0.70-0.83
Flakaliden			Top	81.4 (2.2)			41.5 (6.5)	0.20 (0.03)	0.52-0.80
		CA	B.H.				84.2 (2.1)*	0.12 (0.01)	0.38-0.61
		CE	B.H.				87.5 (0.6)*	0.13 (0.01)	0.41-0.65
	2000			/	/	/			
		ILA	B.H.				88.8 (1.4)*	0.14 (0.01)	0.46-0.78
		ILE	B.H.				90.2 (0.5)*	0.15 (0.02)	0.56-0.78

* R_G% value are calculated for a portion of the growing season only and therefore do not represent the percentage that represents annual growth respiration in the total annual wood respiration.

Growth respiration and wood construction cost

Rapidly changing respiration rates meant that continuous respiration measurements improved the accuracy of the estimated components of stem respiration. The two methods (mature-tissue method and periodic-growth method) used to separate total respiration into maintenance and growth respiration, led to similar predictions of the wood construction cost for beech, but not for Norway spruce (Table 3). The periodic-growth method (Figure 10b & 10d) was more accurate than the mature-tissue method (Figure 10a & 10c), since the intercept of the relationship between growth and growth respiration passed closer to origo than that of the mature-tissue method for Flakaliden. It also

allowed the two components of stem respiration to separated independently for each cuvette (see Papers I & II for further details). Moreover, similar regressions were produced using total respiration instead of growth respiration with the periodic-growth method; the results for r_G were identical. This result indicates that the periodic-growth method, in contrast to the mature-tissue method, is not sensitive to errors in estimates of maintenance respiration. The r^2 values of the regressions were also higher with the periodic-growth method at Flakaliden (Table 3).

Our mean values of r_G were consistent with those from similar studies, but sometimes among the lower values reported. For beech, r_G on average was close to the theoretical value of 0.25 estimated by Penning de Vries (1974), but the r_G values obtained for the base cuvettes by the periodic-growth method were low. For Norway spruce, the mature-tissue method seemed to underestimate r_G. Similarly, Stockfors & Linder (1998) found r_G values between 0.11 and 0.2, depending on the methods used, but the lower values were obtained with the mature-tissue method. Lavigne & Ryan (1997) estimated that the wood construction cost in Jack pine and Black spruce was between 0.24 and 0.39, and Wullschleger *et al.* (1995) estimated r_G to be 0.21 to 0.25 for *Quercus alba* saplings. Maier (2001) found that r_G was 0.24 for *Pinus taeda*. Using theoretical methods, Chung & Barnes (1977) found the wood construction cost to be 0.12 to 0.15 for *Pinus elliottii*, Carey *et al.* (1997) obtained 0.16 to 0.18 for *Pinus ponderosa,* and Griffins (1994) found 0.12 for *Pinus taeda.*

The use of the mature-tissue method can pose problems, since R_M is assumed to be constant throughout the year, whereas some studies have shown that respiration can acclimate to changes in temperature (*e.g.* Linder & Troeng, 1981; Paembonan *et al.*, 1991) or vary with [N] in the wood (Maier *et al.*, 1998). Since similar results were found by both methods for beech, and because the intercepts of the relationship between carbon fixed and carbon respired (see Figure 10b & 10c) were usually close to zero, it can be concluded that R_{M15} was rather constant throughout the year. For Norway spruce, however, maintenance respiration and r_G were underestimated by the mature-tissue method. The annual mean used to simulate maintenance respiration during the growing season for the mature-tissue method, probably underestimated the real value of maintenance respiration during the growing season.

The results from the periodic-growth method also revealed that the wood construction cost varies with position within the tree (Table 3). The higher values in the upper parts of the trees at Flakaliden, or in the middle of the stem at Hesse, reinforce the hypothesis of an increase of respiration rate, and hence construction cost in the crown, caused by the transport and storage of carbohydrates or other reserve compounds (Lavigne, 1988; Sprugel, 1990). Changes in wood composition with height (Anttonen *et al.*, 200X) could also be responsible for spatial variations in r_G.

