Soil warming increased whole-tree water use of *Pinus cembra* at the treeline in the Central Tyrolean Alps

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This study quantified the effect of soil warming on sap flow density ($Q_s$) of *Pinus cembra* L. at the treeline in the Central Tyrolean Alps. To enhance soil temperature we installed a transparent roof construction above the forest floor around six trees. Six other trees served as controls in the absence of any manipulation. Roofing enhanced growing season mean soil temperature by 1.6, 1.3 and 1.0 °C at 5, 10 and 20 cm soil depth, respectively, while soil water availability was not affected. Sap flow density (using Granier-type thermal dissipation probes) and environmental parameters were monitored throughout three growing seasons. During the first year of treatment, no warming effect was detected on $Q_s$. However, soil warming caused $Q_s$ to increase significantly by 11 and 19% above levels in control trees during the second and third year, respectively. This effect appeared to result from warming-induced root production, a reduction in viscosity and perhaps an increase also in root hydraulic conductivity. Hardly affected were leaf-level net CO₂ uptake rate and conductance for water vapour, so that water-use efficiency stayed unchanged as confirmed by needle δ¹³C analysis. We conclude that tree water loss will increase with soil warming, which may alter the water balance within the treeline ecotone of the Central Austrian Alps in a future warming environment.

**Keywords**: cembran pine, climate change, leaf conductance, sap flow, soil temperature manipulation.

Introduction

High-altitude treelines have raised concern as they may undergo significant ecological alterations through warming under climate change (Walther et al. 2005, Holtmeier and Broll 2007, Wieser et al. 2009). During the last century the global surface temperature has increased by about 0.6 ± 0.2 °C (Jones et al. 1988), and global change models predict further an increase by 1.4–5.8 °C for upcoming decades (IPCC 2013). Changes appear to become most pronounced at high altitude (Beniston et al. 1997, Diaz and Bradley 1997). At the treeline of the central Austrian Alps, the mean annual air temperature during the last 10 years (2000–10) was enhanced on an average by 0.8 °C (i.e., to 3.0 °C) when compared with the mean over the previous 38 years (2.2 °C). Temperature increase apparently was most pronounced during spring (by 1.5 °C) and summer (by 1.4 °C) compared with autumn (by 0.6 °C) and winter (by 0.2 °C), implying early snow melt in spring. As a consequence, the growing season has increased by 4 ± 1 weeks during the last three decades (Wieser 2012). In contrast to temperature, however, annual precipitation has not changed significantly during the past 48 years.

Although effects of climate change on forest ecosystems are uncertain, Wieser et al. (2009) suggested that warming rather than the rising atmospheric CO₂ level will cause alterations in the structure and ecological functioning of the treeline ecotone in the Central Austrian Alps. Increasing air temperature in the snow-dominated regions of treelines in the Central Austrian Alps is expected to change ecosystem characteristics with associated biogeochemical and hydrological cycling (Barnett et al. 2005). In the Central Austrian Alps, summer is the main season of rainfall,
with it occurring every third to fourth day on average (Wieser 2012). Ample precipitation and moderate evaporative demand generally cause soil water content to be sufficiently high to meet the trees’ water demand within the treeline ecotone (Tranquillini 1979). Because soil moisture at the treeline in the Central Austrian Alps seldom drops below 20% vol. (Wieser et al. 2009), treeline trees are rarely forced to restrict transpiration during the growing season (Tranquillini 1979, Mayr 2007, Matyssek et al. 2009). Under ample soil water availability upon climate warming, the water uptake capacity will possibly be enlarged through growth stimulation of the mycorrhizal root system and enlargement of the belowground water-absorbing surface. Additionally, water uptake will also be improved by rising soil temperature through lowered water viscosity (Kaufmann 1975), an increased permeability of root membranes (Goldstein et al. 1985, Wan and Zwiazek 1999, Wan et al. 2001) and aquaporin-mediated changes in root conductivity (McElrone et al. 2007, Ruggiero et al. 2007).

