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Variability of stem and branch maintenance respiration in a *Pinus pinaster* tree

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Summary The relationship between maintenance respiration (R_m) of woody organs and their structural characteristics was explored in adult *Pinus pinaster* Ait. trees. We measured R_m on 75 stem and branch segments of different ages (from 3 to 24 years) and diameters (from 1 to 35 cm). The temperature response of R_m was derived from field measurements based on a classical exponential function with Q_{10} = 2.13. Relationships between R_m and the dimensions of the woody organs were analyzed under controlled conditions in the laboratory.

The surface area of a woody organ was a better predictor of R_m than volume, but surface area failed to account for the observed within-tree variability of R_m among stems, branches and twigs. Two simple models were proposed to predict the variability of R_m at 15 °C in an adult tree. Model 1, a linear function model based on the dry mass and nitrogen concentration of sapwood and phloem tissues, explained most of the variability of R_m in branches and stems (R^2 = 0.97). We concluded that the respective contributions of the phloem and sapwood depend on the location and diameter of the woody organ. Model 2, a power-law function model based on the length, diameter and age of the sample, explained the same variance of R_m as Model 1 and is appropriate for scaling R_m to the stand level. Models 1 and 2 appear to explain a larger variability of R_m than models based on stem area or sapwood mass.

Keywords: model, nitrogen, phloem, sapwood, temperature.

Introduction

Estimation of plant respiration is critical for predicting net primary production (NPP) in a changing climate (Amthor 1991, Carey et al. 1997) because small relative changes in photosynthesis and respiration lead to a large relative change in NPP. Over the past 30 years, plant respiration has been described in terms of two components (Amthor 1989): growth respiration, which corresponds to new tissue construction cost and is temperature-independent; and maintenance respiration of existing tissues, which is temperature-dependent (Penning de Vries 1975). Recently, this approach has been challenged on the basis that plants are composed of different organs for which maintenance respiration corresponds to different physiological functions with different responses to environmental factors (Amthor 2000, Cannell and Thornley 2000, Thornley and Cannell 2000). Thus, in modeling, it is desirable to make explicit the processes that require respiration (e.g., growth, nitrate reduction, symbiotic N_2 fixation, N uptake, other ion uptake and phloem loading) (Cannell and Thornley 2000). Any processes not explicitly modeled can be represented by a residual maintenance respiration term (Cannell and Thornley 2000).

On a dry mass basis, respiration of the aerial woody tissues of a tree is less than that of other organs (Ryan et al. 1994). However, woody tissue respiration plays a significant role in the carbon balance of adult stands (Ryan et al. 1994, Carey et al. 1997, Witowshi 1997) because of the large increase in woody biomass with tree age. Estimating respiration of woody parts is therefore an essential step in modeling tree growth and CO_2 exchanges between forests and the atmosphere (Hagihara and Hozumi 1991).

The two principal roles of the aboveground woody parts are architectural support of the tree and sap conduction between the above- and belowground organs. According to the Munch hypothesis, phloem transport requires no energy other than for phloem loading in the leaves. Moreover, active processes such as nitrate reduction, symbiotic N_2 fixation and uptake of N and other ions do not use significant amounts of energy in woody tissues, suggesting that, for these organs, the only active process for which energy consumption might be appreciable is growth. Within woody organs, respiration in the absence of growth may include CO_2 flux produced by different physiological processes for which the associated energy requirement and CO_2 production are not easily quantifiable (e.g., protein turnover, active transport and secondary metabolism). Therefore, the use of the growth respiration–maintenance respiration paradigm remains appropriate for analyzing respiration of woody tissues. In this study we use the term maintenance respiration (R_m) for all non-growth respiration components.

Growth respiration can be estimated from tissue composition and the energy costs for the construction of each component (Penning de Vries et al. 1974, Frossard et al. 1996). Maintenance respiration of woody tissues, which is less clearly quantifiable than growth respiration, is mainly associated with

phloem and xylem tissues. Their respective respiration rates appear to be strongly related to temperature (Lavigne 1987, Maier et al. 1998) and their dimensions (Ryan et al. 1995).

Among a variety of scaling variables that have been proposed to scale up R_m to the tree and stand levels (Landsberg 1986, Hagihara and Hozumi 1991, Ryan and Waring 1992), surface area (Lavigne et al. 1996), volume and mass (Ryan et al. 1995, Edwards and Hanson 1996) have been widely used. Nitrogen content has also been proposed as a scaling variable, on the basis that (1) R_m is related to the number of living cells (Sprugel 1990), (2) the nitrogen content of a tissue is related to the size of its protein pool, and (3) protein synthesis is the principal component of cell R_m (Brix 1971, Ryan et al. 1996, Maier et al. 1998). The choice of structural variable is critical when scaling R_m from a given axis type to the tree and stand levels. Maier et al. (1998) found that a model that adequately described R_m of the trunk was unable to predict branch R_m correctly.

This paper reports the results of R_m measurements made on adult *Pinus pinaster* Ait. stems and branches, in the field and laboratory. First, an analysis of the response of R_m to temperature was performed based on field measurements. Then, to explore the links between R_m and woody tissue characteristics (dimensions, age and nitrogen content of the phloem and sapwood), a second set of measurements was carried out under controlled conditions. Finally, two models of R_m as a function of the dimensions and age of an axis are proposed and their respective advantages discussed.

Materials and methods

Site

The study was carried out at the Bray site, an even-aged, 27-year-old maritime pine (*P. pinaster*) plantation located 20 km southwest of Bordeaux, France (Table 1). This site has been studied for mass and energy flux and tree growth since 1987 (Berbigier and Bonnefond 1995, Loustau et al. 1998, Bosc 1999, Porté 1999) and is part of the Euroflux and Fluxnet networks. The 1996–1999 mean net ecosystem exchange of the stand (NEE), as determined from eddy covariance continuous measurements, was –530 g C m^{-2} $year^{-1}$ (Berbigier et al. 2001), and mean net aboveground primary production (NPP_a), as estimated from allometric measurements, was 390 g C m^{-2} $year^{-1}$ (Porté 1999, Porté et al. 2002).

Table 1. Climatic and stand characteristics of the Bray site in 1997.

Location	44°42′ N, 0°46′ W
Elevation (m)	60
Topography	Flat
Soil type	Hydromorphic humid podzol
Mean soil depth (m)	0.70
Climate type	Oceanic
Annual rainfall (mm $year^{-1}$)	930
Mean annual temperature (°C)	12.5
Stand area (ha)	16
Standing stock (ha^{-1})	516
Tree age (year)	28
Mean height (m)	18.48 (SD = 1.21)
Mean diameter (cm)	28.14 (SD = 4.74)

Gas exchange system

Respiration of stem or branch segments was measured with a closed gas-exchange system with five chambers of various dimensions (Field et al. 1989). The chambers were made from two opaque plastic (PVC) half-cylinders (0.04–0.5 m in diameter) hinged together. Each end of the cylinder was capped with an annular PVC lid with a central hole allowing the chamber to close tightly around a woody axis. Gas tightness was ensured with a neoprene seal. Air inside the chambers was mixed by means of one or two fans, according to chamber size. The total volumes of the gas exchange system (chamber + closed loop) of the five chambers were 0.327, 1.06, 7.76, 36.5 and 281 dm^3. The chambers were connected to an IRGA CO_2 analyzer (Binos 1, Rosemount, Rungis, France), and an air flow of 1 dm^3 min^{-1} through the IRGA was generated by a membrane pump (N010 KNF 18, Neueberger, Village-Neuf, France). The temperature at a depth of 5 mm below the bark was measured by a copper-constantan thermocouple and continuously recorded together with the IRGA analog output on a 21X data logger (Campbell Scientific, Loughborough, U.K.).

