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The Role of Sapwood Temperature Variations within *Pinus cembra* on calculated Stem Respiration: Implications for Upscaling and Predicted Global Warming

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With 5 figures

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Summary

WIESER G. 2002. The role of sapwood temperature variations within *Pinus cembra* on calculated stem respiration: Implications for upscaling and predicted global warming. – Phyton (Horn, Austria) 42 (1): 1–11, with 5 figures. – English with German summary.

Only a few studies focused on variations in stem respiration within entire trees related to variations within sapwood temperature. In this study, sapwood temperature was measured in 1 cm depth at four positions in the stem of a 50-year-old cembran pine (*Pinus cembra* L.) throughout the year 1995. These temperature data were

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used to estimate variations in CO_2 efflux within the stem, assuming that the temperature dependence of respiration was constant and that there is no difference in the number of living cells in the xylem throughout the entire stem. Respiration was compared on a surface area basis.

South-facing sapwood temperatures were significantly higher than air temperature when compared to north-facing sapwood temperature. As a consequence annual respiration was up to 13% higher on the south than on the north side of the tree. Thus, within-stem variations in temperature have been taken into account when scaling up stem respiration from data obtained from one individual position within a tree.

Zusammenfassung

WIESER G. 2002. Die Variabilität der Stammtemperatur in einer Zirbe (*Pinus cembra* L.) und deren Einfluss auf die berechnete Stammatmung: ihre Bedeutung zur Ermittlung der gesamten Stammatmung und erwartetem Anstieg der Erdoberflächentemperatur. – Phyton (Horn, Austria) 42 (1): 1–11, mit 5 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Nur wenige Studien befassten sich mit Unterschieden der Stammatmung innerhalb eines Baumes, hervorgerufen durch unterschiedliche Stammtemperaturen. In dieser Studie wurde im Jahr 1995 die Stammtemperatur einer erwachsenen Zirbe (*Pinus cembra* L.) an 4 verschiedenen Stellen in 1 cm Holztiefe kontinuierlich gemessen. An Hand dieser Temperaturdaten wurde die Variabilität der Stammatmung innerhalb des Stammes berechnet; und zwar unter der Annahme, dass es keinen Unterschiede in der Temperaturabhängigkeit der Atmung und in der Anzahl lebender Zellen innerhalb des Stamms gibt.

Während auf der Südseite des Stammes die Holztemperatur im allgemeinen über den Werten der Lufttemperatur lag, war die Stammtemperatur auf der Nordseite mit den Werten der Lufttemperatur vergleichbar. Als Folge davon war der jährliche Atmungsverlust auf der Stammsüdseite bis zu 13% höher als auf der Nordseite des Baumes. Daher müssen bei Hochrechnungen zur Bestimmung der Gesamtatmung eines Baumes solche stammspezifische Variationen in der Holztemperatur berücksichtigt werden.

Introduction

Knowledge on gas exchange and dry matter allocation of forest trees is important for the assessment of the role of forest ecosystems as a sink or source in the global carbon cycle and for the understanding of the response of forests to future global changes in atmospheric CO_2 and climate (RYAN & al. 1997). Annual net ecosystem carbon storage depends on the balance between net photosynthesis and respiration. This balance may change with predicted climate warming because respiration is relatively more sensitive to temperature than photosynthesis (RYAN 1991, AMTHOR 1994).

Estimating stem respiration is a difficult task (SPRUGEL & BENECKE 1991, SPRUGEL & al. 1995). In general, temperature response measurements made in chambers during short time periods combined with long term temperature records are frequently used for the upscaling of annual respiration rates. Additional assumptions are that the temperature-respiration relationship is constant within an entire tree and that at a given time stem temperature is the same throughout the stem (TRANQUILLINI & SCHÜTZ 1970, LINDER & TROENG 1981, RYAN & al. 1996, GRANIER & al. 2000).