Although water fluxes between forest ecosystems and atmosphere have been studied intensively, the reasons for the intra-annual variability of transpiration and responses to extreme meteorological conditions such as during the dry summer of 2003 (Reichstein et al. 2002, Breda et al. 2006, Granier et al. 2007) still await clarification for conifers at the treeline. In situ manipulation of soil temperature is a common methodology for assessing potential effects of warming in forest ecosystems, making use of heating cables (Bergh and Linder 1999, Strömgen and Linder 2002), open-top chambers (Danby and Hik 2007), closed-top chambers (Kellomäki and Wang 1998) or greenhouses (Bronson and Gower 2010, Van Herk et al. 2011). Although experimental soil warming with heating cables or greenhouses provides a high degree of temperature control, such approaches cannot be used in remote areas of the treeline ecotone because of high energy requirements. Thus, soil roofing is a potential alternative to investigate the effect of soil temperature on tree-hydrological dynamics. We tested the hypothesis that a slight increase in soil temperature in the absence of other soil disturbance will result in increased canopy transpiration of Pinus cembra L. at the treeline in the Central Tyrolean Alps. Experimental soil warming was incited by roofing throughout three consecutive growing seasons while continuously monitoring sap flow density ($Q_s$) with thermal dissipation probes (Granier 1985). Findings are used to explore tree response in a future warmer environment within the treeline ecotone of the Central Austrian Alps.

**Materials and methods**

**Study site**

The study was carried out in a south-exposed $P$. cembra afforestation at the treeline above Hagent near St Sigmund in the Sellrain Valley, Tyrol, Austria at 2150 m above sea level (a.s.l.; 47°12′24″N, 11°05′04″E). Aspect and slope angle were SSW and 25°, respectively (Kronfuss 1997). During the study period (2011–13) trees were ~25 years old. The stand formed a sparsely open canopy permitting dense understory vegetation comprising dwarf shrubs and herbaceous species. The stand density was 2117 trees ha$^{-1}$ and the basal stem area was 13.7 m$^2$ ha$^{-1}$.

According to a 20-year record of meteorological data (1975–94) at a weather station nearby (1800 m a.s.l.; Kronfuss 1997), the mean annual temperature was 3.2 °C, with February as the coldest ($T_{\text{mean}} = −3.5$ °C) and July as the warmest month ($T_{\text{mean}} = 10.7$ °C). The mean annual precipitation was 909 mm with the majority of rain falling during the growing season from May through October (610 mm). Gneisses and mica schist dominated the geology at the study site. According to the World Base for Soil Resources (FAO 1998), the soil at the study site was classified as a podzolic cambisol (Neuwiniger 1972). A humus layer of 5 cm thickness covered the loamy sand subsoil. The top 25 cm of the subsoil was enriched by 8 ± 3% of organic matter and the soil texture was dominated by sand (71.3 ± 1.4%) and silt fractions (27.8 ± 1.3%) with varying clay contribution (1.0 ± 0.1%). Hydraulic field capacity was 0.24 ± 0.08 m$^3$ m$^{-3}$ at −0.033 MPa (sensu Blume et al. 2010), and the wilting point (at ~1.5 MPa) was reached at 0.07 ± 0.01 m$^3$ m$^{-3}$.

**Experimental design**

Soil temperature manipulation was accomplished by roofing the forest floor according to the approach by Gruber et al. (2010). Roofs needed to withstand high wind velocity without considerably influencing the aboveground microclimate and soil water availability in the rooting zone. They consisted of frames anchored into the soil, covered with a 0.5-mm thick transparent polyvinyl skin. They were installed underneath the canopy at 15 cm above ground around the stems of six individual trees (hereafter ‘warmed’ trees). The area covered around each tree was 16 m$^2$ at least. An identical number of $P$. cembra trees served as control in the absence of soil temperature manipulation (‘control’ trees).