The system was used in manual or automated modes. In manual mode, the organ was enclosed by hand in the chamber only during the measurement. In automated mode, the chamber continuously enveloped the sample; the chamber was flushed with external air to maintain chamber conditions close to external conditions, except for a 2-min period during measurements, which were made every 20 min.

Respiration was calculated according to classical equations for a closed gas-exchange system (Field et al. 1989). The volume of the free space of the chamber (m^3) was calculated as the difference between the volume of the chamber system, including the closed loop to the IRGA cell, and the volume of the axis segment included in the chamber, which was determined assuming the segment was a cylinder. Because the rate of increase of CO_2 concentration ($[CO_2]$) in the chamber was not constant over time at high respiration rates, the initial slope $d[CO_2]/dt_{(t=0)}$ (μmol CO_2 m^{-3} s^{-1}) was calculated from a cubic polynomial function fitted by least-squares regression of $[CO_2]$ over time.

Field measurements

Only one tree was accessible from the 20-m tower erected at the site. A larger tower was used for the eddy covariance and micrometeorological measurements (Berbigier et al. 2001). The selected tree had a circumference at breast height and a total height close to those of the average tree in the stand (height = 17.8 m, diameter at 1.3 m height = 0.25 m). Respiration measurements were made from September 4 to October 16, 1997. Respiration rates of seven segments of four branches (Table 2) were monitored in automated mode for 3 to 7 days. From diameter measurements made with automated micrometer gauges located on six trees and eight branches of the se-

Table 2. Characteristics of branch samples studied in the field, dates of measurement (DOY = Day of year), organ temperature during the measurement periods and parameters of the temperature effect model on maintenance respiration: $R_{m,A} = R_{m,A}(15)Q_{10}^{(T(t-\Delta t)-15)/10}$. Maintenance respiration at 15 °C ($R_{m,A}(15)$), rate of increase in $R_{m,A}$ for a 10 °C increase in temperature (Q_{10}) and hysteresis time lag (Δt) were estimated by nonlinear regression on field measurements.

Field samples	Diameter (cm)	Branching order	Age (year)	Period of measurement (DOY)	Organ temperature (°C)		$R_{m,A}(15)$ (μmol m^{-2} s^{-1})	Q_{10}	Δt (min)	R^2	n
					min–max	mean					
A	3.62	2	6	247.9–253.0	13–33	22	0.796	2.36	15.0	0.96	326
B	3.07	2	5	255.6–262.7	8–33	19.8	0.749	1.83	36.6	0.82	502
C	2.99	2	5	262.7–266.6	17–32	22.6	0.897	2.36	50.2	0.88	280
D	1.15	3	5	266.6–273.2	17–27	20.8	0.598	2.07	0	0.61	135
E	2.72	2	5	293.6–295.5	12–32	21.7	0.368	2.07	17.9	0.87	293
F	1.39	2	5	274.4–279.6	14–31	20.3	1.05	2.08	0	0.95	206
G	1.02	2	4	290.5–293.4	15–35	24	0.594	2.38	17.6	0.84	473

lected tree and recorded continuously (Bosc 1999), it was verified that volume expansion of the stem and branches had ceased by September 4, 1997.

Laboratory measurements

From October 27 to December 6, 1997, additional measurements were made on excised branches and stems in a climate chamber in the laboratory, where ambient temperature was maintained at 15 ± 1 °C and [CO_2] between 350 and 500 ppm. These measurements allowed elimination of the main methodological sources of variation in respiration measurements encountered under field conditions, namely: (1) temporal variation in temperature; (2) spatial heterogeneity of the sample temperature because of solar radiation (Stockfors 2000); (3) CO_2 transport by sap flow (Kakubarri 1988, Hari et al. 1990, Martin et al. 1994, Levy et al. 1999); and (4) photosynthesis of inner bark near the chamber (Levy and Jarvis 1998).

Sample size was again confined to a small number of branches and trees because the site was being managed for wood production by a private owner. Altogether, 69 samples of various dimensions were taken from five trees representative of the average tree in the stand: 26 samples were taken from stems of two trees and 43 samples were taken from branches of five trees.

Two trees were felled for stem respiration measurements. Their stems were cut into five sections (3.7 m length) and transported immediately to the laboratory. On the branchless part of the stem beneath the crown, measurements were made on segments separated by 50 cm intervals. On the stem part within the crown, one segment was selected for respiration measurements on each annual growth unit.

Six branches at various heights in the crown of three trees were selected. After cutting, they were brought to the laboratory and recut under water. On each branch, gas exchange measurements were made on several growth units without needles (3 years and older). A total of 43 branch segment samples were measured.

No significant variation in respiration was observed during the first 48 h after cutting a branch or stem, as previously observed by Levy and Jarvis (1998). For large segments, stabilization of sample temperature to 15 °C took several hours. Consequently, all respiration measurements were performed between 12 and 48 h after cutting. To eliminate the potential effects of CO_2 leakage from the log or branch cut end, measurements were carried out 50 cm from a cut end, where internal lateral CO_2 flux is insignificant (Appendix). Three to four respiration measurements were conducted successively on each sample and the mean retained for further analyses.

Sample characteristics

For samples studied in the field, only nondestructive characteristics were measured: diameter (an electronic caliper with a resolution of 0.01 mm was used), age and branching order (1 for stem, 2 for branches fixed on stem and 3 for branches fixed on second-order branches).

From each sample studied in the laboratory, a slice at mid-length was taken. All unlignified tissues located between xylem and the bark were defined as phloem. Strictly speaking, this compartment also contains cambial tissue. The thickness and diameter over bark and under bark were measured, as well as the limits between the phloem, sapwood and heartwood. These were then separated with a chisel or knife, and dried to constant weight at 65 °C. The nitrogen (N) concentrations of phloem, sapwood and heartwood were measured by a colorimetric technique after hot digestion in sulfuric acid (Technicon analyzer, Technicon, Tarrytown, NY) (Brix 1971).

Data analysis

Maintenance respiration rates of laboratory samples (R_m; μmol s^{-1}) were standardized at 15 °C based on the Q_{10} value calculated from field measurements. The respiration rate was calculated on the basis of area ($R_{m,A}$; μmol CO_2 m^{-2} s^{-1}), sapwood volume ($R_{m,V}$; μmol CO_2 m^{-3} s^{-1}), phloem nitrogen ($R_{m,Np}$; μmol CO_2 (mol N)$^{-1}$ s^{-1}), sapwood nitrogen ($R_{m,Ns}$; μmol CO_2 (mol N)$^{-1}$ s^{-1}) and total nitrogen under bark tissues ($R_{m,N}$; μmol CO_2 (mol N)$^{-1}$ s^{-1}).

