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Forstwesen**Soil drought decreases water-use of pine and spruce but not of larch in a dry inner alpine valley****Bodentrockenheit in einem inner-alpinen Trockental verringert den Wasserverbrauch von Kiefer und Fichte, aber nicht von Lärche**Roman Schuster¹, Walter Oberhuber¹, Andreas Gruber¹, Gerhard Wieser^{2*}

Key words: Plant water availability, climate change, sap flow, soil drought, inner alpine dry valley.

Schlagworte: Pflanzenwasserverfügbarkeit, Klimawandel, Stammfluss, Bodentrockenheit, Inneralpinen Trockental

Abstract

The study quantified the effect of soil water availability on sap flow density (Q_s) of *Pinus sylvestris*, *Picea abies* and *Larix decidua* in a dry inner alpine valley, Tyrol, Austria. To reduce soil water availability we installed a transparent roof construction above the forest floor around 10 trees (6 *P. sylvestris*, 3 *P. abies* and 1 *L. decidua*). Eleven other trees (5 *P. sylvestris*, 3 *P. abies* and 3 *L. decidua*) served as controls in the absence of any manipulation. Roofing reduced soil water availability, while soil temperature was not affected. Sap flow density and environmental parameters were monitored throughout two growing seasons. In *P. sylvestris* and *P. abies* withholding precipitation caused Q_s to decrease by 30 and 19%, respectively below levels in control trees, while no effect of limited soil water availability was detected on Q_s in *L. decidua*. Hardly affected were leaf-level net CO_2 uptake rate and stomatal conductance for water vapor. We conclude that the water-saving strategy of *P. sylvestris* and

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P. abies may be a selective advantage to tolerate future increasing aridity in dry inner alpine valleys, while increasing aridity may be critical for *L. decidua* if aridity will increase in future.

Zusammenfassung

Der Artikel beschreibt die Auswirkung einer reduzierten Bodenwasserverfügbarkeit auf den Wasserhaushalt von Rotföhre (*Pinus sylvestris*), Fichte (*Picea abies*) und Lärche (*Larix decidua*) in einem inneralpinen Trockental, Tirol, Österreich. Unter dem Kronendach von 10 adulten Bäumen (6 *P. sylvestris*, 3 *P. abies* und 1 *L. decidua*) installierten wir eine transparente Dachkonstruktion um durch Regenausschluss eine künstlichen Bodentrockenheit zu erzeugen. Elf weitere Bäume (5 *P. sylvestris*, 3 *P. abies* und 3 *L. decidua*) dienten als Kontrollen. Mit Hilfe von Xylemfluss-Sensoren bestimmten wir über zwei Vegetationsperioden hindurch kontinuierlich den Wasserverbrauch. Verglichen zu Kontrollbäumen verursachte die durch Regenausschluss hervorgerufene Bodentrockenheit eine Verringerung des Wasserverbrauchs bei der Föhre und der Fichte um 30 bzw. 19%. Demgegenüber zeigte die Lärche keine Einschränkung in der Wasserabgabe. Falls sich auf Grund der prognostizierten Klimaänderung in inneralpinen Trockentälern die Verfügbarkeit von Bodenwasser verringert, dürfte langfristig die wassersparende Strategie von Fichte und Kiefer ein selektiver Vorteil gegenüber der Lärche sein, da diese auch bei lang anhaltender Bodentrockenheit ihre Transpiration nicht einschränkt.

