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Transpiration and canopy conductance in an inner alpine Scots pine (*Pinus sylvestris* L.) forest

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Abstract

Canopy transpiration (E_c) of a 150-year old *Pinus sylvestris* L. stand in an inner alpine dry valley, Tyrol, Austria was estimated throughout two growing seasons 2011 and 2012 by means of xylem sap flow measurements. Although there were prolonged periods of limited soil water availability E_c did not show a clear trend with respect to soil water availability and averaged 0.4 ± 0.19 mm day⁻¹ under conditions of non-limiting soil water availability and 0.37 ± 0.17 mm day⁻¹ when soil water availability was limited. This is because canopy conductance declined significantly with increasing evaporative demand and thus significantly reduced tree water loss. The growing season total of E_c was 74 mm and 88 mm in 2011 and 2012, respectively, which is significantly below the values estimated for other *P. sylvestris* forest ecosystems in Central Europe, and thus reflecting a strong adaptation to soil drought during periods of high evaporative.

Introduction

Scots pine (*Pinus sylvestris* L.) is a Eurosibirean conifer tree species forming stands under widely different environmental conditions (Jalas and Suominen, 1993). In Europe the distribution limit ranges from the boreal region in the North to the Mediterranean basin in the south. Contrary to the situation in northern Europe *P. sylvestris* forests in Mediterranean areas suffer from summer drought (Martinez-Vilata et al., 2009). Forest ecosystems in dry inner alpine valleys in Italy, Switzerland and Austria are also characterized by high summer temperatures, low precipitation, and limited soil water availability (Zweifel et al., 2009; Oberhuber and Gruber, 2010; Gruber et al., 2012) and thus are considered to be sensitive to climate change.

Based on several dendroclimatological studies conducted in inner Alpine dry valleys it is well established that radial stem increment of trees growing there is primarily limited by low spring precipitation and soil drought during the growing season (Oberhuber et al., 1998; Levesque et al., 2013). Specifically, dendrochronological studies conducted at inner Alpine

dry valley of the Inn River (Tyrol, Austria) gave evidence that a decrease in radial stem growth in the growing season may be due to a high below ground demand for carbohydrates to ensure adequate water and nutrient uptake in this drought-exposed ecosystem (Oberhuber and Gruber, 2010).

Although data on whole water flux in *Pinus sylvestris* stands have been reported by different authors (e.g. Irvine et al., 1998; Lüttenschwager et al., 1999; Zimmermann et al., 2000; Perks et al., 2004; Poyatos et al., 2008) we are not aware of any study focusing on canopy transpiration of pine stands throughout an entire growing season in inner alpine dry valleys.

As photosynthetic carbon gain and regulation of the tree's water status are inherently linked via the stomata in this study we investigated the influence of soil water availability on canopy transpiration and canopy conductance in a xeric *P. sylvestris* stand growing on a postglacial rock-slide area located in the inner alpine study area based on monitoring xylem sap flow throughout two growing seasons. The sap flow approach provides whole-tree transpiration data as sap flow through tree trunks matches crown transpiration on a daily and seasonal basis (Schulze et al., 1985). As this method provides insights into environmental limitations our specific goals were to study the effect of soil water availability on seasonal variations in sap flow density (Q_s) of *P. sylvestris*, and to analyze the impact of other environmental factors (irradiance and vapour pressure deficit). To achieve this goal we measured Q_s with thermal dissipation probes (Granier, 1985). The measured Q_s patterns were then correlated with available environmental variables using simple regression analysis in order to analyze the effect of soil water content (θ), solar radiation (R) and vapor pressure deficit (D) on transpiration. Finally we also focus on the relevance of canopy conductance in regulating the water loss of *P. sylvestris*, given the importance of this tree species in inner alpine dry valleys.