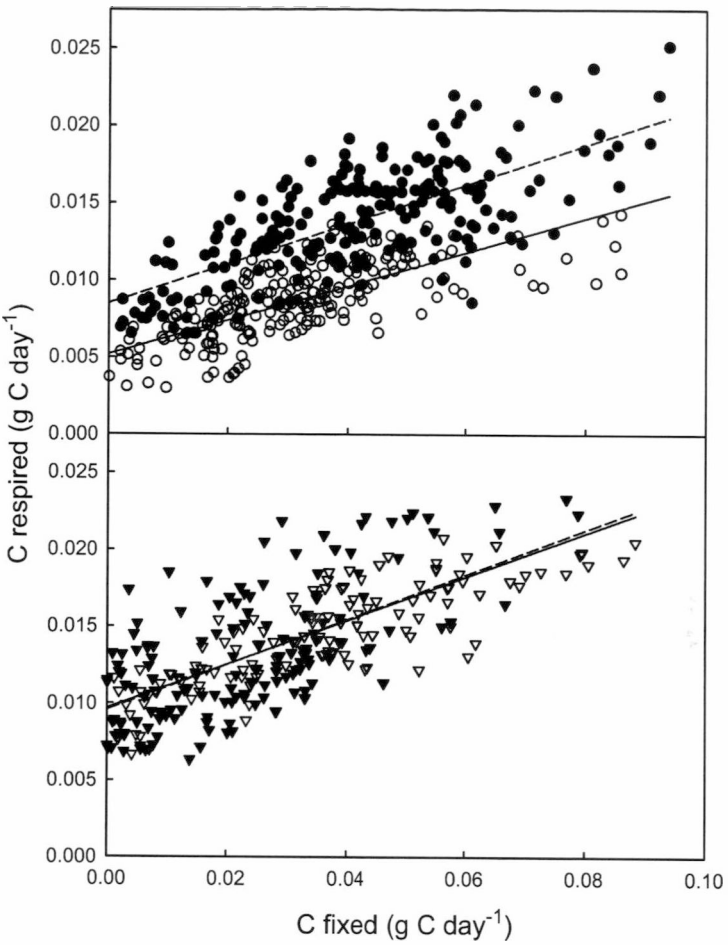


Figure 12. Relationship between carbon fixed in the newly-formed tissue and carbon respired by growth respiration for the CA (o), CE (●), ILA (▽) and ILE (▼) Norway spruce trees at Flakaliden in 2000. The solid and dashed lines represent the average regressions for the three cuvettes in the ambient ($Y = 0.11 * X + 0.005$ on the C plot and $Y = 0.13 * X + 0.009$ on the IL plot) and elevated ($Y = 0.14 * X + 0.010$ on the C plot and $Y = 0.15 * X + 0.010$ on the IL plot) treatments, respectively. The slope of the relationships represents the wood construction cost (r_G). See Papers V for further details.

In beech wood, [C] was not statistically different (*t*-test, $P = 0.32$) between the ambient and elevated treatments (469 mg g^{-1} DM, $SE = 3.0$ and 473 mg g^{-1} DM, $SE = 2.0$, respectively). In the growth rings of year 2000 in Norway spruce, [C] significantly increased in CE trees compared with CA trees, and IL trees had higher [C] than trees on the C plot. Values of [C] were 495.3 ($SE = 0.3$), 503.3 ($SE = 5.4$), 514.3 ($SE = 1.8$), 511.0 ($SE = 3.5$) for CA, CE, ILA, ILE, respectively. Therefore, for both species, the [CO_2] treatment had no significant effect on [C] in the wood after fertilisation.

For beech, [N] in the wood was higher, but not significantly different (*t*-test, $P = 0.07$) for the ambient (10.9 mg g^{-1} DM, $SE = 0.6$) compared to the elevated treatment (9.2 mg g^{-1} DM, $SE = 0.6$). Badeck *et al.* (1997) observed an 11% and 19% drop in [N] for *Castanea sativa* and *Fagus sylvatica* stems, respectively, in elevated [CO_2]. Hättenschwiler *et al.* (1996) observed a decrease in [N] in elevated [CO_2] for Norway spruce, but fertilisation had no effect on [N]. In the present study, the fertilisation treatments had a significant effect on [N], but there was no [CO_2] effect or interaction effect between [CO_2] and fertilisation treatments on [N] in the year 2000 growth ring. However, considering the rings from 1998–2000 together, [N] was 16% higher for CA trees compared to CE trees, and 5.3% lower for ILA trees compared to ILE trees. Nitrogen concentration decreased towards the centre of the stem (Figure 13a), corresponding to the decrease in the percentage of living cells (Stockfors & Linder, 1998).