1. Introduction

Scots pine (*Pinus sylvestris*) forests in inner alpine dry valleys have raised concern as they may undergo significant ecological alterations through warming under climate change (Zweifel et al., 2009; Gruber et al., 2011). During the last century, global surface temperature has increased by about $0.6 \pm 0.2^\circ\text{C}$ (Jones et al., 1988). Global change models predict further increase up to 4°C by the end of this century for Central Europe (IPCC, 2013). In inner alpine valleys in the central Austrian Alps, the mean annual air temperature during the last 10 years (2001-2010) was enhanced on average by 0.5°C (i.e., to 10.3°C) when compared with the mean of the previous 30 years (9.8°C). While the temperatures increase is expected to be more pronounced during the summer (Christensen et al., 2007), summer precipitation is likely to decrease (Maracchi et al., 2005), resulting in more frequent and severe drought events (Schär et al., 2004; IPCC, 2013). Although effects of climate change on forest ecosystems are uncertain, Zweifel et al. (2009) suggested modifications in the abundance of tree species in inner alpine valleys. In dry inner Alpine valleys soil water availability represents a major environmental constraint on the physiological performance of conifers and unusually distinct vegetation dynamics have been reported in Switzerland (Dobbertin et al., 2005; Bigler et al., 2006), Italy (Verturi and Tagliaferro, 1996) and in western parts of the Inn valley, Tyrol, Austria (Oberhuber, 2001; Oberhuber and Gruber, 2010, Schuster and Oberhuber 2013). Increasing air temperature in the Central Austrian Alps are

expected to change ecosystem characteristics with associated biogeochemical and hydrological cycling (Barnett et al. 2005).

Although drought effects on tree tree transpiration has been studied intensively (Pannek and Goldstein, 1999; Reichstein et al., 2002; Breda et al., 2006; Granier et al., 2007; Breshears et al., 2008; Dulamsuren et al., 2009), the 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 in inner alpine dry valleys. In situ manipulation of soil water availability is a common methodology for assessing potential effects of limited soil water availability in forest ecosystems (Lamersdorf et al., 1998; Broken et al., 1999; Corre and Lamersdorf, 2004; Vicca et al., 2012; Leo et al., 2013).

Therefore, our specific goal was to investigate the influence of soil water availability in the absence of other soil disturbance on tree transpiration of co-occurring Scots pine (*P. sylvestris* L.), Norway spruce (*Picea abies* (L.) Karst.) and European larch (*Larix decidua* Mill.) trees. Selected species comprise the major coniferous species in dry, inner alpine valley in Tyrol, Austria and differ with respect to phenological and successional traits. *Larix decidua* and *P. sylvestris* are light demanding species predominating in early successional stages, while *P. abies* is a moderately shade-dominant tree, which predominates in the late-successional stage (Ellenberg and Leuschner, 2010). We hypothesized that a decline in soil water availability in the absence of other soil disturbance will (1) lead to a water-saving strategy and thus reduce canopy transpiration of evergreen *P. sylvestris* and *P. abies* (2) while deciduous *L. decidua* will follow a more risky strategy to withstand soil water shortage. Experimental soil water shortage was incited by roofing the forest floor throughout three consecutive growing seasons while continuously monitoring sap flow density (Q_s) with thermal dissipation probes (Granier, 1985). Findings are used to explore species-specific differences in water strategies, as species-specific differences in water strategies provides a basis for stand level hydrological properties of such forest ecosystems in a future warmer environment in dry, inner alpine valleys.

2. Material and Methods

2.1. Study site

The study was carried out in an open *Pinus sylvestris* forest (Erico-Pinetum typicum; Ellenberg and Leuschner, 2010) growing on postglacial rock-slide area situated 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). During the study period (2011 - 2013), the trees were approximately 100-150 years old with a mean tree height of 18 ± 2 m. The stand density was 2117 trees ha⁻¹ (*Pinus sylvestris* 60%, *Picea abies* 20% and *Larix decidua* 20%) and their diameter at breast height (DBH) averaged 26.5 ± 12.7 m.

The study site is characterized by a continental climate with a mean annual temperature of 7.3°C (long term mean 1911-2012; Ötz, 812 m a.s.l., 5 km south from the study site). The mean annual precipitation was 716 mm, with the minority of rain falling in winter (100 mm) and spring (138 mm). Limestone dominates the geology at the study site. According to the World Base for Soil Resources (FAO, 2006), the soil at the study site was classified as a protorendzina (Oberhuber and Gruber, 2010). A xeric moder of 5-15 cm thickness covered the subsoil. The top 10 cm of the subsoil was enriched by 10 % of organic matter and the soil texture was dominated by sand (91%) and silt fractions (9 %). Hydraulic field capacity was 0.20 m³ m⁻³ (sensu Blume et al., 2010), and the wilting point (at -1.5 MPa) was reached at 0.06 m³ m⁻³ (Leo et al., 2013).