Linear and nonlinear models were fitted with SAS software (SAS 6.11, SAS Institute, Cary, NC). We sought to minimize the weighted residual sum of squares ($\sum(\hat{y}_i - y_i)^2/|y_i|$), so that woody parts with large dimensions did not have a more significant weight in the adjusted model.

Results

Field measurements

Figure 1a illustrates the daily course of R_m of one branch versus its temperature. Maintenance respiration of a given stem or branch sample varied by a factor of 2–3 during the day. At a given temperature, R_m was lower in the morning than in the evening (Figure 1a). Thus, R_m exhibited hysteresis following a counterclockwise time course. Therefore, for each branch segment, the following model was fitted by least squares, nonlinear regression:

$$R_m(t) = R_m(15)Q_{10}^{(T(t-\Delta t)-15)/10} \quad (1)$$

where $R_m(t)$ is measured maintenance respiration rate (μmol s^{-1}) at time t, $R_m(15)$ is maintenance respiration at 15 °C (μmol s^{-1}), Q_{10} is the coefficient by which R_m is increased for a 10 °C increase in temperature, and $T(t - \Delta t)$ is temperature (°C) at time $t - \Delta t$. Parameter Δt describes the hysteresis lag. Values of $R_m(15)$, Q_{10} and Δt, which are fitted parameters, were estimated by nonlinear regression. Because sample temperature was measured only during gas exchange measurements, i.e., every 20 min, the temperature at time $t - \Delta t$ was estimated by a cubic spline fit to the four temperature measurements made around this time. The lag values (Δt) ranged between 0 and 50 min and increased with increasing diameter of the sample (Table 2).

Individual sample Q_{10} values ranged from 1.83 to 2.38 (Table 2). No relationship was evident between Q_{10} values and measurement period or characteristics of the organ, but there was a significant correlation between Q_{10} and the mean temperature of the sample ($R^2 = 0.76$, $P = 0.01$). To obtain a value of Q_{10} representative of the whole data set, allowing us to cover the entire temperature range during the measurement period, the data were standardized as follows. First, the sample respiration rate at the reference temperature $R_m(21.7)$ (21.7 °C was the mean temperature of the data set) was calculated from the individual model of R_m (Table 2); the respiration measurements were then normalized by this value (Figure 1). The Q_{10} value thus obtained was 2.13 (R^2 = 0.851, n = 2212) (Figure 1b).

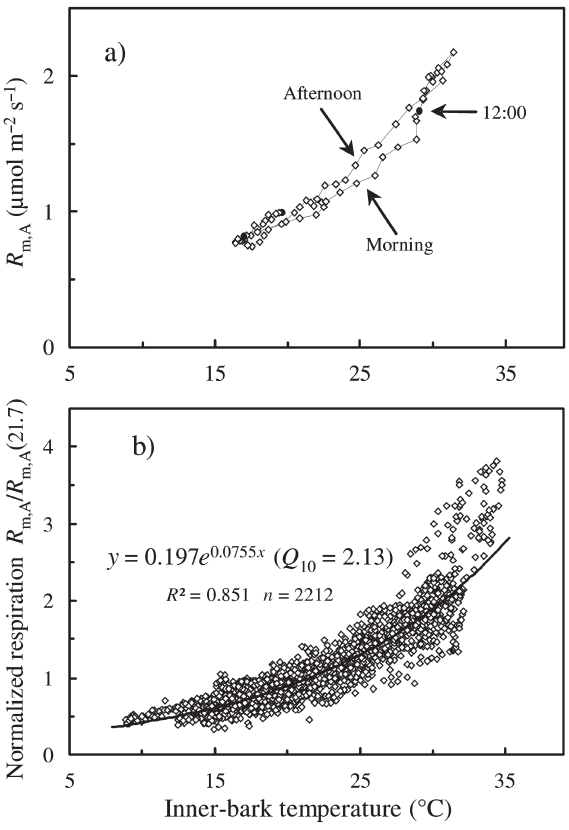

Figure 1. (a) Hysteresis relationship between instantaneous inner-bark temperature and maintenance respiration per unit area ($R_{m,A}$) of a selected branch (sample B) on September 17, 1997. Measurement symbols are connected chronologically. (b) Relationship between inner-bark temperature at time ($t - \Delta t$) and normalized maintenance respiration at time t of all branches used for field measurements.

Relationships between respiration and sample characteristics

The size of the woody organs in terms of diameter, mass of sapwood and phloem increased with age and, for a given age, decreased with branching order (Table 3). Heartwood was observed only in stem segments with a diameter greater than 13 cm. The phloem, forming a thin layer at the surface of the sapwood, contributed a decreasing fraction of the total mass of the axes with increasing age. In addition, this proportion varied according to branching order, being about 5% in the stem, 20% in second-order branches and 33% in third-order branches. Phloem N concentration decreased with the age of stems or branches, but there were no significant differences according to the branching order. Similarly, sapwood N concentration decreased with age and increased with the branching order of the woody organs.

For the 10 groups of samples defined on the basis of their age and branching order (Table 3), the range of maintenance respiration rates standardized at T = 15 °C depended on the units used (Table 3). When expressed per unit of sapwood volume ($R_{m,V}$), the highest rate was 14 times the lowest rate (25.1 and 348.8 μmol CO_2 m^{-3} s^{-1}), whereas when R_m was expressed per unit of area ($R_{m,A}$) the difference was only 2.5 times (0.68 versus 1.72 μmol CO_2 m^{-2} s^{-1}). Maintenance respiration was more uniform when N content in the phloem was the basis of expression ($R_{m,Np}$ = 3.91 to 8.73 μmol CO_2 (mol N)$^{-1}$ s^{-1}, ratio = 2.2) than when N content in the sapwood ($R_{m,Ns}$ = 1.68 to 9.01 μmol CO_2 (mol N)$^{-1}$ s^{-1}, ratio = 5.4) or total N content in living tissues ($R_{m,N}$ = 1.15 to 3.44 μmol CO_2 (mol N)$^{-1}$ s^{-1}, ratio = 3.0) was the basis of expression.

All $R_{m,A}$, $R_{m,V}$ and respiration rates per unit nitrogen ($R_{m,N}$, $R_{m,Ns}$, and $R_{m,Np}$) decreased with axis age. Conversely, different relationships were found with branching order and axis diameter. Respiration rates per unit area ($R_{m,A}$ and $R_{m,Np}$) decreased with increasing branching order, whereas volume-based respiration rates ($R_{m,V}$ and $R_{m,Ns}$) tended to increase (Table 4, Figures 2 and 3). Thus, for a group with the same age

Table 3. Diameter, dry mass per unit length and nitrogen concentration of woody tissues (phloem, sapwood and heartwood) and maintenance respiration per unit area ($R_{m,A}$; μmol m^{-2} s^{-1}), sapwood volume ($R_{m,V}$; μmol m^{-3} s^{-1}), nitrogen in the phloem ($R_{m,Np}$; μmol (mol N)$^{-1}$ s^{-1}), nitrogen in the sapwood ($R_{m,Ns}$; μmol (mol N)$^{-1}$ s^{-1}) and nitrogen in the whole sample ($R_{m,N}$; μmol (mol N)$^{-1}$ s^{-1}) of the *P. pinaster* samples measured in the laboratory. Respiration rates were standardized at 15 °C using a Q_{10} value of 2.13. Samples are grouped by age and branching order class (*n* indicates number of samples). For each parameter, mean and standard deviation are reported (mean ± SD).

