ORIGINAL ARTICLE

Gerhard Wieser · Michael Bahn

Seasonal and spatial variation of woody tissue respiration in a *Pinus cembra* tree at the alpine timberline in the central Austrian Alps

Abstract Total stem, branch, twig, and coarse root respiration (R_t) of an adult *Pinus cembra* tree at the alpine timberline was measured continuously at ten positions from 7 October 2001 to 21 January 2003 with an automated multiplexing gas exchange system. There was a significant spatial variability in woody tissue respiration when expressed per unit surface area or per unit sapwood volume. Surface area related maintenance (R_m) respiration at 0°C ranged between 0.109 and 0.643 μmol m^{-2} s^{-1} and there was no clear trend with respect to tissue type and diameter. Sapwood volume based R_m at 0°C by contrast, varied between 2.5 μmol m^{-3} s^{-1} in the stem and 193.2 μmol m^{-3} s^{-1} in thin twigs in the upper crown. Estimated Q_{10} values ranged from 1.7 to 3.1. These Q_{10} values were used along with R_m at 0°C and annual woody tissue temperature records to predict annual total R_m. Annual total R_m accounted for 73±6% of annual R_t in 2002.

Keywords *Pinus cembra* · Timberline · Coarse root · Stem · Branch and twig respiration

Introduction

Net carbon gain of a tree or a forest ecosystem is the balance between total canopy net photosynthesis and the amount of carbon lost via autotrophic respiration of the foliage and woody tissues. In forest ecosystems the fraction of net photosynthetic production consumed by respiration of foliage and woody tissue is approximately 50–70% (Ryan et al. 1994) and annual woody tissue respiration alone consumes 11–23% of total carbon assimilation (Ryan 1991). Despite the many studies on carbon uptake and foliage respiration in *Pinus cembra* woody tissue respiration received little attention and has only been investigated using cut sections under laboratory conditions (Tranquillini 1959; Tranquillini and Schütt 1970) or in field measurements in weekly or longer intervals (Havranek 1981).

Woody tissue respiration and Q_{10} of forest trees has been shown to vary significantly within an entire tree (Tranquillini and Schütt 1970; Sprugel 1990; Maier et al. 1998; Ceschia et al. 2002; Damesin et al. 2002; Bosc et al. 2003). Therefore, it was the goal of this study to examine the seasonal and spatial variations in stem, branch, twig and coarse root respiration within an entire adult *P. cembra* tree at the upper timberline in the central Austrian Alps.

G. Wieser (✉)
Bundesamt und Forschungszentrum für Wald, Abt.
Forstpflanzenphysiologie,
Rennweg 1,
6020 Innsbruck, Austria
e-mail: gerhard.wieser@uibk.ac.at
Tel.: +43-512-5739335210
Fax: +43-512-5739335250

M. Bahn
Institut für Botanik der Universität Innsbruck, Abt. Ökologie,
Sternwartestraße 15,
6020 Innsbruck, Austria

Materials and methods

The study was carried out in an open, approximately 95-year-old cembran pine stand at the upper timberline at 1,950 m a.s.l. near the Klimahaus Research Station on Mt. Patscherkofel (47°N, 11°E) south of Innsbruck, Austria. The field site is characterized by a cool subalpine climate with low temperatures, the possibility of frost in all months and a continuous snow cover from October until May. Forty years of meteorological data recorded from the weather station at the study site show a mean annual temperature of 2.4°C and the mean annual precipitation is 950 mm.

Scaffolding provides access to the crown of a 9 m high *P. cembra* tree that was not shaded by neighboring trees. Woody tissue respiration was measured by means of a multiplexing, open gas exchange system. Sections of stems, branches, twigs and coarse roots were enclosed permanently in chambers made of clear Perspex and CO_2 evolution through the bark was monitored continuously from 7 October 2001 to 21 January 2003. The chambers were placed selectively at ten positions covering the range of conditions that were expected to reflect the spatial variability of woody tissue respiration within the entire tree (Table 1). The restriction to one single tree was necessary due to the technical requirements of the gas exchange system, and the fact that at the study site the distance from one tree to another is more than 20 m on average.