Two nearby sites (c. 50 m in linear distance) where *Larix decidua*, *Pinus sylvestris* and *Picea abies* grow side by side were selected ("control" and "roofed" plot, respectively) and scaffolds of 16 m height were constructed to reach the upper crowns of all three species at both plots. As the study site was situated in nature reserve the installation of more than one roofed plot and two scaffoldings were not feasible. In both plots all measurements were carried out on dominant randomly selected trees similar in age, diameter and height.

2.2. Manipulation of soil water availability

Soil water manipulation was accomplished by roofing the forest floor according to the approach by Leo et al. (2013). For reducing plant water availability, the roof was installed underneath the canopy 1.0-1.3 m above ground (slope 10-15° from the center to the outer end). The roof consisted of frame anchored into the soil, covered with a 1.2 mm thick transparent rip stop film (hereafter "roofed" plot). The covered area was 240 m² and included 10 trees (6 *P. sylvestris*, 3 *P. abies* and 1 *L. decidua*). Eleven trees (5 *P. sylvestris*, 3 *P. abies* and 3 *L. decidua*) trees served as control in the absence of soil water manipulation ("control" plot). Rain exclusion was operated in 2011 during April throughout October (Leo et al., 2013) and continued throughout each snow free period (March - September) during 2012 and 2013. The roof was removed during the dormant season. As stretching of roots outside roof could not be prevented because restrictions imposed by nature conservation prohibited trenching, roofed trees were able to extract water from outside of the roofed area indicated by $\delta^{18}\text{O}$ analysis (Leo et al., 2013).

2.3. Environmental, sap flow density measurements and tree characteristics

Air temperature (T_a), relative humidity (RH), photosynthetic active radiation (PAR), wind velocity (v) and precipitation (P) were monitored by an automatic weather station (ONSET, Pocasset, MA, USA) 15 m above ground level on top of a scaffolding in the roofed plot. Because the roofed and the control plot were located within less than 50 m in linear distance, records of the above mentioned environmental parameters were regarded as representative for both plots. In order to determine seasonal differences

in soil water content (θ) and soil temperature (T_s) between control and roofed trees three soil moisture sensors (Theta Probe Type ML2x, Delta-T, Cambridge, England) and three soil temperature probes (HOBO Pendant; ONSET, Pocasset, MA, USA) were installed in each plot in 15-20 cm and in 5-10 cm soil depth, respectively. Soil moisture sensors were connected to two DL6 data loggers (one per plot; Delta-T, Cambridge, England), while the soil temperature probes were equipped with internal storages. The measuring interval for soil moisture and soil temperature was 30 minutes. The data logger for all the other environmental parameters was programmed to record 30-min averages of measurements taken every minute.

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 data logger, providing one constant source of electrical power (0.2W) for heating three sensors each. Each sensor consisted of two probes of 20mm in length and 2mm 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 at 20 mm depth in the outer hydroactive xylem on the north-facing side of trees 0.8 m above ground. Accounting for variations in Q_s across the cross-sectional trunk sapwood area, two sensors were also installed at 20 and 40 mm depth in addition to the one at 20 mm in two *P. sylvestris*, two *P. abies*, and one *L. decidua* tree per treatment. Probe positions 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 minutes. Two car batteries (12 VDC, 90 Ah) which were recharged by means of an 80W solar panel in combination with a charge controller each provided power for all electrical equipment.

For each tree Q_s ($\text{g m}^{-2} \text{s}^{-1}$) was calculated from the temperature difference between the two probes (ΔT) relative to the maximum temperature difference (ΔT_m) which occurred at times of zero flow according to the calibration equation by Granier (1987):

$$Q_s = 119 * [(\Delta T_m - \Delta T) / \Delta T]^{1.231} \quad (1)$$

Each night ΔT_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 vapor pressure deficits were mostly low. In addition, during most nights temperature time 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 2012 (March 14 throughout October 27) and 2013 (April 15 throughout October 18).