For practical reasons and to facilitate logistics of soil temperature and soil moisture monitoring (see below), three adjacent trees per treatment were assembled into a plot, resulting in four plots in total. Surface and slope run-off of water was allowed to penetrate the soil (in total 67% of precipitation; Neuwiniger et al. 1988) during and after rainfall. Soil warming was operated in 2011 during July through October and continued throughout each snow-free period (May–October) during 2012 and 2013.

**Environmental, sap flow density measurements and tree characteristics**

Air temperature ($T_a$), relative humidity (CS215, Campbell Scientific, Shepshed, UK), solar radiation ($R_s$; SP1110, Campbell Scientific), wind velocity ($v$; A100R, Campbell Scientific) and precipitation ($P$; ARG100, Campbell Scientific) were monitored at 2 m aboveground. In order to determine seasonal differences in
soil temperature ($T_{\text{soil}}$) and volumetric soil water content ($\theta$) between control and roofed plots, six soil temperature sensors (T 107 Probe, Campbell Scientific) and two soil moisture probes (EC-5, Decagon Devices, Inc., Pullman, WA, USA) were installed in each plot close to the trees used for sap flow measurements. While $T_{\text{soil}}$ was measured at 5, 10 and 20 cm of soil depth (two sensors per plot and depth each), $\theta$ was measured at 10 cm. Data were transmitted to an AM16/32 multiplexer and recorded with a CR1000 data logger (both Campbell Scientific) programmed to record 30-min averages of measurements taken by 1-min intervals.

Sap flow density ($Q_s$) of the selected study trees was monitored by means of the heat dissipation approach according to Granier (1985), using three-channel battery-operated sap flow systems (M1 Sapflow Systems PROSA-LOG; UP, Umweltanalytische Produkte GmbH, Cottbus, Germany). Each system consisted of a three-channel PROSA-LOG datalogger, providing one constant source of electrical power (0.2 W) to heat three sensors each. Each sensor consisted of two probes of 20 mm in length and 2 mm in diameter each. The upper probe of each sensor included the heater, whereas the lower probe was unheated, remaining at trunk temperature for reference. The probes were inserted 15 cm apart from each other in the vertical direction into the outer 20 mm of the xerotic xylem on the north-facing side of trees (Ewers and Oren 2000). Positions were below the transpiring foliage at ~25 cm aboveground to prevent sun exposure (Wieser et al. 2013). Probe positions, in addition, were fully insulated with a thick aluminium-coated foam cover to prevent any direct radiation while providing mechanical protection. The temperature difference between the upper heated probe and the lower reference probe was recorded every 30 min. Two car batteries (12 VDC, 90 Ah), which were recharged by means of an 80 W solar panel in combination with a charge controller each, provided power for all electrical equipment. For each tree $Q_s$ (g m$^{-2}$ s$^{-1}$) was calculated from the temperature difference between the two probes ($\Delta T$) relative to the maximum temperature difference ($\Delta T_m$), which occurred at times of zero flow according to the calibration equation by Granier (1987):

$$Q_s = 119 \times [\frac{\Delta T_m - \Delta T}{\Delta T}]^{1.231}$$

Each night $\Delta T_m$ was determined and used as a reference for the following day. The underlying assumption of zero sap fluxes during the night is justified as vapour pressure deficits were mostly low. In addition, during most nights temperatures temperature courses reached equilibrium between both sensors, suggesting complete refilling of tree-internal water storage. Environmental data and $Q_s$ were monitored continuously throughout the growing seasons 2011 (17 June to 11 October), 2012 (15 May to 4 October) and 2013 (2 May to 8 October).

