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Seasonal Variation of Leaf Conductance in a Subalpine *Pinus cembra* During the Winter Months

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Summary

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Winter leaf conductance of the last three flushes of *Pinus cembra* L. was studied under ambient conditions at the alpine timberline. Changes in leaf conductance paralleled seasonal variations in temperature. During the coldest months, December to March, leaf conductance was almost completely suppressed, even at the highest needle temperatures as compared to spring and fall. Comparing the maximum leaf conductance measured during the day with the minimum air and stem temperature of the previous night showed significant curvilinear relationships. A similar comparison with minimum soil temperature by contrast, resulted in a non significant relationship. Thus, in areas where a continuous snow cover prevents freezing of the soil, as for instance at the alpine timberline or even at high latitudes, stem temperature seems to be a precise predictor of the potential maximum leaf conductance on the following day.

Introduction

Low temperature is one of the most important factors limiting ecosystem processes in high altitude temperate forests. During spring and fall low night temperatures have been shown to reduce leaf conductance on the following day (cf. KÖRNER 1994). However, in earlier studies measurements were only conducted in weekly or longer intervals; but information on long-term responses during the cold season is scare. Furthermore, among temperature variables, the relative importance of stem and needle temperature in influencing leaf conductance received little attention. To examine this question further seasonal changes of leaf conductance in a subalpine cembran pine (*Pinus cembra* L.) tree have been investigated under site

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conditions in situ. The specific objective of this study was to test relationships between selected temperature variables and leaf conductance. For this purpose air, soil, stem, and needle temperatures were used.

Material and Methods

The study site is located at the timberline ecotone in 1950 m a.s.l. near the Klimahaus Research Station on Mt. Patscherkofel south of Innsbruck, Austria (47°N, 11°E). Measurements were carried out on a mature 12-m-high cembran pine (*Pinus cembra* L.) tree from November 2, 1994 to May 22, 1995. The field site is characterised by a cool subalpine climate with low soil temperatures. Frost may occur in all months and snow cover is continuous from October until May.

The upper canopy was accessed by a scaffolding tower. Ambient air temperature and humidity were measured with a Skye SKH 2013 sensor (Skye Instruments, Powys, UK) installed on a horizontal aluminium rod 1 m to the side of the top of the tree. Soil, stem, and needle temperature was measured by means of copper constantan thermocouples.

In situ gas exchange of the last three needle age classes of sun exposed branches was measured continuously with a temperature-controlled chamber (Walz, Effeltrich, Germany) on sun exposed branches 2 m from the top of the tree. The chamber was tracking ambient temperature, while the relative humidity of the air inside the chamber was only monitored with a Vaisala HMP35A probe (Vaisala, Helsinki, Finland).

Both humidity sensors were calibrated against a dew-point mirror before and after the measurement period, respectively. The sensors appeared stable during the experiment exhibiting an absolute accuracy of ± 2 % in relative humidity. Due to technical reasons a transpiration induced increase of the humidity inside the chamber could not be compensated using a by-pass loop (freezing of cold traps). Therefore vapour pressure deficit (VPD) of the air inside the chamber was at an average 0.48 (max. 1.15) hPa lower, as compared to the ambient air outside. Plots of VPD versus stomatal conductance of *Pinus cembra* needles showed that during the vegetation period, when stomatal opening is not hindered by low temperatures and low irradiance an increase in VPD of 10 hPa resulted in a 30 % reduction in stomatal conductance (WIESER 1999). Thus, altogether, the relative error in leaf conductance to water vapour was not higher than 5 %.

Additionally, during the growing seasons 1997 and 1998 xylem sap flux density (GRANIER 1985) was monitored in two trees using Granier-type sensors (UP Umweltanalytische Produkte GmbH, Munich, Germany).

All the data were recorded using a Campbell CR10 data logger (Campblell, Scientific, Shepshed, UK) programmed to record 10 min means of measurements taken every minute. Leaf conductance to water vapour was calculated according to the equations of VON CAEMMERER & FARQUHAR 1981 and related to total needle surface area estimated with grass beads (THOMPSON & LEYTON 1971).