Material and Methods

Study site

The study was carried out in a *Pinus sylvestris* forest (*Erico-Pinetum typicum*, Ellenberg and Leuschner 2010) growing on a postglacial rock-slide area located in the montane belt of the inner Alpine dry Inn valley; Tyrol, Austria (750 m a.s.l.; 47°14'00'' N, 10°50'20'' E) on south exposed slope of 40° inclination (cf. Oberhuber et al., 1998; Oberhuber, 2001). At the time of study (2011-2012) trees were 150 ± 30 years old, the diameter at breast height (DBH) averaged 24.4 ± 4.9 cm, and their height ranged between 4 and 5 m. The stand density was 600 trees ha⁻¹, the basal area was 21.8 m² ha⁻¹, and the leaf area index (LAI) was 0.55 (Oberhuber and Gruber, 2010)

The study site is characterized by a continental climate. According to a long term record (1911 -2012) from a weather station nearby (Ötz 812 m a.s.l., 5 km south from the study area) the mean annual air temperature was 7.3°C and the mean annual precipitation was 718 mm, with spring representing the driest part of the year (March - May; 138 mm).

The geological substrate is limestone. According to the World Base for Soil Resources (FAO 2006) the soil at the study site is classified as a protorendzina (rendzic leptosol; soil profile:

O-A-C). There is a 3 to 5 cm thick xeromoder followed by a 10 cm thick A-horizon above the debris of the parent material. The A-horizon is enriched by 5% of organic matter and the soil texture is dominated by the sand (54%) and the silt fraction (44%) with almost no clay (2%). Based on the water retention curve obtained in the laboratory the water holding capacity at field saturation is $0.42 \text{ m}^3 \text{ m}^{-3}$, the corresponding values for field capacity (-0.033 MPa) and the wilting point (-1.5 MPa ; *sensu* Blume et al. 2010) are 0.23 and $0.07 \text{ m}^3 \text{ m}^{-3}$, respectively.

Environmental measurements

Air temperature, relative humidity (HMP45C, Campbell Scientific, Shepshed, UK), solar radiation (SP-Lite, Campbell Scientific, Shepshed, UK), wind velocity (A100R, Campbell Scientific, Shepshed, UK), and precipitation (ARG100, Campbell Scientific, Shepshed, UK), were monitored 2 m above ground in an open ridge. Soil temperature (Temperature 107 Probe, Campbell Scientific, Shepshed, UK) was monitored at two sites in 5-10 cm soil depth. All these environmental parameters were recorded with a CR10X data logger (Campbell Scientific, Shepshed, UK) programmed to record 30-min averages of measurements taken every minute. Volumetric soil water content (θ) was continuously monitored in 5 - 10 cm soil depth of the A-horizon for a certain time interval of 30 minutes at three sites with capacitive soil moisture sensors (Cyclobis, proprietary development, University Innsbruck, Austria). Due to small-scale variability of the soil structure (cf. Oberhuber and Gruber 2010) records of the two soil temperature and the three soil moisture sensors, respectively were averaged.

Soil water deficit (SWD) was quantified in the form of relative extractable water (REW, dimensionless) and assumed to occur when REW dropped below 0.4 (Granier, 1987; Breda et al., 1995), a value known to cause stomatal closure in *P. sylvestris* (Irvine et al., 1998; Sturm et al., 1998), and to limit crown conductance of *P. sylvestris* in a nearby more mesic *Erico-Pinetum* typicum forest (Leo et al., 2013). As in rendzic leptosols, similar to that at our site, most of the fine roots spread in shallow thin A-horizon and only the tap-root and some fine roots are capable to penetrate into the debris below (Kutschera and Lichtenegger, 2002) we used our θ values observed in 5-10 cm soil depth as a proxy for estimating REW as follows:

$$\text{REW} = (\theta_{\text{act}} - \theta_{\text{m}}) / (\theta_{\text{fc}} - \theta_{\text{m}}) \quad (1)$$

where θ_{act} is the actual soil water content, θ_{m} , is the minimum soil water content observed during the investigation period, and θ_{fc} is the soil water content at field capacity (Granier et al., 2000).