Tree characteristics, including stem diameter at height of sensor installation ($D_s$), projected crown area, 100-needle dry weight and specific leaf area (SLA) were determined in fall 2013. In P. cembra, heartwood and sapwood are clearly distinguishable on the basis of colour. Sapwood cross-sectional area was established from $D_s$ based on measurements along increment cores (5 mm in diameter) taken at sensor height, according to the equation:

$$A_s = 7.89 \times \exp(0.223 \times D_s), \quad R^2 = 0.99$$

Gas exchange measurements

Needle CO$_2$/H$_2$O gas exchange was measured in situ with a portable measurement system (CIRAS 1, PP Systems, Hitchin, Hertfordshire, UK) equipped with a climate-controlled PLC6 leaf chamber, providing standardized conditions of 20 °C air temperature, 50% relative air humidity and 370 μmol CO$_2$ m$^{-2}$ s$^{-1}$. An LED light unit was used to maintain photosynthetic photon flux density of 1500 μmol m$^{-2}$ s$^{-1}$ at the needle surface. In each study tree gas exchange of current-year and 1-year-old needles of sun-exposed twigs was measured repeatedly during the growing season of 2012 (on 24 and 27 July, and 9 August). Gas exchange data were related to projected leaf area.

Stable carbon isotopes

Sun-exposed current-year needles were sampled from all study trees during late-August of 2012 and 2013 each for stable carbon isotope analysis. Needles were dried at 60 °C, ground to fine powder and 2.0 ± 0.05 mg of samples were each weighed into a tin capsule (3.5 × 5 mm, IVA Analysentechnik e.K., Meerbusch, Germany) prior to combustion to CO$_2$ in an elemental analyser (Eurovector EA3000) that was connected to an isotope ratio mass spectrometer (Isoprime, GVI, Manchester, UK). Isotopic abundances were expressed using the δ-notation according to Farquhar and Richards (1984):

$$\delta^{13}C (\%o) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1000$$

where $R_{\text{sample}}$ is the mole fraction of $^{13}$C/$^{12}$C in the sample, and $R_{\text{standard}}$ that of the international IAEA standard V-PDB for carbon. The analytical precision was <0.12‰ (expressed as standard deviation of the internal laboratory standard).

Data analysis

Sap flow density ($Q_s$) and environmental data were available at 30-min resolution. To prevent stem capacitance from biasing the analysis of the transpirational response to variations in environmental conditions (Oren et al. 1998, Ewers et al. 1999), we condensed diurnal courses of $Q_s$ and environmental parameters to daily means. Finally, $Q_s$ data were pooled over all the six trees per treatment. Single variable analyses were used to examine the response of $Q_s$ to $T_{\text{soil}}, R_s$ and $D$ as these environmental
factors have often been found to be closely related to transpiration in conifers at the treeline in the Central European Alps (Anfodillo et al. 1998, Matyssek et al. 2009, Wieser et al. 2013). While relationships between $Q_s$ and $T_{soil}$ and $Q_s$ and $R_i$ were derived by linear regression analysis, the relationship between $Q_s$ and $D$ was analysed using an exponential saturation function:

$$T = a \times (1 - \exp(-b \times D))$$

(4)

where $a$ and $b$ are fitted parameters.

As daily mean $T_{soil}$ and $\theta$ values in the two control and in the two warmed plots, respectively, did not differ significantly (all $P$ values >0.1; one-way analysis of variance (ANOVA)), we used repeated-measures ANOVA (Moser et al. 1990) to test for differences in $T_{soil}$ and $\theta$ between control and warmed plots ($n = 4$ per treatment). Differences in overall mean $Q_s$ between control and warmed trees during the period before roof closure in 2011 and during the periods of roof closure in 2011, 2012 and 2013, respectively, were analysed by one-way ANOVA. One-way ANOVA was also used to test for differences in $D_s$, projected crown area, 100-needle dry weight, SLA, gas exchange parameters and carbon isotope signature between control and warmed trees. A probability level of $P < 0.05$ was considered as statistically significant. Statistical analyses were made with the SPSS 16 software package for Windows (SPSS, Inc., Chicago, IL, USA) and nonlinear curve fits were performed using FigP for Windows (BIOSOFT, Cambridge, UK).