Table 1 Position of chambers and thermocouples installed on the experimental tree, diameter of the respiratory surface at termination of measurements enclosed in the chambers, and corresponding sapwood volume under the bark of the woody tissues selected for respiration measurements in a *P. cembra* tree at the alpine timberline near the Klimahaus Research Station, Mt. Patscherkofel, Tyrol (1,950 m)

Tissue and position	Elevation above ground (m)	Distance to stem (m)	Stem diameter (mm)	Area (cm^2)	Sapwood volume (cm^3)
Stem south	5.9	–	82.0	185	574
Stem south	3.5	–	160.0	234	995
Stem south	1.6	–	320.0	293	1,521
Stem north	1.6	–	320.0	293	1,419
Root north	0	0.7	96	112	872
Root south	0	0.5	123	112	1,514
Branch south	5.5	0.3	18.6	44	20
Branch south	3.5	0.5	47.0	190	171
Twig south	6.9	0.5	17.2	62	26
Twig south	3.5	2.5	7.4	21	3.8

Putty (Terostat, Teroson, Ludwigsburg, Germany) and nonhardening insulating foam was used to ensure a gas-tight seal between the chambers and the bark. Ambient air was continuously sucked through each chamber with flow rates between 0.3 and 6.0 l min^{-1}. All the pneumatic tubing was heated and insulated. CO_2 concentration of the airstreams through the chambers and of the reference air, sampled 2 m above the top of the tree, was measured using an infrared gas analyzer (LI-6262, Li-Cor, Lincoln, Neb.) operating in the absolute mode. The corresponding flow rates were monitored with an electronic mass flow-meter (Model 179, MKS Instruments, Andover, Mass.). All the gas streams were measured alternately by means of a solenoid-based gas-switching system. Each air stream was sampled for 80 s with the first 60 s being ignored in order to allow a total flushing of the gas analyzer. Woody tissue CO_2 efflux rate was based on the surface area enclosed in each chamber and the corresponding sapwood volume under the bark (Table 1).

Simultaneously, tissue temperatures were monitored inside and outside the chambers with 1 mm thin type T thermocouples inserted into the bark down to the cambial surface. Relative to the tissue position outside the chambers mean maximum overheating of the tissue in the chambers reached 2.1 K with absolute maxima up to +8.9 K during short periods of high irradiance but otherwise was negligible.

All the data were transmitted to an AM416 multiplexer (Campbell Scientific, Shepshed, UK) and recorded with a Campbell CR10 data logger, programmed to record 30-min means. The data logger also controlled the switching of the solenoids.

The temperature response of woody tissue respiration was estimated according to the exponential equation

$$R = R_0 \exp [\ln Q_{10}(T/10)], \qquad (1)$$

where R is the woody tissue CO_2 efflux, R_0 is the CO_2 efflux at a tissue temperature of 0°C, Q_{10} is the temperature sensitivity of woody tissue respiration and T is the measured tissue temperature.

The mature tissue method (Amthor 1994; Sprugel et al. 1995) has been used to subdivide total respiration (R_t) into maintenance (R_m) and growth respiration (R_g). Values of R_0 and Q_{10} estimated during the dormant season (December to February) and the annual position specific sapwood temperature records were used with Eq. 1 to estimate annual R_m. Annual R_g was then calculated as the difference between R_t and R_m.

Following the seasonal woody tissue respiration measurements, tissue samples were taken at mid-length of each chamber and nitrogen (N) concentrations of dried and ground sapwood were measured in triplicate by means of an elemental analyzer (Leco CHNS 932, Leco St Joseph, Mich., USA).

Results and discussion

Typical variations in tissue temperature and twig, branch, stem, and coarse root respiration are shown in Fig. 1. Changes in CO_2 efflux generally followed seasonal trends in temperatures (Fig. 1) as has also been observed in other trees species in temperate and boreal forest ecosystems (Linder and Troeng 1981; Havranek 1981, 1985; Edwards and Hanson 1996; Ryan et al. 1996; Lavigne and Ryan 1997; Ceschia et al. 2002; Gansert et al. 2002). CO_2 efflux

Table 2 Spatial variation in annual total (R_t), maintenance (R_m) and growth respiration (R_g) rates per unit surface area (R_A; g cm^{-2} year^{-1}) and per unit sapwood volume (R_S; kg cm^{-3} year^{-1}) during the period 1 January 1 to 31 December 2002

Position	Elevation above ground (m)	R_t		R_m		R_g	
		R_A	R_S	R_A	R_S	R_A	R_S
Stem south	5.9	100.7	3.25	73.6	2.38	27.1	0.87
Stem south	3.5	77.5	1.82	57.0	1.34	20.5	0.48
Stem south	1.5	431.9	7.55	246.8	4.31	185.1	3.24
Stem north	1.5	343.2	7.07	262.3	5.41	80.9	1.66
Root south	0	373.8	2.77	298.6	2.21	75.2	0.56
Root north	0	325.8	4.18	238.5	3.06	87.3	1.12
Branch south	5.5	536.9	117.04	403.3	87.93	133.6	29.11
Branch south	3.5	221.0	24.54	159.1	17.67	61.9	6.87
Twig south	6.9	624.1	149.56	465.5	111.56	158.6	38.00
Twig south	3.5	352.4	199.33	265.4	150.11	87.0	49.22