Stem diameter increment was determined in fall 2014 based on measurements along two increment cores (5 mm in diameter) per tree in parallel to the contour line to avoid reaction wood taken at sensor height. The cores were dried in the laboratory, non-permanently mounted on a holder, and the surface was prepared with a razor blade for visibility enhancement of tree ring boundaries (Pichler, 1990). Ring widths were measured to the nearest 1 μm using a reflecting microscope (Olympus SZ61) and the software package TSAP WIN Scientific. Ring widths of both cores from each sample tree were averaged and individual tree ring chronologies were then checked for dating accuracy using the COFECHA software (Grissino-Mayer 2001). In order to account for the inherent variability in growth among the trees under study not attributable to experimental factors radial stem increment was normalized to the mean radial stem increment obtained in the 3 years before soil water manipulation (2008-2010) commenced.

2.4. Shoot water potential and gas exchange measurements

Measurements of shoot water potential and needle $\text{CO}_2/\text{H}_2\text{O}$ gas exchange was measured repeatedly throughout the growing season of 2012 (May 25 and 26, June 19, July 18, August 1 and 20, and October 7). To facilitate needle water potential and gas exchange measurements, one scaffolding was erected in each plot for accessing top-canopy shoots. Three sample trees (one *Pinus sylvestris*, one *Picea abies*, and one *Larix decidua* tree) were successfully accessed in the control and the roofed plot, respectively. The same trees were also used for examining needle water potential in 2011 (Leo et al. 2013) and growth phenology in 2011 and 2012 (Swidrak et al., 2013).

Shoot water potential (Ψ ; MPa) was measured with a pressure chamber (Model 1000; PMS Instrument Company, Corvallis; Oregon, USA) at different dates on rainless days with clear sky throughout 2012. Needle water potential measurements included the determination of predawn (Ψ_p) and midday (Ψ_m), water potential. While Ψ_p is representative of the mean soil water potential next to the roots because the trees should be in equilibrium with the soil at the end of the night (Havranek and Benecke, 1987), Ψ_m represents the daily minimum Ψ . Water potential measurements were carried out on freshly cut twigs before sunrise between 04:30 and 05:00 (Ψ_p) and at noon (Ψ_m) local time.

In parallel to Ψ needle $\text{CO}_2/\text{H}_2\text{O}$ gas exchange of three selected twigs per tree (6 trees, 18 shoots in total) was measured in situ using a portable gas exchange system (CIRAS 1, PP Systems, Hitchin, Hertfordshire, UK) equipped with a PLC6 leaf chamber under ambient conditions. In order to estimate daily maximum net CO_2 uptake rate (A_{max}), diurnal courses of gas exchange were assessed repeatedly during the growing season of 2012. While gas exchange of *L. decidua* was estimated for short-shoot needles, measurements in *P. sylvestris* and *P. abies* were made in one-year-old-needles after removing the terminal buds in February to prevent the influence of growth respiration on net CO_2 uptake and to avoid nutrient leaching into the new flush (Weikert et

al., 1979). For gas exchange measurements selected twigs were marked at the base to ensure that the same needles of each of the selected twigs (three per tree) were measured throughout the entire daily course. Gas exchange data were related to projected leaf area. In fall, twigs were detached for estimating leaf area by using the open source software ImageJ (<http://rsbweb.nih.gov/ij/index.html>).

2.5. Data analysis

Values of 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 to daily means. Finally, for each species Q_s data were pooled over all the trees per treatment and year (2012 and 2013). Differences in overall mean Q_s between control and warmed *P. sylvestris*, *P. abies* and *L. decidua* trees, respectively during the periods of roof closure in 2012 and 2013 were analyzed by one-way ANOVA. One way ANOVA was also used to test differences in Ψ_p , Ψ_m and gas exchange parameters between control and roofed *P. sylvestris*, *P. abies*, and *L. decidua* 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, USA)