Branching order	Age (year)	Diameter (cm)		Dry mass (g)			Nitrogen concentration (mg g^{-1})				Maintenance respiration					*n*
		Overbark	Underbark	Phloem	Sapwood (× 10^3)	Heartwood (× 10^3)	Phloem	Sapwood	Heartwood	Whole organ	$R_{m,A}$	$R_{m,V}$	$R_{m,Np}$	$R_{m,Ns}$	$R_{m,N}$	
(1)	3–4	6.01 ± 0.235	5.87 ± 0.280	90.1 ± 19.7	1.20 ± 0.146	0.00	5.84 ± 1.37	1.06 ± 0.193	–	1.39 ± 0.171	1.72 ± 0.734	116 ± 44.5	8.73 ± 3.98	3.38 ± 0.618	2.42 ± 0.639	2
	5–7	8.53 ± 1.47	8.37 ± 1.43	143 ± 40.9	2.55 ± 0.879	0.00	5.24 ± 1.16	0.816 ± 0.126	–	1.05 ± 0.0896	1.62 ± 0.158	79.3 ± 16.8	8.26 ± 0.414	3.10 ± 0.891	2.23 ± 0.516	4
	8–12	13.3 ± 1.71	13.0 ± 1.55	260 ± 44.8	6.14 ± 1.51	0.00	4.00 ± 0.825	0.599 ± 0.073	–	0.738 ± 0.0847	1.30 ± 0.256	40.7 ± 9.38	7.23 ± 0.579	2.08 ± 0.478	1.61 ± 0.307	6
	13–19	18.3 ± 1.82	17.4 ± 1.58	392 ± 56.5	10.3 ± 1.39	0.694 ± 0.668	3.44 ± 0.478	0.453 ± 0.0378	0.352 ± 0.0864	0.550 ± 0.0402	1.15 ± 0.185	28.1 ± 4.47	6.59 ± 0.956	1.91 ± 0.450	1.41 ± 0.284	7
	20	24.3 ± 3.18	21.2 ± 1.88	533 ± 97.9	14.0 ± 2.32	2.53 ± 1.36	3.02 ± 0.257	0.467 ± 0.0708	0.368 ± 0.0559	0.533 ± 0.0550	1.13 ± 0.146	25.1 ± 3.74	6.69 ± 1.01	1.68 ± 0.400	1.15 ± 0.146	7
(2)	3–4	2.36 ± 0.645	2.36 ± 0.645	49.0 ± 17.9	0.167 ± 0.0873	0.00	4.94 ± 0.464	1.27 ± 0.209	–	2.16 ± 0.446	1.18 ± 0.302	201 ± 16.9	5.18 ± 1.20	6.30 ± 0.612	2.83 ± 0.482	3
	5–7	2.82 ± 0.856	2.81 ± 0.836	58.4 ± 24.7	0.258 ± 0.170	0.00	4.51 ± 0.473	1.00 ± 0.186	–	1.72 ± 0.344	1.00 ± 0.280	151 ± 57.7	4.86 ± 1.23	5.56 ± 1.68	2.55 ± 0.603	18
	8–12	4.09 ± 0.749	4.02 ± 0.763	101 ± 12.7	0.515 ± 0.218	0.00	3.84 ± 0.183	0.768 ± 0.112	–	1.32 ± 0.105	0.838 ± 0.318	81.1 ± 16.7	3.91 ± 1.82	3.81 ± 0.513	1.85 ± 0.525	4
(3)	3–4	0.93 ± 0.214	0.928 ± 0.214	10.6 ± 2.41	0.0225 ± 0.0125	0.00	5.27 ± 0.265	1.92 ± 0.361	–	3.13 ± 0.640	0.798 ± 0.295	349 ± 114	5.88 ± 2.24	9.01 ± 3.51	3.44 ± 1.18	9
	5–7	1.02 ± 0.178	1.02 ± 0.178	11.8 ± 3.22	0.0275 ± 0.0108	0.00	4.87 ± 0.526	1.54 ± 0.247	–	2.58 ± 0.441	0.680 ± 0.175	272 ± 74.4	5.43 ± 1.14	7.86 ± 2.29	3.18 ± 0.728	9

Table 4. Models of maintenance respiration at 15 °C (R_m) of *P. pinaster* woody parts. Abbreviations: W_s, N_s and W_p, N_p are dry mass (kg) and nitrogen concentration (mg g^{-1}) of sapwood and phloem, respectively; D is diameter of the annual growth unit (m); L is its length (m); and Y is its age (year). An asterisk (*) indicates a value not significantly different from zero.

Model	Equation R_m (15 °C) (µmol s^{-1})	Parameter value				$\frac{\sum(\hat{y}_i - y_i)^2 / \lvert y_i \rvert}{n}$
		a	*b*	*c*	*d*	
1	$R_m = aW_s(N_s - b) + cW_p(N_p - d)$	0.0810	0.0535*	0.722	2.38	0.00672
2	$R_m = aLD^b/Y^c$	41.2	1.44	0.624		0.00680

(3–4 years or 5–7 years) and diameter range, $R_{m,A}$ of the stem was twice the value found for the third-order branches. Similarly, the effect of diameter was different for area-based ($R_{m,A}$ or $R_{m,Np}$) versus volume-based ($R_{m,V}$, $R_{m,Ns}$ and $R_{m,N}$) respiration rates. In branches, area respiration was unaffected by diameter, but in the stem, it decreased slightly with diameter. The volume respiration rate decreased exponentially with axis diameter: the diameter effect was greatest for small diameters (Figures 2 and 3).

Modeling maintenance respiration

Two maintenance respiration models of the woody axes at 15 °C were compared (Table 4). Model 1 was used to investigate the partitioning of R_m between the two living tissues, i.e., the phloem and sapwood. Their respective contributions were made proportional to their mass and nitrogen concentration, i.e., their nitrogen content. Fitting this model to observed data made it possible to estimate the phloem contribution as 34 to 70% of total R_m for stems, and 78 to 88% of total respiration for branches (Figure 4). This result largely reflected a shape effect, sapwood being more important in thicker axes and less important in small branches. Model 2 (Table 4) was designed to allow R_m to be estimated at the stand scale. Because age and size distributions of stems and branches are known for *P. pinaster* stands (Porté et al. 2000, Porté et al. 2002), these variables were chosen as independent variables of the model, making it possible to estimate R_m based on nondestructive measurements. Model 2 was based on the observation that, for a given diameter, R_m decreased with sample age. We note that the form of the model, D^b/Y^c (where D is diameter and Y is