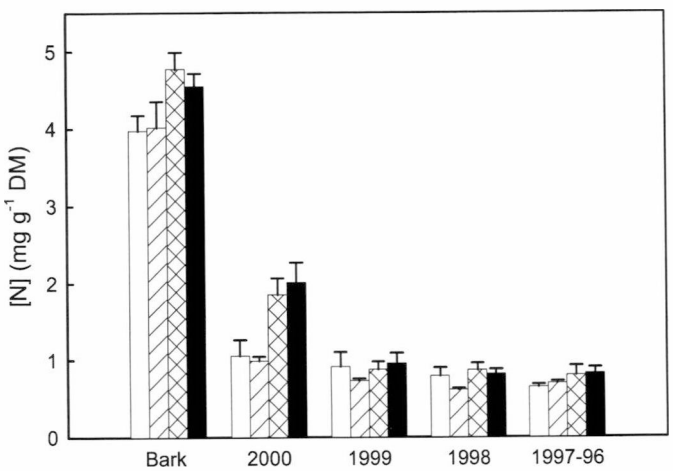


Figure 13. Nitrogen concentration in the bark (including phloem and cambium) and in the 1996–2000 xylem rings for the CA (empty column), CE (striped column), ILA (hatched column) and ILE (filled column) Norway spruce trees enclosed in the Whole Tree Chambers at Flakaliden in 2000.

For beech and Norway spruce, the [CO_2] treatment had no significant effect on carbon concentration in the wood after fertilisation was applied. These results show that a change or an imbalance in wood composition could be the origin of an increase in maintenance respiration for the CE trees. Runion *et al.* (1999) also showed that for *Pinus palustris,* the stem chemical composition (fat, waxes, oils, sugars, starch, cellulose, lignin and tannin) was not affected by elevated [CO_2] when fertilisation was applied. Therefore, fertilisation may have counteracted an increase in maintenance respiration for the beech and spruce trees grown in elevated [CO_2]. Amthor (1989) pointed out that a change in the substrate or in the product of respiration would induce a change in respiration. Further wood analyses are needed in order to understand the small variation in r_G for Norway

spruce, and to determine the exact effects of the [CO_2] treatment on wood composition for both species.

Effect of sapflow on respiration and [CO_2] in the stem

The relationship between the residuals from equation 1 and sapflow, indicated that sapflow had very little effect on respiration at Flakaliden, and no effect at Hesse below a sapflow value of 60 g H_2O m^{-2} s^{-1} (Figure 14). For higher sapflow values at Hesse, the sapflow had a negative effect on stem CO_2 efflux, and represented at most an 18% decrease in CO_2 efflux. Similar stem respiration measurements between the sectioned and non-sectioned samples in Figure 5, indicate that sapflow had no significant effect on respiration rates in Norway spruce. The results obtained for beech confirm the study from Martin *et al.* (1994), which showed that sapflow could reduce stem CO_2 efflux by about 7%. Levy *et al.* (1999), however, showed that CO_2 in the sap, originating from the soil, could have a positive effect on stem CO_2 efflux, and that it could represent up to 12% of the CO_2 efflux measured on the stem. Such effects, however, occurred only in very high sapflow situations, both in our study at Hesse and in those studies. Edwards & Wullschleger (2000), on the other hand, found little evidence of the effect of sapflow on stem respiration. It is possible that CO_2 originating from the soil, and degassing at breast height, could be compensated for by the CO_2 respired at breast height, and transported *via* the sap towards the upper parts of the tree. There degassing would increase, since the sapwood temperature is higher, limiting the amount of CO_2 that can be dissolved in the sap. Moreover, CO_2 would diffuse across the bark more easily at higher stem positions, because the bark is thinner.