3. Results

3.1. Environmental factors

Daily mean PHAR varied between $28 \mu\text{mol m}^{-2} \text{s}^{-1}$ (October 10, 2012) and $686 \mu\text{mol m}^{-2} \text{s}^{-1}$ (June 7, 2013), averaging $390 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 2012 and $388 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 2013 (Fig. 1). Daily mean air temperature (T_a) was 14.1°C in 2012 and 15.0°C in 2013, and varied between 1.9°C on April 8, 2012 and 26.0°C on June 30, 2012 and August 2, 2013 (Fig. 1). Daily mean vapor pressure deficit (D) was 1.2 kPa in 2012, and 1.3 kPa in 2013, approaching zero on rainy days and reaching a maximum of 2.0 kPa on August 5, 2013 (data not shown). Average daily mean soil temperature (T_s) in 5-10 cm soil depth over 2012 and 2013 did not differ significantly ($P > 0.23$) between the control (11.9°C in 2012; 12.0°C in 2013) and the roofed plot (11.7°C in 2012; 12.3°C in 2013) (data not shown).

Precipitation (P) during the study periods 2012 and 2013 amounted 596 and 470 mm, respectively (Fig 1). Due to frequent rainfall over the two investigation periods 2012 and 2013 θ in 15-20 cm soil depth varied between $0.07 \text{ m}^3 \text{ m}^{-3}$ (June 3, 2012) and $0.32 \text{ m}^3 \text{ m}^{-3}$ (April 20, 2013) and averaged 0.13 and $0.15 \text{ m}^3 \text{ m}^{-3}$ in 2012 and 2013, respectively (Fig. 1), indicating that control trees did not suffer from soil drought. Roofing by contrast, caused θ to decline progressively reaching a minimum on July 12, 2012 and July 15, 2013 and stayed close to the wilting point ($0.06 \text{ m}^3 \text{ m}^{-3}$) throughout the end of both investigation periods (Fig. 1).

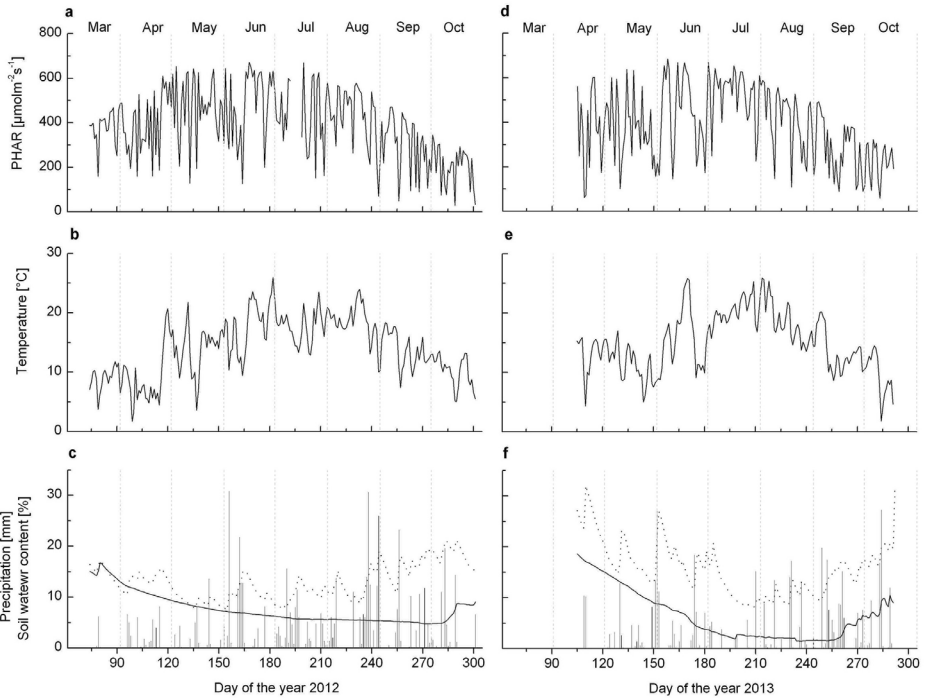


Fig. 1 a, d: Seasonal course of daily mean photosynthetic active radiation (PAR), b, e daily mean air temperature, c, f daily sum of precipitation (bars), and daily mean soil water content in 15 to 20 cm soil depth in the control (dotted line) and the roofed (solid line) plot from March 14, throughout October 27, 2012, and April 15, throughout October 18, 2013.