Sap flow density measurements, estimation of whole tree-water use, canopy transpiration, and conductance

Sap flow density (Q_s) through the trunks of six *P. sylvestris* trees differing in diameter at breast height (DBH) and projected crown area (Table 1) was monitored with thermal dissipation sensors (Granier 1985) by battery-operated sap flow systems (M1 Sapflow

System, PROSA-LOG; UP, Umweltanalytische Produkte GmbH, Cottbus, Germany). Each system consisted of a three-channel PROSA-LOG datalogger and a constant source for sensor heating. Each sensor consisted of a heated and an unheated pair of thermocouples, connected in opposite for measuring temperature difference. In each study tree one 20 mm long sensor was installed into the outer xylem (0-20 mm from the cambium) at breast height. Accounting for variations of Q_s across the cross section trunk sapwood area (Cermák et al., 1992; Köstner et al., 1998) sensors were also installed in the next 20 mm thick xylem band (20-40 mm sapwood depth; termed “inner xylem”) in two of the selected study trees. Sensors were installed 15 cm apart vertically on the north facing side of the stems, 1.3 m above ground. The upper probe of each sensor included a heater that was continuously supplied with a constant power of 0.2 W, whereas the lower probe was unheated, remaining at trunk temperature for reference. The temperature difference between the upper heated probe and the lower reference probe was recorded every 30 minutes. The sensors were shielded with a thick aluminium-faced foam cover to prevent exposure to rain, and to avoid physical damage and thermal influences from radiation.

Power for the sap-flow systems, the environmental sensors, and the data loggers was provided by two car batteries (12 VDC, 90 Ah) which were recharged by means of an 80 W solar panel and a charge controller each. Environmental and sap flow density data were continuously monitored from April 1 until October 14, 2011 and from March 14 until October 20, 2012.

For each sensor Q_s ($\text{g m}^{-2} \text{s}^{-1}$) was calculated from the temperature difference between the two probes (T) relative to the maximum temperature difference (T_m) which occurred at times of zero flow according to the calibration equation determined by Granier (1987) and revalidated by others (Köstner et al., 1998; Clearwater et al., 1999):

$$Q_s = 119 * [(\Delta T_m - \Delta T) / \Delta T]^{1.231} \quad (2)$$

Each night T_m was determined and used as a reference for the following day. This assumption of zero sap fluxes seems reasonable as night-time vapour pressure deficits were mostly low and temperature courses of the sensors reached equilibrium most nights suggesting that refilling of internal reserves was complete.

The sensors in the outer and the inner xylem covered most of the active sapwood which had an average thickness of 41.5 ± 5.4 mm in our study trees. In our study trees Q_s did not vary notably across sapwood depth ($P < 0.5$). In the outer xylem Q_s averaged 3.9 ± 2.6 and 4.8 ± 1.7 $\text{g m}^{-2} \text{s}^{-1}$ in 2011 and 2012, respectively. The corresponding values for the inner xylem were 4.0 ± 2.8 and 4.8 ± 3.01 $\text{g m}^{-2} \text{s}^{-1}$, respectively. Thus, we assumed uniform Q_s across sapwood depth and our installation sampled 100% of the whole water flow in this conifer. Based on this assumption whole-tree water use (WU; kg day^{-1}) was calculated by summing Q_s over a day and multiplying this sum by the tree cross-sectional sapwood area at the height of sensor installation (Table 1).

Sapwood area (A) was estimated from stem diameter at breast height DBH based on measurements on several increment cores of a diameter of 5-mm taken at breast height of study and neighbouring trees, as well as from wood disks of cut trees according to the allometric relationship:

$$A = 0.126 \cdot \text{DBH}^2 + 5.12 \cdot \text{DBH}; R^2 = 0.98 \quad (3)$$

In *P. sylvestris* sapwood and heartwood are clearly distinguishable on the basis of colour. Finally, Q_s was also related to canopy transpiration per unit of ground surface area (E_c ; mm day⁻¹). As in both investigation periods Q_s was not correlated with DBH ($R^2 > 0.15$, $P > 0.45$) daily Q_s sums estimated for our six study trees were averaged and the mean was multiplied with the estimated stand level sapwood area (Zimmermann et al., 2000; Oishi et al., 2010). A stand level sapwood area of 10.5 cm² m⁻² was used for up-scaling.