However, mean sapwood temperatures may vary significantly at different positions within the stem (EDWARDS & HANSEN 1996, STOCKFORS 2000). Therefore, it was the goal of this study to compare stem respiration calculated from actual sapwood temperature variations within the stem of a 50-year old cembran pine (*Pinus cembra* L.) and periodically obtained respiration-temperature response measurements carried out on the north-facing part of the stem throughout the year 1979 by HAVRANEK 1981. Moreover, because warmer temperatures increase the rates of all biochemical and physiological processes in trees (JARVIS 1995) I also focused on possible impacts of predicted global warming on stem respiration. All the calculations were made under the assumption that within the entire stem there is no difference in (1) surface area related respiration, (2) in sapwood volume, (3) in the number of living cells in the xylem and phloem, (4) in maintenance respiration throughout the year, and (5) in the temperature-dependence of respiration (Q_{10}).

Material and Methods

Measurements were made on adult cembran pine (*Pinus cembra*) trees near the Austrian Timberline Research Station, (1950 m a.s.l.; 47°N, 11°E) on Mt. Patscherkofel south of Innsbruck, Austria. Above-canopy air temperature and sapwood temperatures were measured with 1mm thin copper constantan thermocouples throughout the year 1995. Air temperature was measured under an inverted white plastic cup installed on a horizontal aluminum rod about 1 m to the side of the top of the tree. Sapwood temperature measurements were made in 1 cm depth in 7.0, 4.0 and 1.7 m on the south and in 1.7 m stem height on the north side of the stem, respectively. Temperature data were collected with a Campbell CR10 data logger (Campbell Scientific, Ltd. Shepshed, UK), programmed to record the 10-minute means of measurements taken every minute.

Observations of CO_2 efflux from the north-facing part of the stem were carried out over short periods in each month from February until December 1979 (HAVRANEK 1981). These in situ measurements were made using unclimatised clear "Perspex" chambers which enclosed a part of the circumference of the stem at breast height. Using an open system air with flow rates between 100 and 450 l h^{-1} was sucked through the chamber and then conducted to the reference cell of the gas analyser (UNOR 4, Maihak, Hamburg, Germany). Further details regarding the construction and measurement instrumentation are reported by HAVRANEK 1981.

For each sample period I determined relationships between total stem respiration (R_t) and sapwood temperature according to the formula:

$$R_t = R_0 * \exp^{(k*T)} \qquad (1)$$

where R_0 is the respiration rate at 0 °C, k is a temperature coefficient and T is the sapwood temperature in °C. In this relationship k is related to the common Q_{10} because:

$$Q_{10} = \exp^{(10*k)} \quad (2)$$

the increase factor for a 10°C rise in temperature. Values of R_t were extrapolated throughout 1995 by applying these Q_{10} values to observed diurnal and seasonal changes in sapwood temperature.

The subtraction method was used to subdivide total respiration into growth (R_g) and maintenance respiration (R_m) (c.f. SPRUGEL 1990, SPRUGEL & BENECKE 1991). Values of R_0 and k estimated during the dormant season (November to December) were used in equation 1 for calculating R_m. R_g was then calculated as the difference between R_t and R_m.

Results and Discussion

Seasonal changes in the temperature-respiration relationship are shown in Fig. 1A. On a relative scale however, all these temperature-respiration relationships were similar (Fig. 1B) strongly suggesting a constant Q_{10} throughout the year. As both R_t and R_m involve the same biochemical pathways (LEVY & JARVIS 1998) and are equally dependent on temperature, seasonal changes in the temperature-response relationship

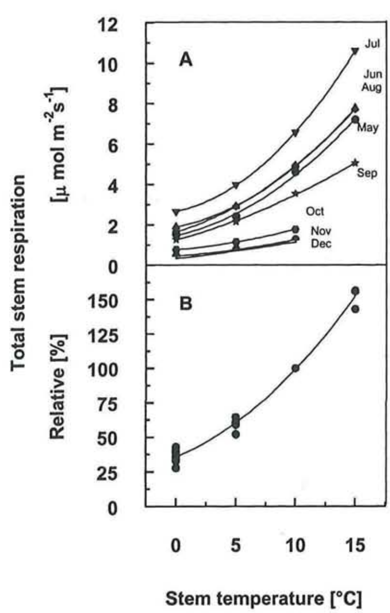

Fig. 1. Absolute (A) and relative (B) rates of total stem respiration (R_t) over different ranges of sapwood temperature in *Pinus cembra* at 1.7 m stem height. Relative values were obtained by setting R_t to 100% at a sapwood temperature of 10 °C. (Modified after HAVRANEK 1981).

appear to be dependent on the metabolic activity of the living cells in the xylem and phloem. This idea is further corroborated by the observation that night-time foliage respiration of *Pinus cembra* needles was found to be significantly lower during the period of winter dormancy when compared to the growing season (PISEK & WINKLER 1958, WIESER 1997).