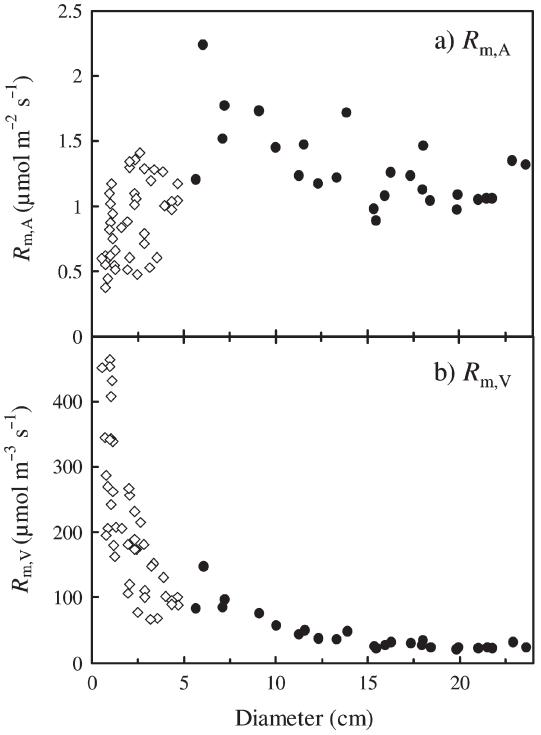

Figure 2. Relationship between segment diameter and maintenance respiration expressed per unit area (a) and volume (b). Symbols: ◇ = branches and ● = stems.

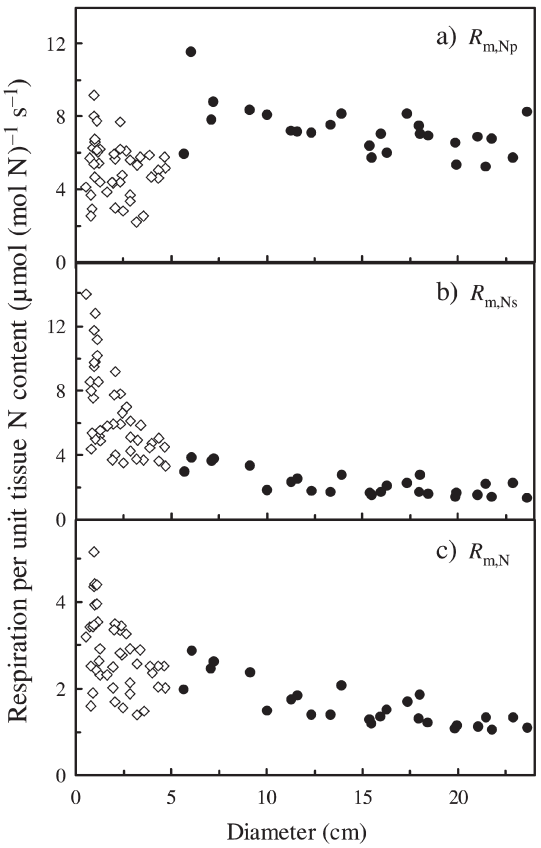

Figure 3. Maintenance respiration of woody samples per unit of nitrogen contained in the phloem (a) or sapwood (b) and per unit total nitrogen content (c), according to their diameter. Symbols: ◇ = branches and ● = stems.

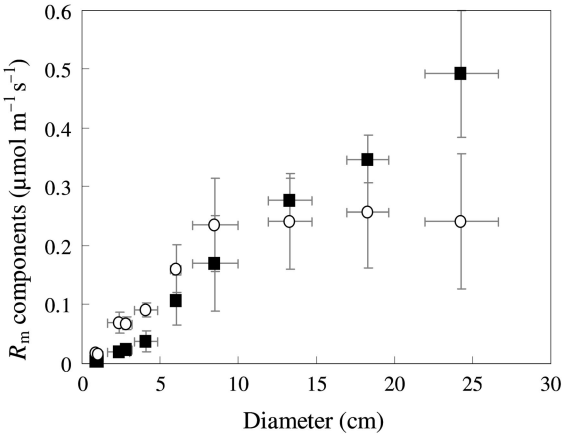

Figure 4. Relationship between organ diameter and maintenance respiration (R_m) of phloem and sapwood as estimated from Model 1, for sample groups defined in Table 3. Symbols: ■ = sapwood component and ○ = phloem component. Standard deviations of R_m components and of diameter by sample groups are indicated.

age), is analogous to a growth rate averaged over the life span of the woody organ.

Statistical performances of the models were similar (Figure 5). Both explained more than 97% of the variance in R_m. No significant deviation from 1 was observed in the slope of the relationship between observed and modeled data and the intercept was not significantly different from zero.

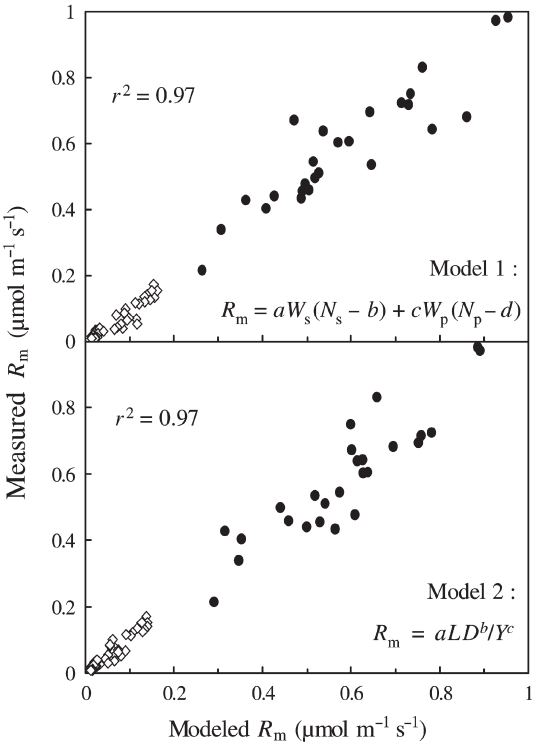

Figure 5. Comparison between measured maintenance respiration (R_m) values and values estimated with Models 1 (a) and 2 (b) (Table 4). Symbols: ◇ = branches and ● = stems.

Discussion

Continuous diameter recordings on the stem and seven branches of the tree used for the field measurements of R_m (Bosc 1999) showed that radial growth stopped between the beginning of July and mid-August. Because several authors have shown that growth respiration of stems continues for 4 to 6 weeks after diameter growth has ceased (Havranek 1985), our first field measurements made in early September may include a growth respiration component. Therefore, assuming that growth rate and maintenance components have the same temperature dependency, respiration measurements in the field were used to study only the short-term temperature dependency of R_m. We found no evidence of a change in sample Q_{10} during the field study (Table 2). Laboratory measurements extending from October 27 to December 6 were interpreted as reflecting strictly R_m.

We observed a hysteresis in the respiration–temperature relationship during field measurements. This phenomenon showed a slight, nonsignificant dependence on the organ considered. A similar observation has been made on larger stem pieces where a hysteresis lag of 2 or 3 h was estimated (Ryan et al. 1995, Lavigne et al. 1996). Three explanations of the hysteresis have been proposed: (1) heterogeneity of organ temperature because of heat storage in the living tissues (Kakubarri 1989, Stockfors 2000); (2) delay between CO_2 production in living tissues and CO_2 efflux at the organ surface (Hari et al. 1990); and (3) CO_2 export and import by xylem sap flow (Kakubarri 1988, Hari et al. 1990, Martin et al. 1994, Levy et al. 1999). For *P. pinaster*, explanations 1 and 2 are unlikely because of the lack of a significant relationship between the hysteresis lag, Δt, and sample diameter.