Crown conductance related to ground surface area (g_c) was estimated from E_c using a simplified inverted Penman-Monteith equation (cf. Luis et al., 2005):

$$g_c = \gamma \lambda E_c / \rho c_p D \quad (4)$$

where γ is the psychrometric constant, λ is the latent heat of water vaporisation, ρ is the density of the air, c_p is the specific heat of air at constant pressure, and D is the vapour pressure deficit calculated from air temperature and relative humidity (see above). The term g_c represents the total average water vapour conductance and includes boundary layer and aerodynamic conductance (Köstner et al., 1992; Ryan et al., 2000). However, due to the open well ventilated canopy at our study site (33% canopy coverage; Oberhuber and Gruber 2010), and hence a strong coupling to the atmosphere, we assumed that g_c closely approximated average stomatal conductance (Köstner et al., 1992; Oren et al., 1998; Ryan et al., 2000).

Data analyses

In this study we emphasized on the comparison of transpiration characteristics of *P. sylvestris* as affected by soil water availability (SWA). Because of the large variation in Q_s among individual study trees and with respect to investigation period (2011 and 2012) we used normalized Q_s for our analysis. This was achieved by converting Q_s values of each tree to a ratio of the maximum daily mean value observed during the measurement periods (Table 1). Subsequently, each tree had a maximum normalized Q_s of 1, and thus permitting a better comparison of Q_s to environmental variables (Luis et al., 2005; Du et al., 2011).

Values of Q_s and of environmental variables were available at 30-min resolution. In order to reduce the dimension of the data sets and to avoid the problem that stem capacitance may affect the analysis of transpiration responses to variation in environmental conditions (Oren et al., 1998; Ewers et al., 1999) we averaged diurnal values of Q_s and environmental parameters to daily means. Finally the data sets were pooled over all the six trees and season (2011 and 2012).

Regression analyses were performed to analyze the response of normalized Q_s values to soil water content (θ), solar radiation (R), and vapour pressure deficit (D). While correlation of normalized Q_s with θ and R was obtained by linear regression analysis, the relationship between normalized Q_s and D was analyzed using the following exponential saturation function:

$$Q_s = (1 - \exp(-a + D)) \quad (5)$$

where a is a fitting parameter.

The response of g_c to D was examined using the Lohammer type equation:

$$g_c = g_{cmax} * (1 / (1 + (D/a))) \quad (5)$$

where g_{cmax} is the maximum canopy conductance observed during the study period and a is a fitting parameter. All the analyses were performed using the SPSS 16 software package (SPSS Inc. Chicago, USA).

Results

Environmental conditions

Seasonal patterns of environmental parameters obtained during the study periods 2011 (April 1 to October 14) and 2012 (March 14 to October 20) are shown in Fig. 1. Daily mean solar radiation (R) varied between 6 (June 8, 2011) and 388 W m⁻² (April 2, 2012) and averaged 178 W m⁻² in 2011 and 191 W m⁻² in 2012. Daily mean air temperature (T_a) was 15.4°C in 2011 and 14.9°C in 2012 and varied between 2.1°C on March 21, 2012 and 26.4°C on July 1, 2012 (data not shown). Daily mean vapour pressure deficit (D) was 0.6 and 0.9 kPa in 2011 and 2012, respectively. It was close to zero on rainy days and reached values up to 1.82 kPa on May 12, 2012 (Fig. 1). Daily mean wind velocity (v) averaged 0.5 m s⁻¹ in both investigation periods (data not shown). Daily mean soil temperature (T_s) in 5-10 cm soil depth generally followed seasonal trends in T_a averaged 15.2° in 2011 and 16.5 °C in 2012. T_s varied between 1.8°C on March 4, 2011 and 24.4°C on July 3, 2012 (data not shown).