Seasonal changes in the temperature-respiration relationship (Fig. 1A) and observed daily and seasonal changes in sapwood temperature measured throughout 1995 were used for calculating R_t and R_m. As a typical example the seasonal variations of sapwood temperature and R_t are shown for the north-side of the tree trunk (Fig. 2). In general, R_t was greatest during the vegetation period and was reduced to the level of R_m during the dormant season. After a significant increase in late April R_g appeared to be relatively constant and approached 80% of R_t throughout the growing season (Fig. 2). This pattern coincided with the pattern of radial increment growth (Fig. 2) as also observed in *Larix decidua* (MATYSSEK 1985), *Pinus radiata* and *Nothofagus truncata* (BENECKE 1985).

Sapwood temperature and respiration rates were greater on the south than on the north side of the stem (Figures 3 and 4). Temperature differences between sapwood and the air were quite large, especially on the south side of the stem (Fig. 3). The high temperature difference between south-facing sapwood and air temperature at the tree trunk resulted from the exposure to direct sunlight and might also be related to the large heat capacity of the woody tissue (RYAN 1990). Sapwood temperature on the north side by contrast, was more comparable to air temperature as also observed by EDWARDS & HANSON 1996.

The lower temperature difference between south-facing sapwood and the air at 4 and 7 m stem height (Fig. 3) resulted from less exposure to direct sunlight due to self shading by branches and twigs, a higher average wind velocity, and hence probably also from the cooling effect of foliage transpiration.

Temperature related differences in south- and north-side R_t were quite significant throughout the year. For example, at the stem base periods occurred when R_t of the south-facing tissue was up to 35% higher than in the north-facing tissue (Fig. 4).

Similar differences in south- and north- side stem respiration rates were also reported for *Quercus alba, Quercus prinus* and *Acer rubrum* by EDWARDS & HANSON 1996. Overall, when compared to the north side of the stem at 1.7 m stem height observed differences in sapwood temperature within the stem accounted for up to 14 and 16% in annual R_t and R_m, respectively (Table 1). The observed decrease in R_t and R_m with increasing stem height at the south side (Table 1) coincided with a decrease in mean sapwood temperature and a smaller temperature amplitude in the upper parts of the stem (Fig. 3). Furthermore, there is also a positive relationship