Maintenance respiration rates and Q_{10} values obtained for *P. pinaster* were similar to those of other pine species (Ryan et al. 1994). The temperature dependency of R_m of *P. pinaster* woody parts followed an exponential response similar to those reported for many pine species (Ryan 1990, Carey et al. 1997). The model adjusted for all organs resulted in a Q_{10} = 2.13, which fitted well to the entire data set, except at high temperatures for a few measurements of sample G, which had the highest individual Q_{10}. Most previous studies on maintenance respiration of the woody parts of pine species have been concerned with the main stem, with fewer studies of branch maintenance respiration (Ryan et al. 1994, Damesin et al. 2002, Ceschia et al. 2003). Ryan et al. (1994) reported values of the reference rate of maintenance respiration, $R_m(15)$, ranging from 0.8 to 62 nmol C (mol C)$^{-1}$ s^{-1} according to the pine species and axis type (trunk, branch, twig) considered. For *P. pinaster*, stem $R_m(15)$ (1.13 and 1.72 μmol m^{-2} s^{-1}) was close to that in *Pinus taeda* L. (0.64–1.47 μmol m^{-2} s^{-1}), but less than that in *Pinus contorta* Dougl. (6.5 μmol m^{-2} s^{-1}). Branch $R_m(15)$ in *P. pinaster* (0.68–1.18 μmol m^{-2} s^{-1}) was larger than in *P. taeda* (0.36–0.60 μmol m^{-2} s^{-1}) (Maier et al. 1998) and less than in *P. contorta* (4.3 and 1.3 μmol m^{-2} s^{-1}) (Ryan et al. 1994).

Efflux of CO_2 from the axis, as measured in both field and laboratory experiments, can be attributed to respiration alone

because all laboratory measurements were made in the dark in opaque chambers. In the field, we observed that the youngest branches and twigs had significant photosynthetic capacity, indicated, for example, by their chlorophyll content. However, for this species, neither the CO_2 assimilation rate of the bark nor the refixation rate of CO_2 respired has been quantified. This phenomenon appears to be significant for other species (Levy and Jarvis 1998) and may play an important role in the carbon balance of woody organs.

For *P. pinaster*, R_m of woody organs was more closely correlated with organ surface area than with organ volume. Moreover, the relationship between respiration and tissue N content was largely dependent on the diameter of the woody sample. The amount of N contained in the phloem was strongly correlated with the woody surface area, whereas the amount of N contained in sapwood or in whole woody organs was correlated with volume. From our measurements, it was not possible to predict respiration from N content alone. Similarly, for *P. taeda*, Maier et al. (1998) observed no simple relationship between R_m and N, and used two separate models for the branches and stem, both based on the N content of the external 2 cm of wood. Our results suggest that the contribution of tissue respiration to CO_2 efflux rate at the surface of the axis changed according to the tissue location within the axis, with deeper tissues having a lower respiration rate per unit nitrogen.

Respiration of woody parts of *P. pinaster* varied with age and branching order, regardless of measurement basis (length, diameter, volume, or nitrogen concentration): no single size variable described the variation in respiration within a whole *P. pinaster* tree. Similar results were obtained by Levy and Jarvis (1998) in two sahelian shrub species (*Guiera senegalensis* J.F. Gmel. and *Combretum micranthum* G. Don). Taking into account the different respiration rates of the sapwood and phloem tissues, these authors demonstrated how the relationships between R_m and area or volume change with stem diameter. Model 1, which partitions R_m between phloem and sapwood, suggests that R_m per unit nitrogen was greater in phloem than in sapwood (cf. values of c and a in Table 4). This result is consistent with recent experiments carried out in vitro on wood cores in *Pseudotsuga menziesii* Mirb. (Pruyn et al. 2002). We conclude that the phloem respiration was the larger component of respiration in small woody organs (diameter < ~0.10 m) (Figure 4), whereas sapwood respiration was dominant for the largest organ. This conclusion may justify the use of surface area or sapwood volume for scaling R_m to the tree or stand level (Ryan et al. 1994, Edwards and Hanson 1996).

An original and practical result of our work is the strong relationship between R_m and organ age, as described in Model 2 by the scaling factor D^b/Y^c. Model 2 explains most of the variability of respiration among woody segments. Model 2, which can be rewritten using surface area (S; m^2) or volume (V; m^3) of the organ ($R_m = aLD^{1.44}/Y^c = a'SD^{0.44}/Y^c = a''V/D^{0.56}/Y^c$), also reveals that there is an additional dependence of stem or branch R_m on D and Y and that this dependence can be formalized in a simple equation that may be used for upscaling. From Model 2 we can infer that, for a given diameter, R_m of an organ decreases by 65% when its age doubles, whereas at a given age, R_m is increased by 271% when the diameter doubles. This amplification of respiration with diameter is greater than a strict respiration–area relationship (200%) but smaller than a respiration–volume relationship (400%). The scaling factor $D^{1.44}/Y^{0.624}$ (= $(D^2)^{0.72}/Y^{0.624}$) (Table 4) is approximately proportional to $(S_c/Y)^\alpha$, where S_c is the cross-sectional area of the organ (m^2) and α is a constant. It may therefore be interpreted as a surrogate of secondary growth rate. Lavigne and Ryan (1997) found a similar result among tree stems. The observation (Ryan et al. 1996) that the lower branches of a *P. radiata* D. Don canopy had a lower maintenance respiration rate than branches in the upper two thirds of the canopy, which have a greater growth rate, are also consistent with our findings. Physiological causes of differences between the respiration rates of young and older branches remain to be clarified, in terms of protein turnover, active transport processes, storage and release of carbohydrate reserves and secondary metabolism. The allocation of phloem nitrogen between active metabolite pools and reserve proteins may also differ and lead to a discrepancy between respiration rates when expressed on a nitrogen content basis.

Conclusion

Respiration characteristics of *P. pinaster* are similar to those of other pine species in terms of temperature dependence and maintenance respiration rate. We found that branch age, independently of diameter, had a major influence on R_m. This influence was partly explained by temporal changes in woody tissue composition and by a change in tissue respiration rate per unit dry mass (linked to their nitrogen content). Models 1 and 2 allow us to better explain and predict R_m than models based on area or volume relationships alone. In particular, for scaling woody tissue R_m to the tree and stand levels, the new and practical Model 2, $R_m = aLD^b/Y^c$, can be used when data on the distribution of woody tissues according to age, length and diameter are available. These data can be obtained directly by nondestructive measurements of tree architecture or estimated by tree architecture modeling (De Reffye et al. 1997, Bosc 2000).

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References

Amthor, J.S. 1989. Respiration and crop productivity. Springer-Verlag, New York, 214 p.

Amthor, J.S. 1991. Respiration in a future, higher-CO_2 world. Plant Cell Environ. 14:13–20.

Amthor, J.S. 2000. The McCree–de Wit–Penning de Vries–Thornley respiration paradigms: 30 years later. Ann. Bot. 86:1–20.

Berbigier, P. and J.M. Bonnefond. 1995. Measurement and modelling of radiation transmission within a stand of maritime pine (*Pinus pinaster* Ait). Ann. Sci. For. 52:23–42.