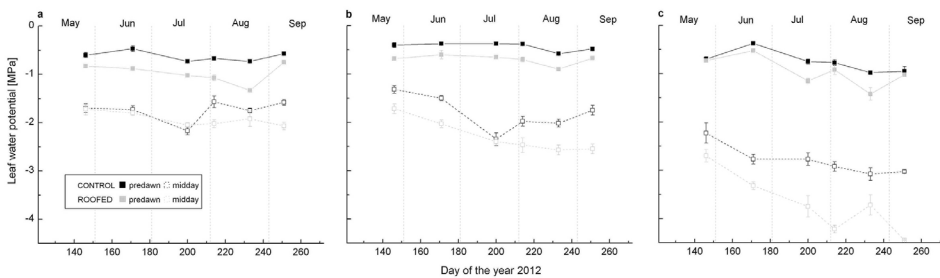


Fig. 2: Seasonal course of predawn and midday leaf water potential in control and roofed *Pinus sylvestris* (left), *Picea abies* (middle), and *Larix decidua* trees (right) obtained throughout the investigation period 2012. Values are the mean \pm SE of three measurements per species and treatment.

Seasonal patterns of predawn (Ψ_p) and midday (Ψ_m), water potential also reflected differences in plant available water between control and roofed trees. During the growing season 2012 Ψ_p of control trees never dropped below -1.0 MPa whereas Ψ_p of roofed trees reached -1.5 MPa (Fig. 2). Midday water potential fell below -2.5 MPa in

	<i>Pinus sylvestris</i>		<i>Picea abies</i>		<i>Larix decidua</i>	
Year	Control	Roofed	Control	Roofed	Control	Roofed
2011	0.52	0.31	0.78	0.48	0.60	0.53
2012	0.72	0.55	0.76	0.67	0.91	1.11
2013	0.63	0.37	0.96	0.41	1.57	0.99

Table 1: Normalized stem diameter increment at height of sensor installation in control and roofed *P. sylvestris*, *P. abies*, and *L. decidua* trees selected for sap flow measurements. Stem diameter increment was normalized to the mean radial stem increment obtained in the 3 years before soil water manipulation (2008-2010) commenced. Values are the mean of one or two to six trees per treatment.

control trees and was in general considerably above the values of roofed trees (Fig. 2) indicating a lower amount of plant available water.

3.2. Stem increment

Radial stem increment averaged for the three years (2008-2010) preceding the drought experiment did not differ significantly between control and roofed trees (all $P > 0.18$). The three-year average for the control trees was 0.77 ± 0.14 mm for *P. sylvestris*, 1.04 ± 0.18 mm for *P. abies*, and 0.21 ± 0.07 mm for *L. decidua*. The corresponding values for roofed *P. sylvestris*, *P. abies*, and *L. decidua* trees were 0.59 ± 0.16 , 1.02 ± 0.26 , and 0.33 ± 0.11 mm, respectively. Withholding precipitation throughout three growing seasons caused normalized radial stem increment to decline on average by 34% in *P. sylvestris* ($P = 0.08$), 37% in *P. abies* ($P = 0.04$), and 15% in *L. decidua* ($P = 0.68$) below the corresponding levels of control trees (Table 1).

Year	Species	Treatment	0-20 mm	20-40 mm	P
2012	<i>P. sylvestris</i>	Control	4.47 (0.19)	3.55 (0.15)	< 0.001
		Roofed	3.09 (0.10)	2.88 (0.10)	< 0.001
	<i>P. abies</i>	Control	3.13 (0.12)	0.96 (0.04)	< 0.001
		Roofed	2.60 (0.17)	0.98 (0.04)	< 0.001
2013	<i>P. sylvestris</i>	Control	2.04 (0.07)	2.07 (0.08)	0.62
		Roofed	1.38 (0.06)	1.58 (0.06)	< 0.001
	<i>P. abies</i>	Control	3.17 (0.12)	1.35 (0.05)	< 0.001
		Roofed	2.49 (0.10)	1.22 (0.05)	< 0.001
<i>L. decidua</i>	Control	3.05 (0.14)	2.11 (0.05)	< 0.001	
	Roofed	3.53 (0.09)	1.97 (0.05)	< 0.001	