Fig. 1 Time courses of mean daily twig, branch, stem, and coarse root cambium temperature (*T*; *white line*), and corresponding daily mean area-based respiration (*R*; *black line*) between 7 October 2001 and 21 January 2003. *Gray bars* indicate the daily maximum and minimum *T*
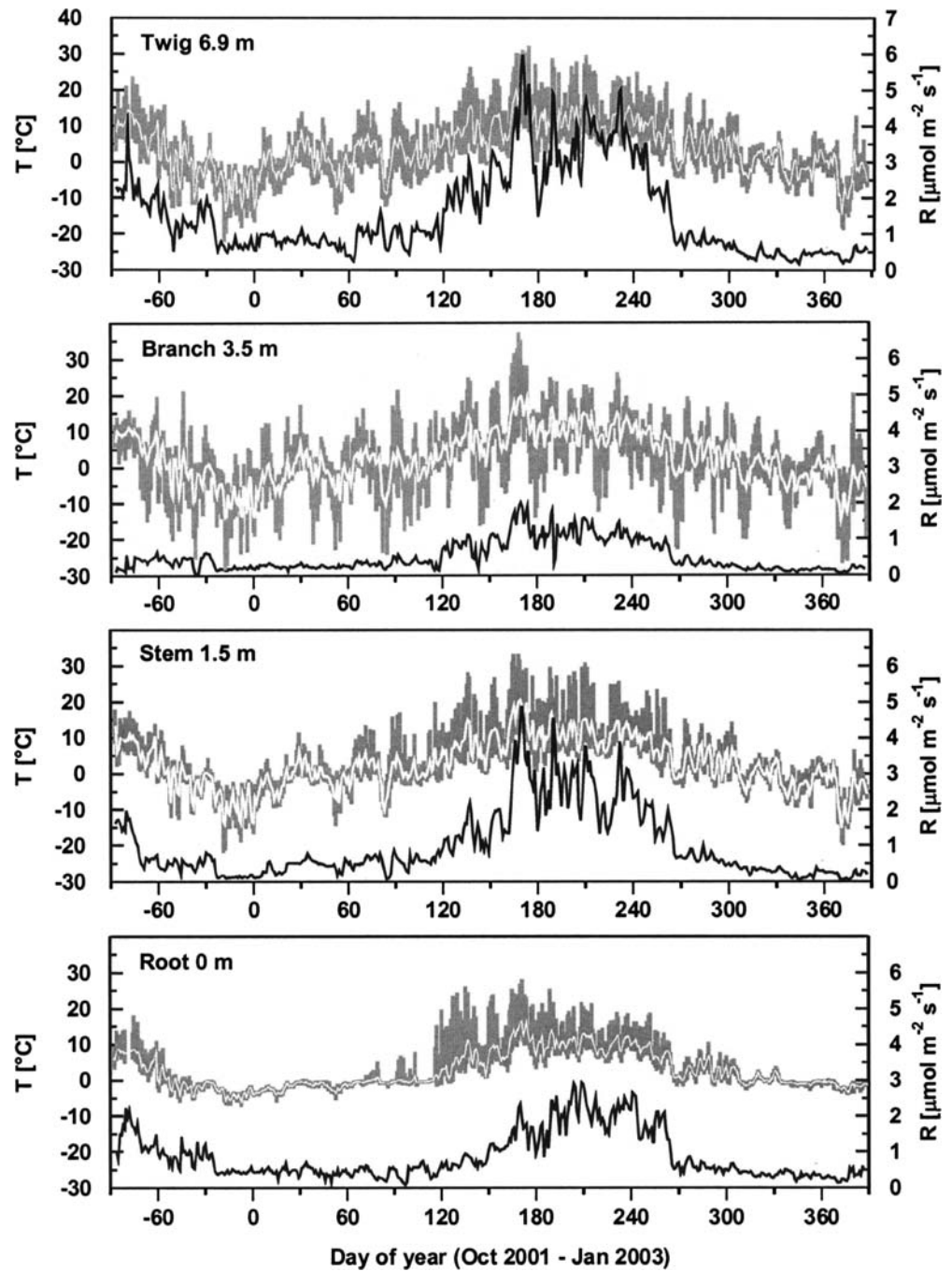