**Results**

**Environmental conditions**

Daily mean solar radiation ($R_i$) varied between 18 (18 September 2011) and 347 W m$^{-2}$ (27 June 2011), averaging 161 W m$^{-2}$ in 2011, 170 W m$^{-2}$ in 2012 and 161 W m$^{-2}$ in 2013 (Figure 1). Daily mean air temperature ($T_{air}$) was 9.5 °C in 2011, 9.2 °C in 2012 and 8.1 °C in 2013, and varied between −4.2 °C on 16 May 2012 and 18.4 °C on 20 August 2012 (Figure 1). Daily mean vapour pressure deficit ($D$) was 0.33 kPa in 2011, 0.24 kPa in 2012 and 0.22 kPa in 2013, approaching zero on rainy days and reaching a maximum of 1.2 kPa on 23...
August 2011 (Figure 1). Daily mean wind velocity averaged 4.5 m s⁻¹ throughout the 3-year study period (data not shown). Precipitation during the study periods 2011, 2012 and 2013 amounted to 602, 889 and 816 mm, respectively. Due to frequent rainfall over the years (Figure 1) soil water content (θ) in 10 cm soil depth varied between a maximum of 0.44 m³ m⁻³ on 2 June 2013 and a minimum of 0.18 m³ m⁻³ on 1 August 2013. Average θ over 2011, 2012 and 2013 did not differ significantly (P ≥ 0.30 each) between control (0.31 m³ m⁻³) and warmed plots (0.29 m³ m⁻³, Table 1).

Before roof closure (DOY 169–182 in 2011) daily mean soil temperature (Tsoil) did not differ significantly (P = 0.68) between control and treatment plots (Figure 2). During periods when roofs were installed, daily mean Tsoil in 5 cm soil depth of the control varied between 1.5 °C on 1 June 2013 and 17.5 °C on 25 August 2011 (Figure 2). In parallel, roofing caused Tsoil to average +1.6 ± 0.2, +1.3 ± 0.2 and +1.0 ± 0.1 °C above corresponding control levels at 5, 10 and 25 cm soil depth, respectively (P < 0.021 consistently; Table 1). Temperature differences between warmed and control plots were linearly correlated with R (Figure 3, during the study period of 2013).

**Structural features of the study trees**

In 2010, the year preceding the warming experiment, Dₜ did not differ significantly (P = 0.66) between control and warmed trees and averaged 8.1 ± 0.6 and 8.5 ± 0.5 cm, respectively. Soil warming had no effect on growth. After 3 years of treatment, Dₜ (P = 0.65) and Aₜ (P = 0.80) did not differ significantly between control and warmed trees (Table 2). Soil warming during three growing seasons did not affect SLA or 100-needle dry weight. In 2013 current-year needle SLA was 43.3 ± 1.4 cm² g⁻¹ in control and 43.2 ± 1.4 cm² g⁻¹ in warmed trees (P = 0.89). Correspondingly, 100-needle dry weight was 1.79 ± 0.09 and 1.77 ± 0.06 g, respectively (P = 0.88).

**Sap flow density and influencing factors**

Seasonal courses in sap flow density (Qₛ) in general followed those of R and D (Figure 4; cf. Figure 1). Before roof closure in
In July 2012, mean rates of net photosynthesis ($P_n$) and transpiration ($E$) along with stomatal conductance for water vapour ($g_{w0}$) of current-year and 1-year-old needles from warmed trees displayed an increase of 3–19% above respective levels of control trees (Table 3). Warming also caused an increase in instantaneous water-use efficiency (WUE) and intrinsic water-use efficiency (iWUE) in 1-year-old needles, which opposed the findings in current-year needles (Table 3). Such differences, however, failed to be statistically significant. Neither did $\delta^{13}$C of sun-exposed current-year needles yield a significant response in 2012, with $-27.00 \pm 0.14\%$ in control and $-26.69 \pm 0.16\%$ in warmed trees ($P = 0.24$). Corresponding $\delta^{13}$C levels in 2013 were $-26.13 \pm 0.16\%$ and $-26.18 \pm 0.21\%$, respectively ($P = 0.83$), reflecting some tendency to increase over the data of 2012.