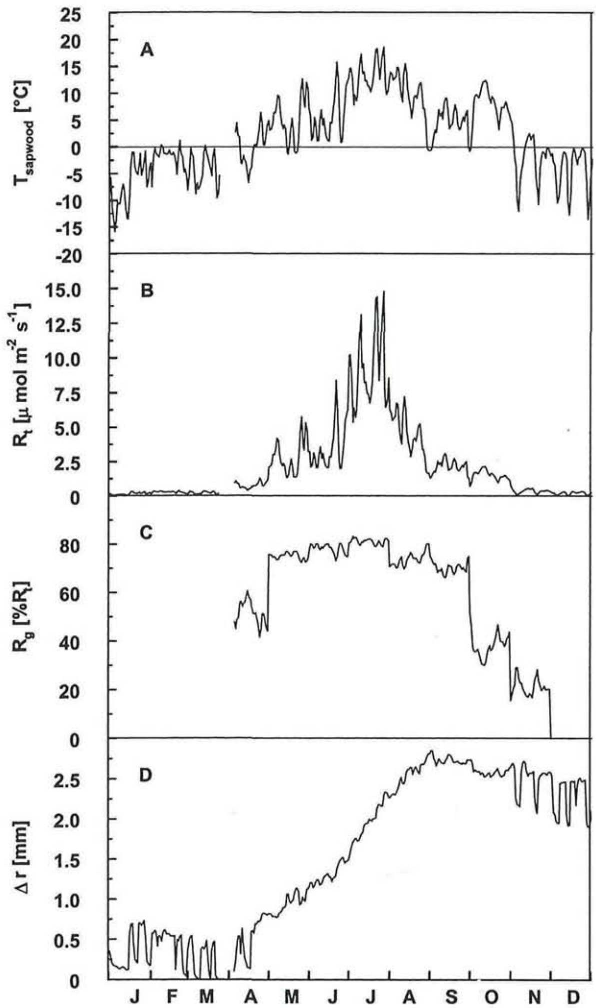

Fig. 2. Time course of (A) sapwood temperature ($T_{sapwood}$), (B) daily mean total stem respiration (R_t), (C) growth respiration (R_g) in % of R_t, and (D) radial stem growth increment (Δr) on the north side of the stem 1.7 m above the tree base during January 1 to December 31, 1995. Increment measurements by point dendrometers (Data Loris K., HAVRANEK W. M. and WIESER G. unpubl.). Some data from March and April are missing due to a data logger failure.

between stem respiration related to surface area and the reciprocal stem diameter (TRANQUILLINI & SCHÜTZ 1970, LEVY & JARVIS 1998); and hence probably also in sapwood volume (LAVIGNE 1987) because the number of living cells in the xylem increases with increasing thickness of the stem. However, this was not investigated.

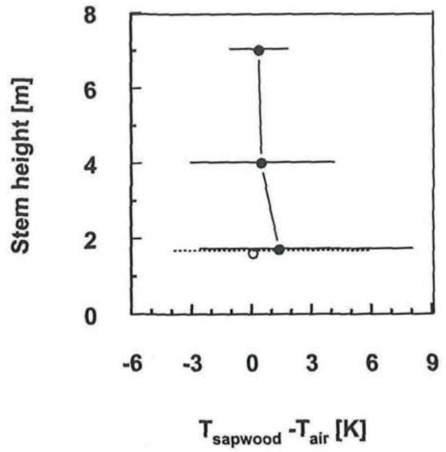

Fig. 3. Seasonal daily temperature difference between air temperature and south (●) and north (○) facing sapwood temperature in relation to stem height of *Pinus cembra* during January 1 to December 31, 1995. Horizontal bars indicate the range of maximum daily overheating and maximum daily undercooling.

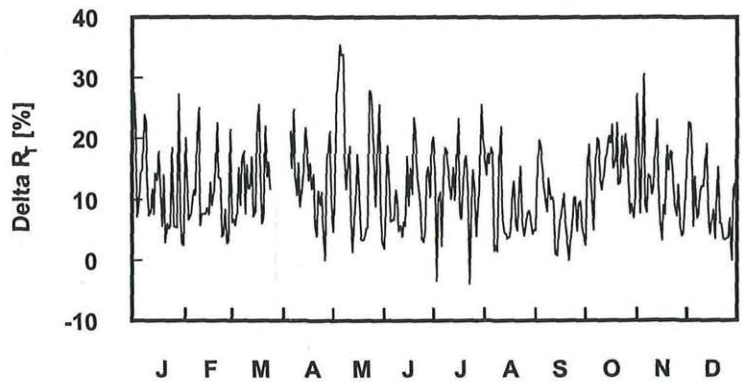

Fig. 4. Difference between daily mean total stem respiration (R_t) on the south and the north side of the stem 1.7 m above the tree base during January 1 to December 31, 1995. Y ordinate values are R_t south – R_t north. Some data from March and April are missing due to a data logger failure.

Table 1.
Annual total (R_t) and maintenance stem respiration (R_m) in *Pinus cembra* during 1995. Maintenance respiration rates are based on measured temperature-respiration responses obtained during the dormant season and monitored sapwood temperatures throughout the year.