Analysis of data was based on half hour means.

Results and Discussion

Changes in leaf conductance generally followed seasonal trends in temperature. The fall decline and the spring increase in leaf conductance was coincident with seasonal temperature trends (data not shown). In general, leaf conductance was negligible during the winter months (December to March) even at the highest needle temperatures when compared with conductance values during the spring and fall (Fig. 1). During the winter months, when the stomata were completely closed, daily maximum leaf conductance in *Pinus cembra* was around

3 μmol m^{-2} s^{-1} on average. Similar leaf conductance values during the cold season were also reported for *Picea abies, Pinus sylvestris* (KÖRNER 1994), *Picea rubens* (SCHABERG & al. 1995), *Pinus contorta, Pinus ponderosa, Pinus flexilus, Pseudozuga menziesii, Abies lasicocarpa, Picea engelmannii* (SMITH & al. 1984) and, *Nothofagus solandri* (MCCRACKEN & al. 1985).

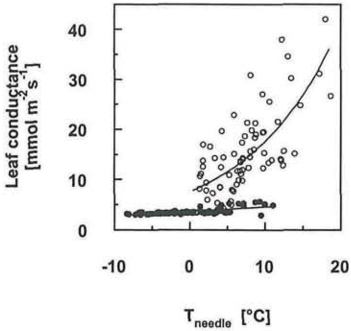

Fig. 1. Maximum daily leaf conductance of current- to two-year-old *Pinus cembra* needles in relation to the maximum needle temperature (T_{needle}) during the winter (●), spring and fall (○). Winter refers to December through March. Spring and fall values were fit by monoexponential regression: y = 7.5 ∗ exp (0.08 ∗ x), r² = 0.54.

Parallel trends in temperature and leaf conductance were also supported by correlation analysis (Fig. 2). Minimum air temperatures of the previous night less than -6.5 °C caused daily maximum leaf conductance approaching minimum values. This is in coincidence with findings from earlier studies on conifers (KAUFMANN 1976, FAHEY 1979, GRAHAM & RUNNING 1984, SMITH & al. 1984, KÖRNER & PERTERER 1988, WANG & ZWIAZEK 1999).

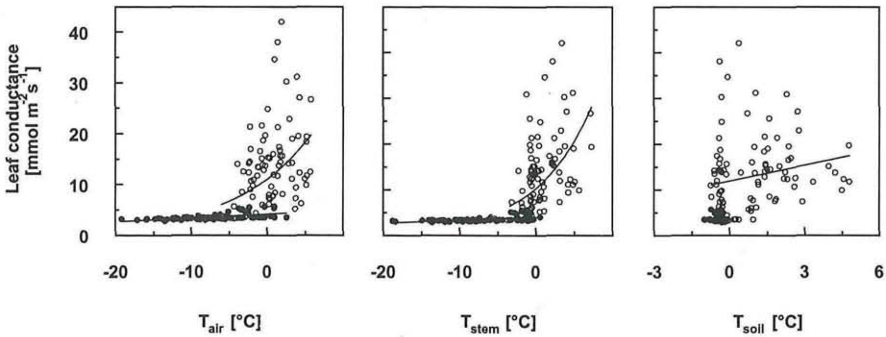

Fig. 2. Maximum daily leaf conductance of current- to two-year-old *Pinus cembra* needles in relation to the previous night minimum air temperature (T_{air}, left); stem temperature 5 cm below the north facing stem surface, 1.5 m above ground (T_{stem}, middle); and soil temperature at 10 cm depth (T_{soil}, right) during the winter (●), spring and fall (○). Winter refers to December through March. Spring and fall values were fit by monoexponential or linear regression: T_{air}: y = 10.34 ∗ exp (0.13 ∗ x), r² = 0.34; T_{stem}: y = 10.39 ∗ exp (0.15 ∗ x), r² = 0.45; T_{soil} : y = 1.16 ∗ x + 11, r² = 0.04.