### Table 2. Stem diameter at height of sensor installation ($D_s$), sapwood cross-section area ($A_s$) and sap flow density ($Q_s$) of *P. cembra* trees selected for sap flow measurements during the study periods 2011 (2 July–11 October), 2012 (15 May–4 October) and 2013 (2 May–8 October). $A_s$ was estimated from $D_s$ according to Eq. (2). Values are the mean ± SE of six trees per treatment. Significant differences ($P < 0.05$) between control and warmed trees are marked in italics.

<table>
<thead>
<tr>
<th>Tree</th>
<th>$D_s$ (cm)</th>
<th>$A_s$ (cm$^2$)</th>
<th>$Q_s$ (g m$^{-2}$ s$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>8.6 ± 0.6</td>
<td>9.2 ± 0.7</td>
<td>9.8 ± 0.7</td>
</tr>
<tr>
<td>Warmed</td>
<td>9.0 ± 0.5</td>
<td>9.6 ± 0.5</td>
<td>10.2 ± 0.6</td>
</tr>
</tbody>
</table>

2011 (DOY 169–182) daily mean $Q_s$ did not differ significantly between control and warmed trees ($P = 0.84$; Figure 4) and averaged 5.37 ± 0.59 and 5.41 ± 0.60 g m$^{-2}$ s$^{-1}$, respectively. Even after roof closure on 2 July 2011 control and warmed trees resembled each other with respect to $Q_s$ (Figure 4), in the absence of a warming effect during the first year of treatment (Table 2; $P = 0.68$). However, during the second (2012) and third year (2013), soil warming caused daily mean $Q_s$ of warmed trees to increase significantly, on average, by 11 and 19% (both $P < 0.001$), respectively, above levels of control trees (Table 2).

Three years of soil warming did not modify the response of $Q_s$ to $T_{soil}$, $R_s$ and $D$. Examined at a daily timescale these results generally reflected positive correlations between $Q_s$ and the three environmental factors. When correlating $Q_s$ with $T_{soil}$ in 5 cm soil depth, $R$ and $D$ throughout the study period of 2013, both in control and warmed trees a linear increase was found with $T_{soil}$ ($P < 0.001$ each; Figure 5). Linear positive correlations also existed with $R$ in control ($R^2 = 0.68$) and warmed trees ($R^2 = 0.50$; $P < 0.001$ each; Figure 6). With respect to $D$, $Q_s$ increased sharply at low $D$, and tended to saturate at mean daily $D$ values >0.2 kPa, in both control and warmed trees. $D$ explained 62 and 67% of the variation in $Q_s$ in control and warmed trees, respectively ($P < 0.001$ each; Figure 7).

### Leaf-level gas exchange and carbon isotope signature

In July 2012, mean rates of net photosynthesis ($P_n$) and transpiration ($E$) along with stomatal conductance for water vapour ($g_{w0}$) of current-year and 1-year-old needles from warmed trees displayed an increase of 3–19% above respective levels of control...
Discussion

The experimental approach was appropriate to manipulate $T_{\text{soil}}$ enabling the clarification of tree water use in situ under a wide range of environmental conditions. Differences in $T_{\text{soil}}$ between control and warmed plots largely depended on radiative warming, i.e., by incoming $R_S$ (Figure 3). Moreover, treatment differences in daily mean $\theta$ stayed within the typical variation at the study site (Neuwinger 1972, 1980), which confirmed the employed roofing system to prevent any shortage in soil water availability (Figure 1; Table 1).