The total sum of precipitation (P) during the investigation periods 2011 and 2012 were 567 and 605 mm, respectively. In April 2011 P was six times lower (6 mm) as compared to the long term mean (1911-2012; 38 mm) and thus resulting in low volumetric soil water content (θ) values down to 0.05 m³ m⁻³ (Fig. 1). Ample P from May throughout August 2011 (440 mm; long term mean 456 mm) caused θ to reach values up to 0.22 m³ m⁻³ throughout the summer (Fig. 1). During a rainless period at the end of August 2011 θ tended to decline and remained at low values till mid October and then increased again due to ample P (Fig. 1). In 2012 by contrast, the sum of P for the period of March and April (79 mm) was comparable to the long term mean of 74 mm and thus resulting in high θ values at the beginning of the growing season (Fig. 1). From May throughout August 2012 P (377 mm) was 17 % lower

than the long term mean and thus triggering lower θ values during the summer of 2012 as compared to the previous year. Frequent P events with more than 10 to 15 mm day⁻¹ during fall 2012 caused θ to remain at high values during September and October 2012 (Fig. 1).

Based on an REW value of 0.4 ($\theta = 0.12 \text{ m}^3 \text{ m}^{-3}$) limited SWA represent 54 % of the growing season in 2011 and 30% of the growing season 2012. Limited SWA occurred for a 40 day period in spring 2011 beginning in April, during several days between end of May and mid June and for another 50 days beginning on August 20, 2011 (Fig. 1). In 2012 limited SWA occurred mainly during May until mid July (about 55 days) and another few days during spring and fall (Fig 1).

Sap flow density and influencing factors

To elucidate response patterns of Q_s to environmental factors daily mean normalized Q_s were correlated with R and D conditions obtained at the study site 2 m above ground. Examined at a daily time-scale for the two growing seasons these results reflected positive relationships between normalized Q_s and both atmospheric factors. We obtained linear correlation between normalized Q_s and R at R^2 levels of 0.67 and 0.28 under conditions of non-limiting and limiting SWA (both P values < 0.001; Fig. 2).

With respect to D normalized Q_s increased sharply at low D and tended to saturate at daily mean D values > 0.8 kPa under non-limiting SWA and >1.2 kPa when SWA was limiting (Fig. 2). D explained 73 and 39% (both P values < 0.001) of the variation in normalized Q_s under conditions of non-limiting and limiting SWA, respectively (Fig. 3). Despite a noticeable decrease in normalized Q_s at R and D values < 250 W m⁻² (Fig. 2) and 0.8 kPa (Fig. 3), respectively there were no significant differences between SWA in the relationship between normalized Q_s and both environmental parameters ($P = 0.31$). After pooling data across both growing seasons normalized Q_s averaged 0.52 ± 0.23 under conditions of non-limiting SWA and 0.47 ± 0.21 during periods of limiting SWA (Fig. 3, box plot). In contrast to normalized Q_s and hence also canopy transpiration (E_c) canopy conductance related to ground surface area (g_c) declined with increasing D (Fig. 4) and D explained 41 and 25% (both P values < 0.001) of the variation in g_c under conditions of non-limiting and limiting SWA, respectively (Fig. 4).

Whole tree water use, canopy transpiration and canopy conductance

Maximum whole tree water use (WU) varied between 8.1 and 25.4 kg day⁻¹ and averaged $14.5 \pm 5.5 \text{ kg day}^{-1}$ in 2011 and $15.1 \pm 4.8 \text{ kg day}^{-1}$ in 2012 (Table 1) Canopy transpiration per unit of ground surface area (E_c) generally followed seasonal trends in R and D (Fig. 1), was close to zero on rainy days (September, 6 2011) and reached maximum values up to and 0.75 mm day⁻¹ (August, 17 2011) during cloudless days with high evaporative demand and non-limiting SWA (Fig. 5). Aggregated over both growing seasons E_c averaged 0.40 ± 0.19 and $0.37 \pm 0.17 \text{ mm day}^{-1}$ under conditions of non-limiting and limiting SWA, respectively. Total growing season E_c was 74 mm in 2011 (April 1 until October 14) and 88 mm in 2012 (April 21 throughout October 9).