Table 3 Spatial variation in temperature sensitivity (Q_{10}) and woody tissue respiration at 0°C (R_0) during the dormant season (December–February) in a *P. cembra* tree at the alpine timberline near the Klimahaus Research Station, Mt. Patscherkofel, Tyrol (1,950 m). The r^2-value represents the proportion of variability in CO_2 efflux explained by tissue temperature

Position	Elevation above ground (m)	R_0 (µmol m^{-2} s^{-1})	Q_{10}	r^2
Stem south	5.9	0.134	1.95	0.55
Stem south	3.5	0.109	1.71	0.56
Stem south	1.5	0.398	2.48	0.56
Stem north	1.5	0.394	2.69	0.87
Root south	0	0.444	3.10	0.57
Root north	0	0.385	2.85	0.72
Branch south	5.5	0.643	2.16	0.60
Branch south	3.5	0.232	2.59	0.85
Twig south	6.9	0.636	2.59	0.78
Twig south	3.5	0.352	2.61	0.85

was highest during the growing season and was reduced to the level of maintenance respiration during the winter. The fall decline and spring increase in respiration was coincident with seasonal temperature trends (Fig. 1).

Cumulative R_t measured during 2002 varied between 77.5 and 624.1 g cm^{-2} surface area year^{-1} and between 1.82 and 199.3 kg cm^{-3} sapwood volume year^{-1}, respectively (Table 2). Annual R_m accounted for 73±6% of R_t (Table 2). For pine and spruce trees Ryan (1990) reported stem R_m values between 60 and 40% of R_t during the growing season, but no estimates for the entire year. Estimates presented in this study however, include an extensive period of dormancy (≈5 months) without growth, and thus reduced annual R_g considerably to 27 ±6% of R_t (Table 2).

The magnitude of area-based R_m normalized to 0°C ($R_{m,0}$) varied considerably within the entire tree (Table 3): it increased along the stem with increasing height, and decreased both, vertically and horizontally with increasing depth of the canopy. Similar heterogeneities in area-based woody tissue CO_2 efflux within entire trees have also been described by others (Linder and Troeng 1981; Havranek 1985; Sprugel 1990; Edwards and Hanson 1996; Ryan et al. 1996; Maier et al. 1998; Ceschia et al. 2002; Gansert et al. 2002).

Although at a given temperature, respiration per unit surface area was significantly lower during the dormant season than at other times during the year, the Q_{10} value remained constant throughout the year (Fig. 2). The Q_{10} values estimated for the ten positions within the tree (1.71–3.10; Table 3) were within the range of 1.0–3.9 reported for other conifers (Sprugel 1990; Ryan 1990; Ryan et al. 1994; Carey et al. 1997; Lavigne 1996; Lavigne et al. 1996; Lavigne and Ryan 1997; Stockfors and Linder 1998). Woody tissue temperature accounted for 55–87% of the variation in R_m (Table 3, Fig. 2) and the remaining variation might be attributed to spatial variations in the micro-environment, and thus affecting the boundary layer conductance (Martin et al. 1999) and hence also CO_2 efflux within the entire tree.

$R_{m,0}$ values were also related to twig, branch, stem, and root diameter. Area-based $R_{m,0}$ did not show any clear trend with respect to diameter and averaged 0.37 ±0.17 μmol m^{-2} s^{-1} (Fig. 3). However, when related to sapwood volume, $R_{m,0}$ significantly increased with decreasing diameter and was up to 70-fold higher in thin twigs of the upper crown than in the stem and in coarse roots with diameters >80 mm (Fig. 3) as also observed by others (Ryan et al. 1996; Ceschia et al. 2002; Damesin et al. 2002; Bosc et al. 2003).

Woody tissue nitrogen (N) concentration has also been proposed to be a scaling variable for R_m (Ryan 1991; Sprugel et al. 1995), and a strong relationship between R_m and N has been shown to exist in several forest tree species (Kawahara et al. 1976; Ryan et al. 1994; Maier 2001). Conversely, in *Pinus pinaster* (Bosc et al. 2003), *Pinus taeda* (Maier et al. 1998), and *Fagus sylvatica* (Ceschia et al. 2002) the relation between R_m and tissue N content has been show to be also dependent on the diameter of the
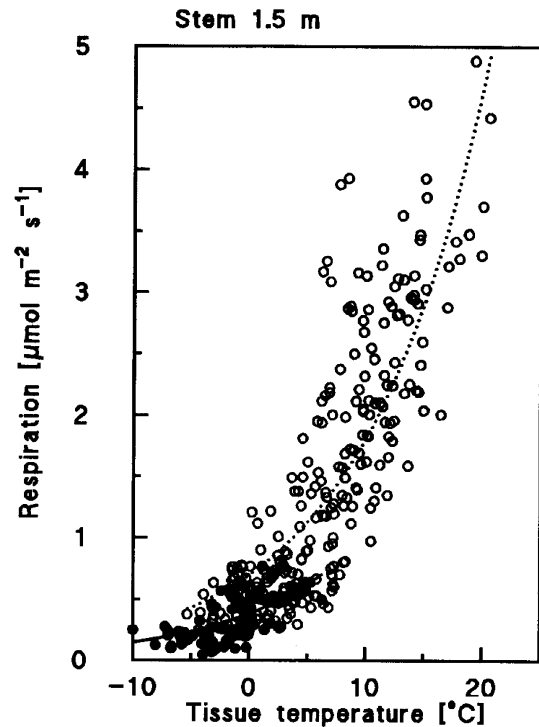