The correlation improved if the minimum stem temperature of the previous night was used instead of minimum air temperature. Daily maximum leaf conductance approached minimum values whenever minimum stem temperature of the previous night decreased to less than -5 °C (Fig. 2). A similar comparison with the minimum soil temperature resulted in a less significant relationship (Fig. 2). By contrast, at a low elevation site KÖRNER 1994 observed a close linear correlationship between minimum soil temperature of the previous night and daily maximum leaf conductance in Pinus sylvestris and Picea abies, the latter approaching minimum values whenever soil temperature decreased to +1°C.

The specific physiological mechanisms responsible for these observed low temperature induced reductions in leaf conductance are still under debate. Soil water uptake by the roots is severely restricted by low soil temperatures (KOZLOWSKY 1943, KRAMER & BOYER 1995, BOYCE & LUCERO 1999, WAN & al. 1999) and ceases completely when soil temperatures falls below -1°C (LARCHER 1957, TRANQUILLINI 1979). At the study site, a continuous snow cover throughout the cold season prevented soil freezing. During the cold season soil temperatures were high enough (cf. Fig. 2) that serious interference with soil water uptake by the roots can be excluded as a limiting factor (HAVRANEK 1972, DAY & al. 1990).

However, a decrease in soil temperatures can reduce the water flow through the roots (WAN & al. 1999) as a result of decreased root permeability and increased water viscosity (KAUFMANN 1975). Additionally, an inhibition of sapwood water movement through the stem can be linked to cold temperatures of the above-ground tissue (HADLEY & SMITH 1987). ZIMMERMANN 1964 found that stem temperatures below -2°C stopped the ascent of sap. Similarly, in *Pinus cembra* sap flow approached zero at air temperatures below –2.5 °C (Fig. 3). Thus, when the flow rate through the tree is low, the stomata close to maintain a positive water balance.

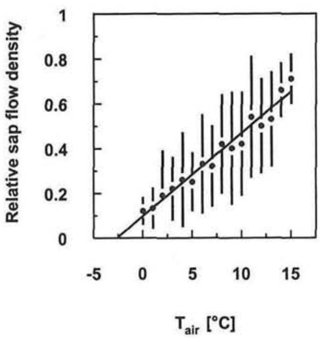

Fig. 3. Correlation between daily average air temperature (T_{air}) and daily average relative sap flow in *Pinus cembra*. Each point is the mean of 10 to 25 values collected during the growing seasons 1997 and 1998. Relative values were obtained by setting the daily maximum average sap flow density to 1. The points were fitted by linear regression: y = 0.037 * x + 0.097, $r^2 = 0.98$. Since daily average stem temperature correlates linearly with daily average air temperature this regression holds also for stem temperature ($T_{stem} = 1 * T_{air} - 0.02$; $r^2 = 0.84$; WIESER unpublished).

A rapid decline in xylem sap flow as a result of freezing might also influence the release of abscisic acid (TESKY & al. 1983), which is known to influence stomatal aperture. Measurements of abscisic acid contents on five *Pinus cembra* trees at the same study site confirmed that abscisic acid concentrations of the needles were approximately 50% higher during the cold season when compared to summer values ($p < 0.05$; CHRISTMANN & al. 1999).

Conclusions

During the cold season daily maximum leaf conductance of *Pinus cembra* at high altitude is limited significantly by low night temperatures. Stomatal closure due to subfreezing air and stem temperatures minimises water loss during the winter when water uptake by the roots and xylem transport is severely impeded or even impossible. Furthermore, it appears that in areas where a continuous snow cover prevents freezing of the soil stem temperature is a very precise predictor of daily maximum leaf conductance in *Pinus cembra*. Although such temperature adaptations in leaf conductance contribute to the survival of conifers at the alpine timberline and even in the boreal zone, further investigations are necessary in order to determine the influence on tissue temperatures on leaf conductance and water transport in conifers under field conditions. Additionally the role of abscisic acid in the down regulation of leaf conductance during the cold season must be investigated further under field conditions.

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