Position	Height (m)	Stem diameter [mm]	R_t [mol m^{-2}]	R_m [mol m^{-2}]
Stem south	7.0	50	69.6	21.1
Stem south	4.0	14	72.7	21.8
Stem south	1.7	300	78.3	23.6
Stem north	1.7	300	68.4	20.3

The ability to detect differences between respiration rates within the stem illustrates the importance of measuring sapwood temperature at different points within an entire tree. When R_t at the tree trunk was calculated using the average temperature of the south- and the north-facing sapwood I found that the average sapwood temperature underestimated annual R_t on the south side of the stem by 6.4% and overestimated annual R_t on the north side by 7.1%, respectively. Using air temperature to calculate R_t, annual R_t would have been underestimated by 18 and 3% on the south- and the north-side, respectively. Therefore, it is important to use correct sapwood temperatures rather than air temperatures when calculating R_t, because sapwood temperatures vary significantly within an entire stem and differ substantially from air temperature (Fig. 3; cf. also BENECKE 1985, RYAN 1990, EDWARDS & HANSEN 1996). However, the assumption that the temperature-respiration relationship is constant within an entire stem has to be examined in further field experiments.

In forest ecosystems the fraction of net photosynthetic production consumed by respiration of foliage, woody tissue and roots is approximately 50–70% (RYAN 1991). For *Pinus cembra* TRANQUILLINI & SCHÜTZ 1970 calculated that within a year 23% of the carbon fixed by net photosynthesis is lost by stem respiration. Thus respiratory fluxes play an important role in tree growth and in forest productivity. However, the carbon balance of trees may change with predicted climate warming. Model estimations predict that a 3–4 °C increase in global temperature will reduce productivity (VEMAP MEMBERS 1995) because respiration increases more rapidly than photosynthesis (RYAN 1991, AMTHOR 1994). JONES & al. 1988 and WUEBBLES & al. 1999 presented surface air temperature data giving evidence that the Earth's climate has warmed during the last century. Changes appear to be significant in the European Alps (BENISTON & al. 1997, DIAZ & BRADLEY 1997). On a regional scale this trend could also be documented for the timberline ecotone in the Central Austrian Alps, especially during the 1990s (Fig. 5), where the mean annual temperature increased by 0.8 K when compared to the 27-yr period before.

Calculations based on the Q_{10} values shown in Fig. 1 suggest that an increase in mean annual air temperature of 1.0 °C will increase annual R_t of *Pinus cembra* by about 10%. On the other hand, respiration rates may acclimate and adjust to new temperatures. There is evidence that at a given temperature species from warmer environments have lower respiration rates than those from colder environments (REICH & al. 1996). Especially in summer differences can be up to 50%, as shown for *Picea abies* by PISEK & WINKLER 1958. On the long term however, respiration may also be limited by the supply of substrate (DEWAR & al. 1999) and hence, must be linked with carbon uptake (SAXE 2001). Thus, when biomass data become available, photosynthesis and respiratory losses of foliage, stem, branches, coarse, and

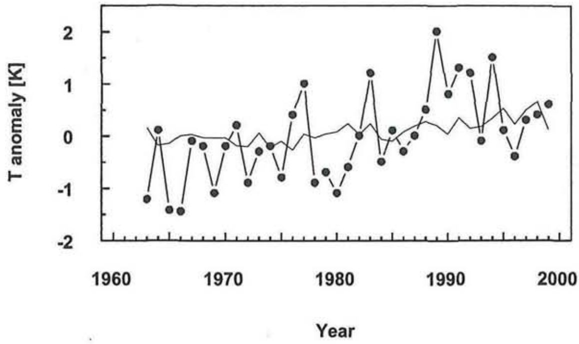

Fig. 5. Global warming on the northern hemisphere (thin line; source: Climate Research Unit, University East Anglia, Oct. 2001, http://www.cru.uea.ac.uk) with strong regional deviations at the Austrian Timberline Research Station, Klimahaus, 1950 m a.s.l. Mt. Patscherkofel, Innsbruck, Austria (●).

fine roots can be extrapolated to the whole tree and in combination with soil respiration data to the stand level. Such data are essential for evaluating possible effects of climate change on carbon cycling and carbon sequestration in forest ecosystems at the timberline ecotone.

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