Fig. 2 Daily mean stem respiration in relation to daily mean cambium temperature on the south side of the stem 1.5 m above ground during the dormant season (December–February; *filled symbols*) and during March–November (*open symbols*). Values were fit by exponential regression: dormant season: $R=0.398 \exp[\ln 2.48 (T/10)]$, $r^2=0.56$; March–November: $R=0.690 \exp[\ln 2.56(T/10)]$ $r^2=0.68$

tissue sample, and the authors used two separate regressions for the stem and branches, respectively. In *P. cembra* however, we lack evidence for a relationship between R_m and sapwood N content ($r^2=0.07$ and 0.02 for area and sapwood volume based $R_{m,0}$, respectively; $n=10$). This is because sapwood N content did not differ significantly within the stem, branch, twig, and coarse root sections under study and averaged independently from diameter 4.0±0.7 mg per g sapwood dry mass (Fig. 3). Similarly, in the boreal zone, an ecotone with environmental conditions comparable to the alpine timberline (Havranek and Tranquillini 1995), stem R_m of field grown *Picea abies* (Stockfors and Linder 1998), *Picea mariana*, *Pinus banksia*, and *Populus tremuloides* trees (Lavigne and Ryan 1997) was also unrelated to N content. Thus, metabolic constraints resulting from low temperatures at timberline may override those related to tissue N content.

We conclude that sapwood volume based R_m values are best suited for scaling up woody tissue respiration of *P. cembra* to the tree and stand level, although effects of tissue diameter should be accounted for. Thus, it remains to be determined to what extent higher R_m values in thin branches and twigs result from crown position and/or ontogenetic effects due to differences in the proportion of young versus old tissues and xylem versus phloem biomass.
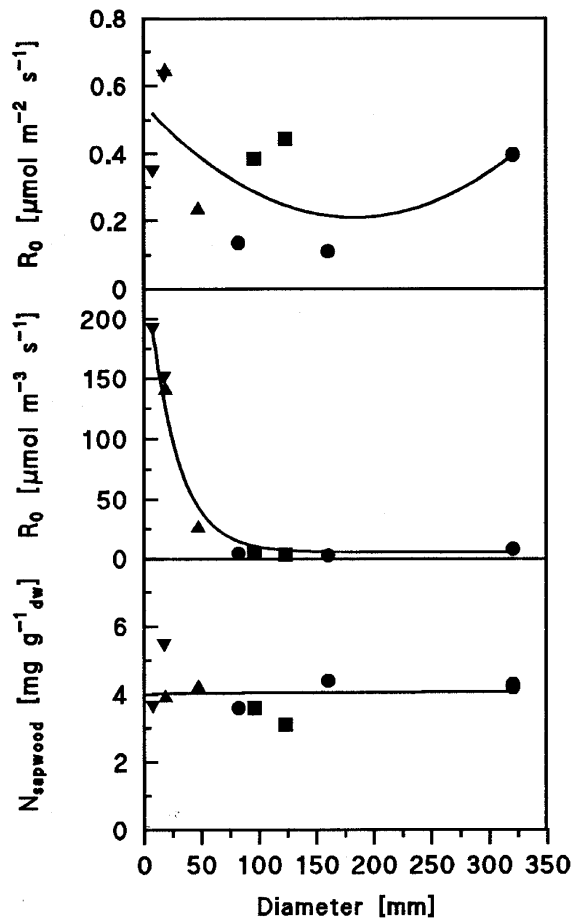
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Fig. 3 Respiration rate at a tissue temperature of 0°C (R_0) calculated per surface area (*top*), or per sapwood volume (*middle*), and sapwood nitrogen concentration (N) of coarse roots (*filled square*), stem sections (*filled circle*), branches (*filled triangle*), and twigs (*inverted filled triangle*) as a function of tissue diameter

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