A similar seasonal trend was also observed for g_c (Fig. 5). Throughout the entire investigation period g_c varied between 0.23 mm s⁻¹ on April 9, 2011 and 2.54 on June 11,

2012 and averaged 1.29 ± 0.36 and $0.86 \pm 0.40 \text{ mm s}^{-1}$ under conditions of non-limiting and limiting SWA, respectively ($P = 0.20$).

Discussion

In the present study we focused on seasonal variations in E_c of a 150-year-old *P. sylvestris* forest in an inner-Alpine dry valley of the Inn River (Tyrol, Austria) where trees had no access to ground water (Leo et al., 2013) and SWA in the main rooting zone was limited due to a low water holding capacity of the A-horizon. In accordance with previous studies carried out in other *P. sylvestris* forests (Sturm et al., 1998; Zimmermann et al., 2000; Verbeeck et al., 2007; Poyatos et al., 2008) also at our site normalized Q_s values have been found to increase linearly with increasing R (Fig. 2) and tended to saturate at high D (Fig. 3).

In forest ecosystems with a high level of coupling between the canopy and the atmosphere (Jarvis and McNaughton 1986), as is typically the case in open stands, the tendency for E_c to saturate at high D can (Fig. 3) primarily be to a decrease in g_c with increasing D (Fig. 4) as also observed by others (Lopushinsky, 1986; Meinzer et al., 1993; Granier et al., 1996, 2000; Hogg and Hurdle, 1997; Zimmermann et al., 2000; Luis et al., 2005; Wieser and Leo, 2012). Stomatal closure due to increasing evaporative demand in terms of D has also been found in *P. sylvestris* at the leaf level (Sturm et al., 1998) as well as in drought exposed *Larix decidua* trees in a Mongolian forest-steppe ecotone (Dulsamsuren et al., 2009) and in Mediterranean tree species (Epron and Dryer, 1978; Borghetti et al., 1998; Medivilla and Escudero, 2003; Peters et al., 2008) and thus significantly reducing tree water loss during periods of high evaporative demand. This drought adaptation mechanism of *P. sylvestris* fits to a typical water-saving strategy (*sensu* Levitt, 1980) as has also been reported previously for other *P. sylvestris* stands in Austria (Leo et al., 2013), Switzerland (Zweifel et al., 2009), Scotland (Irvine et al., 1998; Perks et al., 2004), Spain (Llores et al., 2008), Mongolia (Dulsamsuren et al., 2009), and Siberia (Sugimoto et al., 2002).

Soil water reserves demonstrated clear seasonal variations when approximating REW from soil moisture measurements in the A-horizon (Fig. 1). Based on a REW of 0.4. ($\theta < 0.12 \text{ m}^3 \text{ m}^{-3}$) limited SWA represented half of the growing season 2011 (107 days or 54%) and nearly a third of the growing season 2012 (66 days, or 30%). Even so, we did not detect any significant drought effects on transpiration, even during a 31 day period in fall 2011 when θ values in the A-horizon were close to the wilting point ($0.07 \text{ m}^3 \text{ m}^{-3}$). In contrast to our findings Sturm et al (1996) reported that transpiration in a *P. sylvestris* forest in Germany was strongly limited when θ dropped below $0.12 \text{ m}^3 \text{ m}^{-3}$, whereas Lagergren and Lindroth (2002) reported a decrease in the transpiration of *P. sylvestris* in Sweden at a threshold of $0.10 \text{ m}^3 \text{ m}^{-3}$. Irvine et al. (1998) and Leo et al. (2013) demonstrated that under conditions of artificial soil drought canopy transpiration of Scots pine was significantly reduced when θ dropped below $0.12 \text{ m}^3 \text{ m}^{-3}$. Our results suggest that for *P. sylvestris* growing in inner alpine dry valleys the SWA threshold is below $0.12 \text{ m}^3 \text{ m}^{-3}$ and thus suggesting a great tolerance of this tree species to limited SWA of the top soil. One assumption to explain this observation is that roots which extend below the A-horizon penetrate into the debris of the parent material are able to tap water from deeper pools when the upper layers are exhausted to