Table 2: Seasonal averaged sap flow density (Q_s ; $\text{g m}^{-2} \text{s}^{-1}$) \pm SE in 0-20 and 20-40 mm sapwood depth in control and roofed *P. sylvestris*, *P. abies*, and *L. decidua* for the periods 2012 (March 13 - July 4) and 2013 (April 15 - October 21). Values are the mean \pm SE of one or two to six sensors per treatment. Differences in Q_s between control and roofed trees are indicated as P values and significant differences ($P < 0.05$) between control and roofed trees are marked in bold and italics.

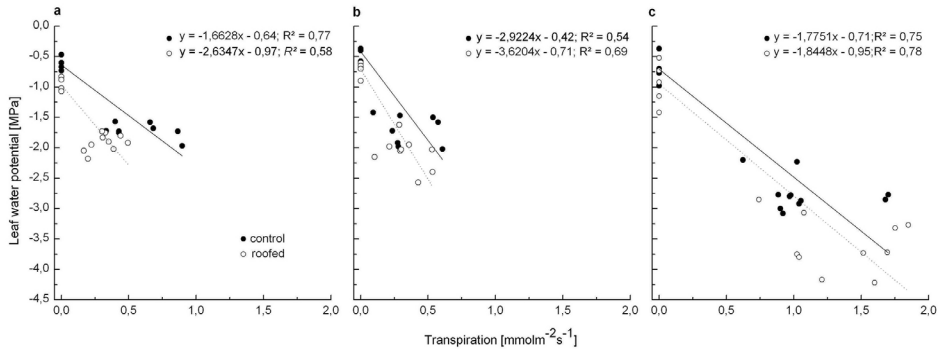


Fig. 3: The relationship between transpiration and leaf water potential in control and roofed *Pinus sylvestris* (left), *Picea abies* (middle), and *Larix decidua* trees (right) obtained throughout the investigation period 2012. Values are the mean \pm SE of three measurements per species and treatment.

3.3. Sap flow density, leaf level transpiration and plant water status

Seasonal courses of sap flow density (Q_s) in each of the experimental trees in 0-20 mm (Fig. 3) and 20-40 mm sapwood depth (data not shown) largely reflected seasonal trends in PHAR and D (cf. Fig. 1). In general, there was a decline from 0-20 mm to 20-40 mm in the growing season mean Q_s for *P. sylvestris*, *P. abies* and *L. decidua* of 20 - 69% (all $P < 0.05$), except for *P. sylvestris* in 2013 where there was an increase (Table 2). During the second (2012) and third year (2013) withholding water generally caused daily mean Q_s in 0-20 mm sapwood depth of roofed *P. sylvestris* and *P. abies* trees to decline by 30 and 19% respectively below the levels of control trees (Table 2). The corresponding values for 20-40 mm sapwood depth were 19 and 4% (Table 2). In *L. decidua* by contrast withholding water had no effect on Q_s and roofed trees was at average 15% above the corresponding values of control trees (Table 2).

The impact of plant water status is also reflected in different slopes of the transpiration (E) to needle water potential (Ψ) relationship in *P. sylvestris* and *P. abies* trees. Withholding water caused a steeper slope in the (Fig. 4). In *L. decidua* by contrast, (Fig. 4) withholding water did not affect the in Ψ /E relationship (Fig. 4).