Berbigier, P., J.M. Bonnefond and P. Mellmann. 2001. CO_2 and water vapour fluxes for 2 years above Euroflux forest site. Agric. For. Meteorol. 108:183–197.

Bosc, A. 1999. Etude expérimentale du fonctionnement hydrique et carboné des organes aériens du Pin maritime (*Pinus pinaster* Ait.): intégration dans un modèle Structure-Fonction appliqué à l'analyse de l'autonomie carbonée des branches de la couronne d'un arbre adulte. Thése de Doctorat de l'Université Victor Segalen Bordeaux 2, 225 p.

Bosc, A. 2000. EMILION, a tree functional-structural model: presentation and first application to the analysis of branch carbon balance. Ann. For. Sci. 57:555–569.

Brix, H. 1971. Effects of nitrogen fertilization on photosynthesis and respiration in Douglas-fir. For. Sci. 4:407–414.

Cannell, M.G.R. and J.H.M. Thornley. 2000. Modelling the components of plant respiration: some guiding principles. Ann. Bot. 85: 45–54.

Carey, E.V., R.M. Callaway and E.H. DeLucia. 1997. Stem respiration of ponderosa pines grown in contrasting climates: implications for global climate change. Oecologia 111:19–25.

Ceschia, E., C. Damesin, S. Lebaube, J.-Y. Pointailler and E. Dufrêne. 2003. Spatial and seasonal variations in stem respiration of beech trees (*Fagus sylvatica*). Ann. For. Sci. In Press.

Damesin, C., E. Ceschia, N. Goff, J.M. Ottorini and E. Dufrêne. 2002. Stem and branch respiration of beech: from tree measurements to estimations at the stand level. New Phytol. 153:159–172.

David, R.L. 2000. Handbook of chemistry and physics. 81st Edn. Chapman and Hall, CRC Press, 2556 p.

De Reffye, P., T. Fourcaud, F. Blaise, D. Barthélémy and F. Houllier. 1997. A functional model of tree growth and tree architecture. Silva Fenn. 31:297–311.

Edwards, N.T. and P.J. Hanson. 1996. Stem respiration in a closed-canopy upland oak forest. Tree Physiol. 16:433–439.

Field, C.B., J.T. Ball and J.A. Berry. 1989. Photosynthesis: principles and field techniques. *In* Plant Physiological Ecology: Field Methods and Instrumentations. Eds. R.W. Pearcy, J. Ahleringer, H.A. Mooney and P.W. Rundel. Chapman and Hall, London, pp 209–253.

Frossard, J.S., C. Gary, N. Brisson, F. Tabourel and B. Adam. 1996. Energétique et croissance: du tissu à la plante entière. Actes de l'école des chercheurs INRA en bioclimatologie, Tome 1: de la plante au couvert végétal. Le Croisic, France, pp 181–196.

Hagihara, A. and K. Hozumi. 1991. Respiration. *In* Physiology of Trees. Ed. Raghavendra. Wiley Interscience Publication, New York, pp 87–110.

Hari, P., P. Nygren and E. Korpilahti. 1990. Internal circulation of carbon within a tree. Can. J. For. Res. 21:514–515.

Havranek, W.M. 1985. Gas exchange and dry matter allocation in larch at the alpine timberline on Mount Patscherkofel. *In* Establishment and Tending of Subalpine Forest: Research and Management. Eds. H. Turner and W. Tranquiliini. Eidg. Anst. Forstl. Versuchswes. Mitt. 270:135–142.

Kakubarri, Y. 1988. Diurnal and seasonal fluctuation in the bark respiration of standing *Fagus sylvatica* trees at Solling, West Germany. J. Jpn. For. Soc. 70:64–70.

Kakubarri, Y. 1989. Diurnal and seasonal fluctuation in the bark respiration of standing *Quercus acutissima* trees in Nakaisu, Japan. Ann. Sci. For. 46:529–531.

Landsberg, J.J. 1986. Physiological ecology of forest production. Academic Press, London, 198 p.

Lavigne, M.B. 1987. Differences in stem respiration responses to temperature between balsam fir trees in thinned and unthinned stands. Tree Physiol. 3:225–233.

Lavigne, M.B. and M.G. Ryan. 1997. Growth and maintenance respiration rates of aspen, black spruce and jack pine stems at northern and southern BOREAS sites. Tree Physiol. 17:543–551.

Lavigne, M.B., S.E. Franklin and E.R. Hunt. 1996. Estimating stem maintenance respiration rates of dissimilar balsam fir stands. Tree Physiol. 16:687–695.

Levy, P.E. and P.G. Jarvis. 1998. Stem CO_2 fluxes in two sahelian shrub species (*Guiera senegalensis* and *Combretum micranthum*). Funct. Ecol. 12:107–116.

Levy, P.E., P. Meir, S.J. Allen and P.G. Jarvis. 1999. The effect of aqueous transport of CO_2 in xylem sap on gas exchange in woody plants. Tree Physiol. 19:53–58.

Loustau, D., J.C. Domec and A. Bosc. 1998. Interpreting the variations in xylem sap flux density within the trunk of maritime pine (*Pinus pinaster* Ait.): application of a model for calculating water flows at tree and stand levels. Ann. Sci. For. 55:29–46.

Maier, C.A., S.J. Zarnoch and P.M. Dougherty. 1998. Effects of temperature and tissue nitrogen on dormant season stem and branch maintenance respiration in a young loblolly pine (*Pinus taeda*) plantation. Tree Physiol. 18:11–20.

Martin, T.A., R.O. Teskey and P.M. Dougherty. 1994. Movement of respiratory CO_2 in stems of loblolly pine (*Pinus taeda* L.) seedlings. Tree Physiol. 14:481–495.

Penning de Vries, F.W.T. 1975. The cost of maintenance processes in plant cells. Ann. Bot. 39:77–92.

Penning de Vries, F.W.T., A.H.M. Brunsting and H.H. van Laar. 1974. Products, requirements and efficiency of biosynthesis: a quantitative approach. J. Theor. Biol. 45:339–377.

Porté, A. 1999. Modélisation des effets du bilan hydrique sur la production primaire et la croissance d'un couvert de Pin maritime (*Pinus pinaster* Aït) en Lande humide. Thèse de Doctorat de l'Université de Paris XI, Orsay, France, 197 p.

Porté, A., A. Bosc, I. Champion and D. Loustau. 2000. Estimating the foliage biomass and area of maritime Pine (*Pinus pinaster* Ait.) branches and crowns with application to modelling the foliage area distribution in the crown. Ann. For. Sci. 57:73–86.

Porté, A., P. Trichet, D. Bert, D. Loustau. 2003. Allometric relationships for branch and tree woody biomass of maritime Pine (*Pinus pinaster* Ait.). For. Ecol. Manage. In press.

Pruyn, M.L., B.L. Gartner and M.E. Harmon. 2002. Within-stem variation of respiration in *Pseudotsuga menziesii* (Douglas-fir) trees. New Phytol. 154:359–372.

Ryan, M.G. 1990. Growth and maintenance respiration in stems of *Pinus contorta* and *Picea engelmannii*. Can. J. For. Res. 20:48–57.