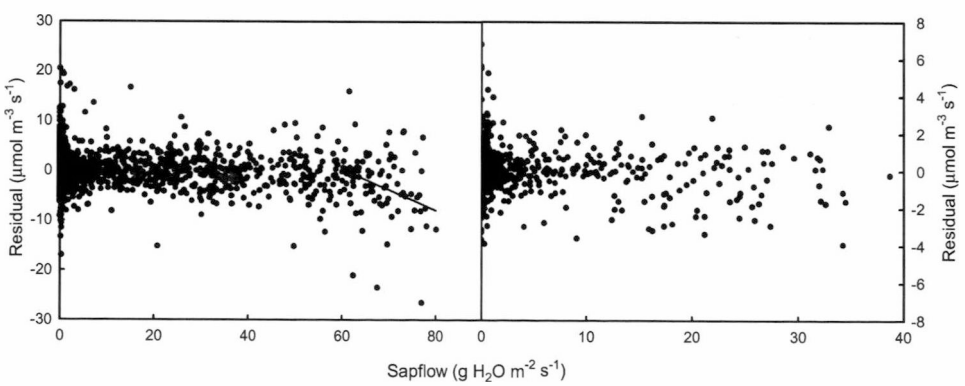


Figure 14. Effect of sapflow on stem respiration residuals from equation (1) for beech (a) and Norway spruce (b). The solid line represents the regression for beech when sapflow exceeds 60 g H_2O m^{-2} s^{-1} with $Y = -0.41 * X + 24.8$ and $r^2 = 0.1$.

The experiment made at Flakaliden in October 1999, showed that the [CO_2] in the cuvette increased till the fifth day, then, on average, stabilised at *ca.* 10,000 µmol mol^{-1} (Figure 15). The variation between trees was rather high, and may have been caused by the distance between the cuvette and the ground. All of the

cuvettes were 1 m above the ground, except on the tree with the higher [CO_2], on which the cuvette was positioned 60 cm above the ground.

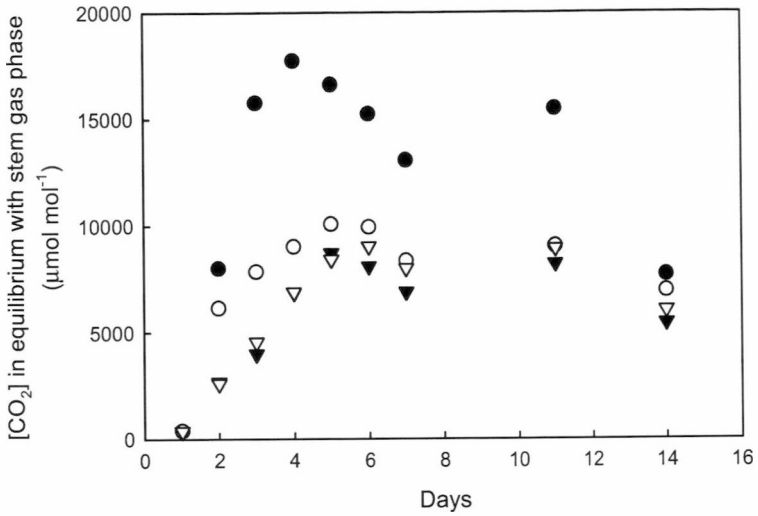


Figure 15. Increase and stabilisation of the [CO_2] in equilibrium with the stem gas phase, measured at a height of 1 metre (o, ▼, ▽) and 0.6 m (●), respectively, on Norway spruce IL trees at Flakaliden in 1999. Each symbol represents a different tree.

In the present study, estimates of stem internal [CO_2] are in good agreement with those of Hari *et al.* (1991) and Eklund (1990), who found [CO_2] in the gas phase in equilibrium with the sapwood close to 10,000 µmol mol^{-1} during the autumn in Norway spruce. Eklund (1990) also showed that the concentration varied with the same pattern as stem respiration throughout the season (with a peak close to 110,000 µmol mol^{-1} in the middle of the growing season). This could mean that a fairly constant proportion of the CO_2 respired by the stem or originating from the soil, is transported in the sap and is brought to the upper parts of the tree, where degassing could occur or where the CO_2 could be re-assimilated by needles or leaves. Levy *et al.* (1999) estimated that such a re-assimilation could represent between 0.5 and 7.1% of typical leaf photosynthesis.

Finally, stem CO_2 efflux depends on cell respiration, but also on the [CO_2] gradient between the inner parts of the stem and the atmosphere. Since the [CO_2] inside the stem is very high, the [CO_2] gradient would not be greatly affected by a 350 µmol mol^{-1} increase in atmospheric [CO_2]. Therefore, stem CO_2 efflux should not change, as long as respiration is not affected by changes in the percentage of living cells or in wood composition.