maintain a favorable water status (Dawson, 1994; Villar-Salvador et al., 1997; Sarris et al., 2013). Access to deep soil water reserves has been reported for a Scots pine forest in Belgium (Vincke and Thiry, 2008), a mixed broadleaved deciduous forest in North Carolina (Oishi et al., 2010), and a Canary island pine forest in Tenerife (Luis et al. 2005). Even if only a few fine roots are present in deeper and wet layer of the subsoil debris they significantly can contribute too water uptake in Scots pine (Vincke and Thiry, 2008) as root distribution is not necessarily correlated with water uptake (Bishop et al., 1998; Wattenbach et al., 2005).

Although maximum WU rates obtained for *P. sylvestris* at our study site (Table 1) were broadly in line with data reported for other conifer tree species comparable in DBH (Wullschleger et al., 1998) our maximum E_c of 0.75 mm day^{-1} (Fig. 5) is significantly below the range of $1 - 6 \text{ mm day}^{-1}$ obtained for evergreen coniferous forests during the course of an entire growing season (Pallardy et al., 1995) and might be attributed the low LAI (0.55) and the low canopy coverage of 33% (Gruber et al., 2012) at our study site. The maximum E_c value obtained at our site however, is comparable to the value of $0.72 \pm 0.3 \text{ mm day}^{-1}$ reported for 28 and 243-year old Scots pine stands in Siberia similar in LAI and canopy coverage (Zimmermann et al., 2000) as at our site. Our annual growing season E_c of 74 and 88 mm estimated for 2011 and 2012, respectively was about four to seven times lower than transpiration rates reported for evergreen forest ecosystems in Central Europe ($300\text{--}600 \text{ mm year}^{-1}$; Köstner, 2001; Larcher, 2001). Our estimated E_c however, was comparable to the value estimated for a drought affected *P. sylvestris* forest in north east Germany ($82\text{--}113 \text{ mm}$; Lüttenschwager et al., 1999), and even more than two times above the value estimated for a spares pine cover in Central Siberia (33 mm ; Zimmermann et al., 2000). Obviously such low daily and total growing season E_c values are quite rare and restricted to extreme climatic and/or soil conditions (Lüttenschwager et al., 1999; Luis et al., 2005; Nadhezhkina et al., 2007; Poyatos et al., 2008; Kucerova et al., 2010).

Conclusions

In conclusion our results suggest that in inner alpine dry valleys *P. sylvestris* is well adapted to cope with high evaporative demand even under limited SWA in the top soil. Due to the combination of a declining g_c in response to increasing evaporative demand and access to deep soil water reserves E_c was at relatively high values during periods when the top soil was dry. This is because g_c of *P. sylvestris* trees declines rapidly with increasing evaporative demand. Although under conditions of limited SWA *P. sylvestris* needles in inner alpine dry valleys of Austria (Schuster et al. unpublished observations) and Switzerland (Zweifel et al., 2009) close their stomata disproportionally more than co-occurring tree species rain at regular intervals (every 1-3 weeks; Zweifel et al., 2009) prevents complete stomatal closure and thus allowing *P. sylvestris* to maintain stem growth (Gruber et al., 2010; Oberhuber and Gruber, 2010) and prevented depletion of non structural carbohydrate reserves throughout the growing season (Gruber et al., 2012). At our study site Gruber et al. (2012) also observed an increased allocation of non structural carbohydrates to roots and associated mycorrhiza in response to soil drought. The latter is a well known phenomenon (Millard et al., 2007; McDowell et al., 2008), and enables adequate and sufficient water and nutrient supply under conditions of limited SWA (Waring and Schlesinger, 1985). Finally, estimates of $\delta^{18}\text{O}$