Ryan, M.G. and R.H. Waring. 1992. Maintenance respiration and stand development in a subalpine lodgepole pine forest. Ecology 73:2100–2108.

Ryan, M.G., S.T. Gower, R.M. Hubbard, R.H. Waring, H.L. Gholz, W.P. Cropper, Jr. and S.W. Running. 1995. Woody tissue maintenance respiration of four conifers in contrasting climates. Oecologia 101:133–140.

Ryan, M.G., S. Linder, J.M. Vose and R.M. Hubbard. 1994. Dark respiration of pines. Ecol. Bull. 43:50–63.

Ryan, M.G., R.M. Hubbard, S. Pongracic, R.J. Raison and R.E. McMurtrie. 1996. Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. Tree Physiol. 16:333–343.

Sprugel, D.G. 1990. Components of woody-tissue respiration in young *Abies amabilis* (Doug.) Forbes trees. Trees 4:88–98.

Stockfors, J. 2000. Temperature variations and distribution of living cells within tree stems: implications for stem respiration modeling and scale-up. Tree Physiol. 20:1057–1062.

Thornley, J.H.M. and M.G.R. Cannell. 2000. Modelling the components of plant respiration: representation and realism. Ann. Bot. 85: 55–67.

Weiss, R.F. 1974. Carbon dioxide in water and seawater: the solubility of a non-ideal gas. Mar. Chem. 2:203–215.

Witowshi, J. 1997. Gas exchange of the lowest branches of young Scots pine: a cost-benefit analysis of seasonal branch carbon budget. Tree Physiol. 17:757–765.

Appendix

Laboratory measurements of respiration were made on cut branches and logs. Because cut sections of these axes could lose CO_2 and thus falsify respiration measurements, we modeled this effect to determine the optimal location on the excised samples for measurement of respiration. In the model, CO_2 flux in samples is based on the following simplifications: (1) the system is assumed to be a cylindrical volume of water without mass transfers; (2) CO_2 is uniformly produced by respiration in the cylinder; (3) CO_2 solubility and diffusivity in the system are similar to those of CO_2 in water; and (4) the system temperature is 15 °C.

For a sample slice whose thickness is dx (m), the variation in CO_2 concentration C over time is:

$$\frac{dC}{dt}(x,t) = R_{m,V} - R^*_{m,V}(x) + F_l \quad \text{(A1)}$$

where t is time (s), x is distance to the cut end (m), $R_{m,V}$ is maintenance respiration per unit volume (μmol m^{-3} s^{-1}), $R^*_{m,V}$ is apparent maintenance respiration corresponding to the flux of CO_2 through the bark of the sample (measured flux) (μmol m^{-3} s^{-1}), and F_l is lateral diffusive flux of CO_2 (μmol m^{-3} s^{-1}) (Figure A1). The expressions for $R^*_{m,V}$ and F_l are:

$$R^*_{m,V}(x) = G_c \frac{pCO_{2i}(x) - pCO_{2a}}{P} \frac{4}{\phi} \quad \text{(A2)}$$

$$\text{with } pCO_{2i}(x) = C(x)/K^*_h$$

$$F_{l_1} = D_c \frac{d^2C}{dx^2}(x) \quad \text{(A3)}$$

where G_c is bark–air conductance for CO_2 (μmol m^{-2} s^{-1}), $pCO_{2i}(x)$ and pCO_{2a} are the partial pressures of CO_2 in the system at x and in air (μmol mol^{-1}), respectively, P is atmospheric pressure (Pa), K^*_h is the solubility constant (Henry's law) for all CO_2 products in water, $4/\phi$ is the ratio of sample perimeter over the section (ϕ is the sample diameter (m)) and D_c is the diffusivity constant of CO_2 in water.

When stability is reached,

$$\frac{dC}{dt}(x,t) = 0$$

and we obtain the following differential equation for $C(x)$:

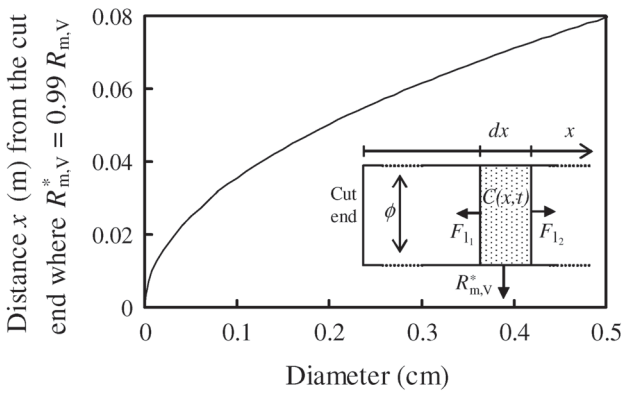

Figure A1. Effect of sample diameter on distance from the cut end of the section (x) where the apparent maintenance respiration ($R^*_{m,V}$) (flux measured with gas exchange system) is equal to 99% of $R_{m,V}$. The smaller diagram illustrates the components of the model.

$$(R_{m,V} + G_c\, pCO_{2a}\frac{4}{\phi}) - \frac{4G_c}{\phi K_h}C(x) + D_c\frac{d^2C}{dx^2}(x) = 0 \quad \text{(A4)}$$

If we consider that, at the cut end ($x = 0$), aqueous CO_2 concentration in the sample is in equilibrium with air CO_2 pressure ($C(0) = K^*_h\, pCO_{2a}$), and that, for a point in the sample that is infinitely far from the cut end, there are no lateral fluxes ($R^*_{m,V}(+\infty) = R_{m,V}$), it is possible to solve the equation and to express $R^*_{m,V}(x)$ from $R_{m,V}$ by using Equation A2:

$$R^*_{m,V}(x) = (1 - e^{kx})R_{m,V} \quad \text{(A5)}$$

$$\text{with } k = \sqrt{\frac{4G_c}{\phi K^*_h D_c}}$$

The physical constants K^*_h = 440 μmol m^{-3} Pa^{-1} (Weiss 1974) and $D_c = 1.45 \times 10^{-9}$ m^2 s^{-1} (David 2000) at 15 °C are known; however, G_c is unknown for *P. pinaster* and no literature reference for another species was found. The difference between $R^*_{m,V}$ and $R_{m,V}$ increases with decreasing G_c (Equation A5). Therefore, for maximum precaution, we estimated G_c from the equation $G_c = R_{m,V}P/(pCO_{2i} - pCO_{2a})$ based on data that minimized G_c; i.e., maximal pCO_{2i} = 25,000 Pa (25%) (Chase 1930 cited by Levy et al. (1999)) and minimal measured $R_{m,A}$ = 0.5 μmol m^{-2} s^{-1}. The G_c value thus obtained was 2 μmol m^{-2} s^{-1}.

We calculated the distance for which $R^*_{m,V}(x)$ is equal to 99% of $R_{m,V}$ as a function of diameter (Figure A1). For the diameter range of studied samples (0.6–25 cm), this distance was less than 6 cm. Therefore, to avoid effects of cutting on the respiration measurements made in the laboratory, no measurements were carried out on the first 50 cm from the cut section. For branches, we plunged the cut section in water; this was unnecessary for the trunk sections because these were fully covered by natural resin.