In our study, 3 years of soil warming did not cause any response in stem diameter increment of $P$. cembra (Table 2). As $P$. cembra exhibits determinate shoot growth, in any year growth is primarily impelled by the bud formation occurring in the previous year (Tranquillini 1979). Additionally, in alpine ecosystems, growth response to warming is mediated through a time lag by one or more years after initiation of warming (Danby and Hik 2007, Hagedorn et al. 2010). Responses during the extraordinary warm year of 2003 support our result, as the growth of $P$. cembra at the treeline in the Austrian Alps was hardly affected by a 4 °C warmer summer (Oberhuber et al. 2008). Neither was a growth response during 2003 observed in Swiss alpine and subalpine forests (Jolly et al. 2005).

Changes in $Q_s$ observed in our study may also be related to treatment-induced alterations in leaf area. In $P$. cembra both cumulative projected foliage area ($A_f$) and sapwood cross-sectional area ($A_s$) increase exponentially with stem diameter reflecting a stable $A_f$ to $A_s$ ratio of 0.45 m$^2$ cm$^{-2}$ (Matyssek et al. 2009). Stable $A_f$ to $A_s$ ratios have also been observed in other conifers (Waring and Running 1985, Waring and Schlesinger 1985) and reflect a long-term adjustment between water demand of the foliage and water supply through the trunk (Tyree and Zimmermann 2002). In our study however, we detected no soil warming effect on sapwood area (Table 2), implying that leaf area was also not affected.

Seasonal patterns in $Q_s$ were similar to those reported from other $P$. cembra stands at the treeline in the Central Austrian (Wieser and Leo 2012, Wieser et al. 2013) and the north-eastern Italian Alps (Anfodillo et al. 1998). We detected no significant treatment effects on $Q_s$ during the first year of warming (Figure 4, Table 2). Similarly, Van Herk et al. (2011) reported that soil warming by 5 °C failed to affect $Q_s$ in Pinus mariana in northern Manitoba, Canada, throughout one growing season.

Table 3. Net photosynthesis ($P_n$; µmol m$^{-2}$ s$^{-1}$), transpiration ($E$; mmol m$^{-2}$ s$^{-1}$), stomatal conductance for water vapour ($g_{H_2O}$; µmol CO$_2$ H$_2$O mol$^{-1}$) and intrinsic water-use efficiency (iWUE; µmol CO$_2$ mol$^{-1}$), of current-year and 1-year-old needles of control and warmed $P$. cembra trees obtained in July 2012, and corresponding $P$ values. Values are related to projected leaf area and are the mean of six trees ±SE per treatment.

<table>
<thead>
<tr>
<th></th>
<th>Current-year needles</th>
<th>1-year-old needles</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Control</td>
<td>Warmed</td>
</tr>
<tr>
<td>$P_n$</td>
<td>14.20 ± 1.72</td>
<td>14.88 ± 1.33</td>
</tr>
<tr>
<td>$E$</td>
<td>4.45 ± 0.42</td>
<td>4.75 ± 0.35</td>
</tr>
<tr>
<td>$g_{H_2O}$</td>
<td>317 ± 31</td>
<td>374 ± 31</td>
</tr>
<tr>
<td>WUE</td>
<td>3.31 ± 0.27</td>
<td>3.18 ± 0.22</td>
</tr>
<tr>
<td>iWUE</td>
<td>0.044 ± 0.003</td>
<td>0.041 ± 0.002</td>
</tr>
</tbody>
</table>

Figure 6. Daily mean sap flow density ($Q_s$) as a function of solar radiation ($R$) for the control (black circles and line) and the warmed treatment (grey circles and line) in the third year of soil warming. Points are mean values of six trees. Points were fit by linear regressions: control: $y = 0.015R + 1.39$, $R^2 = 0.68$, $P < 0.001$; warmed: $y = 0.014R + 2.18$, $R^2 = 0.50$, $P < 0.001$.

Figure 7. Daily mean sap flow density ($Q_s$) as a function of vapour pressure deficit ($D$) for the control (black circles and line) and the warmed treatment (grey circles and line) in the third year of soil warming. Points are mean values of six trees. Points were fit by exponential saturation functions: control: $y = 4.19(1 - \exp[-1.39D])$, $R^2 = 0.62$, $P < 0.001$; warmed: $y = 5.56(1 - \exp[-1.53D])$, $R^2 = 0.67$, $P < 0.001$. 