Scaling up woody respiration to stand level

Annual estimates of aboveground woody respiration (R_{AG}) at Hesse in 1997, are shown in Table 4. R_{AG} was 245 and 289 g C m^{-2} ground surface a^{-1} when volume- and surface area-based respiration rates, respectively, were used to scale up

woody respiration. R_{AG} represented close to 30% of the total ecosystem respiration, and growth respiration accounted for about 35% of R_{AG} (Paper III). Branches accounted for 11% and 53% of the total wood volume and area, respectively, but represented close to 50% of R_{AG} (for further details concerning beech allometry, see Paper III). At Flakaliden in 1999, R_{AG} was 64 and 134 g C m^{-2} ground surface a^{-1} on the C and IL plots, respectively. Growth respiration represented 40% and 47% of total aboveground woody respiration at stand level on the C and IL plots, respectively, and branch respiration was close to 45% of R_{AG} on both plots at Flakaliden. In other studies, growth respiration ranged from 15% in *Pinus ponderosa* (Carey *et al.*, 1997) to 77.5% in *Pinus taeda* (Ryan & Waring, 1992).

Table 4. *Annual estimates for stems and branches of maintenance, R_M, growth, R_G, and total annual respiration at the stand level for Hesse in 1997 and Flakaliden on the C and IL plots in 1999. Units are g C m^{-2} ground surface area a^{-1}. For further information concerning the global-warming scenarios and [CO_2] effects on maintenance or growth respiration, see text*

		Stem Respiration		Branch Respiration		Total
		R_M	R_G	R_M	R_G	
Hesse 1997 Volume-based Q_{10} and R_{15}		75	47.4	79	43.2	245
Hesse 1997 Surface based Q_{10} and R_{15}		95	68.4	88	37.9	289
Hesse 1997 Volume based Q_{10} and R_{15} + Global warming		89.7	68.4	111	37.9	307
Flakaliden 1999	C plot	15.6	19.3	22.4	6.6	63.8
	IL plot	27.7	46.8	43.3	16.0	134
Flakaliden 1999 + Global warming	C plot	19.1	19.3	27.9	6.6	72.8
	IL plot	33.8	46.8	54.1	16.0	151
Flakaliden 1999 + Global warming +[CO_2] effect	C plot	47.8	21.2	69.8	7.2	146
	IL plot	33.8	48.3	54.1	16.7	153

Our estimates of R_{AG} were in the range of values reported in other studies. Edwards & Hanson (1996) found R_{AG} values of 149–204 g C m^{-2} a^{-1} in a mixed Oak and Red Maple stand. For *Pinus radiata* stands, R_{AG} was 373–727 g C m^{-2} a^{-1} (Ryan *et al.*, 1996), between 52 and 162 g C m^{-2} a^{-1} for conifers in different climates (Ryan *et al.*, 1995), 54 g C m^{-2} a^{-1} for *Pinus ponderosa* stands (Law *et*

al., 1999) and up to 1314 g C m^{-2} a^{-1} for rain forests (Müller & Nielson, 1965; cited in Ryan *et al.*, 1994b). Because bark assimilation was not taken into account in the present study, the net values of R_{AG} are overestimated. On a cold winter day at Hesse in 1997, bark assimilation compensated for stem respiration at breast height, and several other studies have shown the importance of bark assimilation (Foote & Schaedle, 1976a;1976b; Linder & Troeng, 1980; Sprugel & Benecke, 1991; Cernusak & Marshall, 2000). Therefore, accurate estimates of this flux are now required.

Since the percentage of growth respiration in total respiration was lower at Hesse compared with Flakaliden, and r_G was higher, the carbon-use efficiency (CUE) was lower at Hesse. The CUEs were close to 0.58 at Hesse in 1997, 0.73 and 0.74 at Flakaliden in 1999 on the C and IL plots, respectively. These results indicate that the two forests of similar stand ages are not equally efficient in fixing carbon in the wood, and that fertilisation does not increase CUE. Ryan *et al.* (1996) and Maier (2001) found CUE values of 0.66 and 0.63 for *Pinus radiata and Pinus taeda*, respectively, and in both studies fertilisation had no effect on CUE. Stem CUE values ranging between 0.37 and 0.59 are also reported for three boreal tree species (Lavigne & Ryan, 1997). Stockfors & Linder (1998) estimated growth respiration to be close to 50% of total respiration at Flakaliden in 1993, in the same Norway spruce stand. The increasing proportion of maintenance respiration in total respiration for aging forests, corresponding with a decrease in carbon-use efficiency, could therefore cause a decline in forest NPP with time. Such issues were already discussed by Peet (1980), Murty *et al.* (1996) and Yoder *et al.* (1994). Ryan & Waring (1992) found that a decrease in stomatal conductance and photosynthetic efficiency was also responsible for declining forest productivity in aging forests. Grier *et al.* (1981) and Gower *et al.* (1995) assumed a reduced N availability in aging forest stands. Murty *et al.* (1996) tested those hypotheses in a G'DAY model, and found that a decrease in stomatal conductance and photosynthetic efficiency could be responsible for declining NPP in aging forests. However, their simulations of stand annual respiration were based on breast-height measurements only, and they considered that branches were composed entirely of sapwood. More recently, Mäkelä & Valentine (2001) showed that sapwood respiration alone could contribute to a downward trend in the NPP/GPP ratio with time.