isotope ratios of precipitation, xylem, and soil water in different soil depths (Sarris et al., 2013) combined with assessments of absorptive root areas in different soil layers by earth impedance methods (Cermak et al., 2013a, b) are necessary to shed light on the accessibility of different water sources for transpiration (Leo et al., 2013) of trees in inner alpine dry valleys.

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Fig. 1. Seasonal course of daily mean solar radiation (R), vapour pressure deficit (D), daily sum of precipitation (P) and soil water content (θ) in 5 to 10 cm soil depth between April 1 until October 14, 2011 and from March 14 until October 20, 2012. The dotted line indicates soil water deficit.

Fig. 2.

Normalized daily mean sap flow density (Q_s) as a function of solar radiation (R) under non limiting (black circles and line) and limiting soil water availability (grey circles and line). Points are mean values of six trees and were fit by linear regressions: non limiting SWA: $y=0.003R+0.08$; $R^2 = 0.67$, $P < 0.001$; limiting SWA: $y=0.002R+0.17$; $R^2 = 0.28$, $P < 0.001$.

Fig. 3.

Normalized daily mean sap flow density (Q_s) as a function of vapour pressure deficit (D) under non-limiting ($REW > 0.4$; black circles and line) and limiting soil water availability ($REW \leq 0.4$; grey circles and line). Points are mean values of six trees and were fit by exponential saturation functions: non limiting SWA: $y=1-\exp(-1.66 \cdot D)$; $R^2 = 0.73$, $P = 0.001$; limiting SWA: $y=1-\exp(-0.98 \cdot D)$; $R^2 = 0.39$, $P = 0.001$. Box plots on the right show median, lower (25%) and upper (75%) quartile and minimum and maximum normalized daily mean Q_s non-limiting (n-l) and limiting (l) soil water availability (SWA) with the center line, the box and the whiskers, respectively.

Fig. 4.

Daily mean canopy conductance (g_c) as a function of vapour pressure deficit (D) under non limiting ($REW > 0.4$; black circles and line) and limiting soil water availability ($REW \leq 0.4$; grey circles and line). Points are mean values of six trees and were fit by Lohammer type regression analysis: non limiting SWA: $y = 2.5 \cdot (1 / (1 + (D/0.76)))$; $R^2 = 0.41$, $P = 0.001$; limiting SWA: $y = 2.5 \cdot (1 / (1 + (D/0.41)))$; $R^2 = 0.25$, $P = 0.001$; $g_{cmax} = 2.3 \text{ mm s}^{-1}$.

Fig. 5. Seasonal course of daily canopy transpiration (E_c), and mean daily canopy conductance (g_c) between April 1 until October 14, 2011 and from March 14 until October 20, 2012. Grey horizontal bars represent periods of limited soil water availability.

Table 1

Biometric data, maximum sap flow density (Q_{smax} ; $\text{g m}^{-2} \text{s}^{-1}$) and whole tree water use (WU_{max}) of the six study trees obtained in 2011 and 2012.

Tree	DBH [cm]	Sapwood area [cm ²]	Sapwood depth [cm]	Projected crown area [m ²]	Q_{smax}		WU_{max}	
					2011	2012	2011	2012
1	28	241	4.6	7.67	12.2	11.0	25.4	22.9
2	18	133	3.6	2.1	12.4	12.5	14.2	14.3
3	22	173	4.0	4.5	7.8	10.8	11.7	16.1
4	32	292	5.0	6.2	5.3	6.3	13.4	15.9
5	21	163	3.9	5.8	8.7	9.6	12.3	13.5
6	20	152	3.8	3.2	7.7	6.2	10.1	8.1