Table 3. Net photosynthesis ($P_n$; µmol m$^{-2}$ s$^{-1}$), transpiration ($E$; mmol m$^{-2}$ s$^{-1}$), stomatal conductance for water vapour ($g_{H_2O}$; µmol CO$_2$ H$_2$O mol$^{-1}$) and intrinsic water-use efficiency (iWUE; µmol CO$_2$ mol$^{-1}$), of current-year and 1-year-old needles of control and warmed $P$. cembra trees obtained in July 2012, and corresponding $P$ values. Values are related to projected leaf area and are the mean of six trees ±SE per treatment.
During the second and third year, soil warming significantly increased $Q_s$ (Figure 4, Table 2). Independent of the treatment $Q_s$ was linearly correlated with $T_{soil}$ as also observed in a snow cover manipulation experiment by Mellander et al. (2004). Hence, $T_{soil}$ appears to determine water transportation along the soil–plant–atmosphere continuum, with low $T_{soil}$ restricting water uptake (cf. Figures 2 and 4). In cold soils increased water viscosity and decreased root permeability are known to limit water uptake in conifers (Kramer 1940, 1942, Kaufmann 1975, Lopushinsky and Kaufmann 1984, Goldstein et al. 1985, Wan and Zwiazek 1999), contributing to low $Q_s$ as observed in trees growing on our control plots (Figures 4 and 5). There is also evidence that the functioning of aquaporins (membrane-bound water channel proteins) is temperature dependent (Yang et al. 2011). In the absence of statistical significance, in our study soil warming appeared to stimulate foliar gas exchange (Table 3). Furthermore, $Q_s$ was considerably higher in warmed than in control trees (Figures 6 and 7) as related to the same reference levels in $R$ and $D$, emphasizing the influence of root zone temperature on aboveground metabolism (Havranek 1972, Gruber et al. 2010, Wieser et al. 2010).

Additionally important is the effect of $T_{soil}$ on $Q_s$ at high altitude as low soil temperatures limit fine-root growth (Häserl et al. 1999, Pregitzer et al. 2000, Oberhuber 2007). In $P$. cembra fine-root elongation rate peaks in July, increases with $T_{soil}$ and ceases at rooting zone temperatures below 3–5 °C (Turner and Streule 1983). Thus, particularly in open stands, as was the case at the study site, soil warming might have enhanced root production in the uppermost soil layers during the second (2012) and third (2013) years of treatment, given that soil warming started immediately after each snow melt (Figure 2). In such a case, it is likely that the water uptake capacity became improved upon enlargement of the absorbing surface area belowground. Such an effect was probably absent during the first year of treatment, when soil warming was started in July, i.e., after the seasonal period of maximum fine-root elongation.

Conclusions

In accordance with our hypothesis, soil warming led to an increase in $Q_s$ of $P$. cembra trees at the treeline in the central Austrian Alps. During the first year of treatment, no warming effect was detected on $Q_s$. In the second and third year, however, the effect appeared to result from warming-induced root production, a reduction in viscosity and perhaps an increase also in root hydraulic conductivity. Although radial stem growth and sapwood area increment did not reflect response to warming, $T_{soil}$ was increased to an extent relevant for treeline water budgets. Presuming a future environment with unchanged precipitation but increased surface temperatures, both tree-level water loss and carbon uptake may increase. Conversely, the response to warming may be transitory as advancing stand development may become resource limited. Such a development in net primary productivity emerged from the long-term FACE study reported by Norby et al. (2010). Consequently, further clarification of future treeline scenarios will require a combination of prolonged experimental soil warming and nutrient availability analysis. We conclude from the present study that tree water loss may increase with soil warming in a future environment, affecting the water balance within the treeline ecotone of the Central Austrian Alps.

Conflict of interest

None declared.

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References