When Q_{10} and R_{15} were derived from breast-height measurements only, and applied to entire trees at Hesse, R_{AG} was 235 (volume based) and 810 (surface-area based) g C m^{-2} ground surface a^{-1}, considering a r_G value of 0.38 (Paper IV). At Flakaliden, when Q_{10} and R_{15} derived from breast height measurements only were used for scaling-up, R_{AG} was 44 and 94 g C m^{-2} a^{-1} on the C and IL plots, respectively. At Hesse, failure to consider stem and branches as different compartments when scaling-up aboveground woody respiration, produced errors in R_{AG} estimates of 28% and 111% for volume- and surface area-based calculations, respectively. At Flakaliden, this error was 30% of R_{AG} for both the C

and the IL plots. Such errors would probably increase with increasing tree size. The large error related to the use of surface area for beech is a new indication that volume is the best basis for expressing stem respiration in young beech trees. Finally, further experiments are needed to assess the variation in r_G within trees. If this observation is confirmed, spatial variation in r_G should also be integrated into our models.

The global climate change perspective

The effects of a global climate change on stand woody respiration are summarised in Table 4 for Hesse and Flakaliden. At Hesse, global warming would induce a 25% increase in R_{AG}. At Flakaliden, global warming that affected maintenance respiration only, would induce a 14% and 13% increase in R_{AG} on the C and IL plots respectively. Including a $[CO_2]$ effect on respiration, R_{AG} would increase by 14% on the IL plot and by a factor of 2.3 on the C plot. This important change in R_{AG} is mainly due to a 2.5-fold increase in R_M on the C plot. Fertilisation moderately increased r_G, but strongly limited an increase in R_M. It is impossible to know what would have been the effect of a $[CO_2]$ increase on the C balance at Hesse, but possibly R_M would have increased in the absence of fertilisation.

Conclusions

Because the balance between net photosynthesis and ecosystem respiration will determine whether a forest ecosystem will act as a source or a sink of carbon, it has become crucial to improve our understanding of forest carbon cycles, in order to estimate forest carbon budgets accurately. From the present study, it is apparent that a failure to consider variation in respiration rates within a tree, would produce large errors in modelled carbon budgets. When modelling, more attention must be given, in particular, to branch respiration, since this component represents close to 50% of total aboveground woody respiration.

Woody respiration varied rapidly throughout the season, in consequence of changes in temperature and growth. It also varied strongly within the tree, in consequence of temperature gradients, spatial variation in secondary growth, spatial variation in the distribution of the living cells within the organs, and organ vitality. Transport and storage of carbohydrates, and changes in wood composition along the stem, may also contribute to the spatial variability in woody respiration. Sapflow had little effect on stem CO_2 efflux at breast height, but could increase the fluxes in the higher parts of the tree.

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respiration is unlikely to be affected directly by a change in atmospheric [CO_2], but global warming could increase aboveground woody respiration of a young beech forest by 25%. For Norway spruce, based on the predicted climate scenario for Flakaliden, woody respiration would increase by *ca.* 14%. In addition, an increase in atmospheric [CO_2] could induce a large increase in stem respiration in an unfertilised stand, in consequence both of a rise in the wood-construction cost (+10%), and of a strong effect on maintenance respiration. The causes of the increase in respiration with high [CO_2] are unclear, but an imbalance in wood composition in the tissue could be involved. Fertilisation apparently counteracted this imbalance, in both beech and Norway spruce, and could therefore limit the rise in forest woody respiration levels with global climate change.

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