3.4. Leaf level gas exchange

In 2012 mean rates of daily maximum net photosynthesis (A_{max}) and transpiration (E) of one-year-old roofed *P. sylvestris* and *P. abies* trees displayed a decline of 15 to 50% below respective levels of control trees, which however was only statistically significant for E in *P. sylvestris* (Table 3). In short shoot needles of *L. decidua* by contrast withholding precipitation caused an increase in A_{max} and E (Table 3). Withholding precipitation caused a decline in stomatal conductance for water vapor (g_{H_2O}) in all the three species investigated (Table 3). Withholding water also caused instanta-

	<i>Pinus sylvestris</i>			<i>Picea abies</i>			<i>Larix decidua</i>		
	Control	Roofed	P	Control	Roofed	P	Control	Roofed	P
A_{max}	4.54±0.50	3.40±0.30	0.058	3.47±0.41	2.96±0.30	0.404	6.57±0.69	6.95±0.51	0.704
E	0.50±0.08	0.30±0.04	0.029	0.38±0.07	0.25±0.05	0.164	0.85±0.14	1.12±0.13	0.220
g_{H_2O}	32.93±5.96	14.28±1.40	0.005	15.00±2.59	12.73±1.98	0.483	60.06±10.46	54.79±6.74	0.722
WUE	8.04±0.91	10.19±1.94	0.344	7.79±1.38	9.34±2.59	0.585	8.34±0.70	6.52±0.77	0.121
iWUE	0.207±0.056	0.248±0.020	0.488	0.291±0.066	0.244±0.029	0.530	0.132±0.022	0.131±0.009	0.978

Table 3: Mean daily maximum net photosynthesis (A_{max} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), transpiration (E; $\text{mmol m}^{-2} \text{s}^{-1}$), stomatal conductance for water vapour (g_{H_2O} ; $\text{mmol m}^{-2} \text{s}^{-1}$), instantaneous water use efficiency (WUE; $\mu\text{mol CO}_2 \text{ H}_2\text{O mol}^{-1}$); and intrinsic water use efficiency (iWUE; $\mu\text{mol mol}^{-1}$), of one year old needles of control and roofed *P. sylvestris* and *P. abies* trees and short shoot needles of control and roofed *L. decidua* trees obtained in 2012, and corresponding P values. Values are the mean \pm SE of three measurements per species and treatment and are related to projected leaf area.

neous water-use efficiency (WUE) to increase in *P. sylvestris* and *P. abies* and to decline in *L. decidua* while the opposite was observed for intrinsic WUE (Table 3).

4. Discussion

In our study withholding precipitation caused radial stem increment to decline in all the three species more intensely (Table 1; Swidrak et al., 2013) than net photosynthesis (Table 3). Moreover, although at a nearby xeric site radial growth of *P. sylvestris* was drastically reduced (Oberhuber and Gruber 2010) carbohydrate pools were not depleted, when compared to our more mesic site (Gruber et al., 2011), suggesting that soil drought may uncouple growth from photosynthesis (Muller et al., 2011). Limited radial growth upon limited soil water availability (Eilmann et al., 2009) has also been observed in the central Wallis, Switzerland (Zweifel et al., 2006).

Our experimental approach was appropriate to manipulate soil water availability, enabling for clarifying water dynamics of co-occurring conifers in situ under a wide range of environmental conditions. Although $\delta^{18}\text{O}$ analyses of the xylem indicated that roofed trees were able to extract water from outside the roofed area (Leo et al., 2013) seasonal patterns of Ψ_p and Ψ_m (Fig. 2) reflected differences in plant available water between control and roofed trees (Leo et al. 2013). Moreover, treatment differences in daily mean soil temperature stayed within the typical variation at the study site (Oberhuber and Gruber, 2010; Swidrak et al., 2013), which confirmed the employed roofing system to prevent any change in soil temperature.

Changes in Q_s in our study may be related to treatment induced alterations in tree water relations. This is reflected in altered correlations between the rate of leaf level transpiration (E) and shoot water potential in *P. sylvestris* and *P. abies* (Ψ ; Fig. 4). In previous studies withholding water also caused a steeper slope in Ψ/E relationship in *P. sylvestris* and *P. abies*, suggesting a "long-term change in the tree-water status" due to a decrease in conductance of water flow from the soil to the foliage (Schulze and Hall, 1982; Matyssek et al., 2010). In *L. decidua* by contrast, three years of withholding precipitation in our study did not cause any response in plant water status

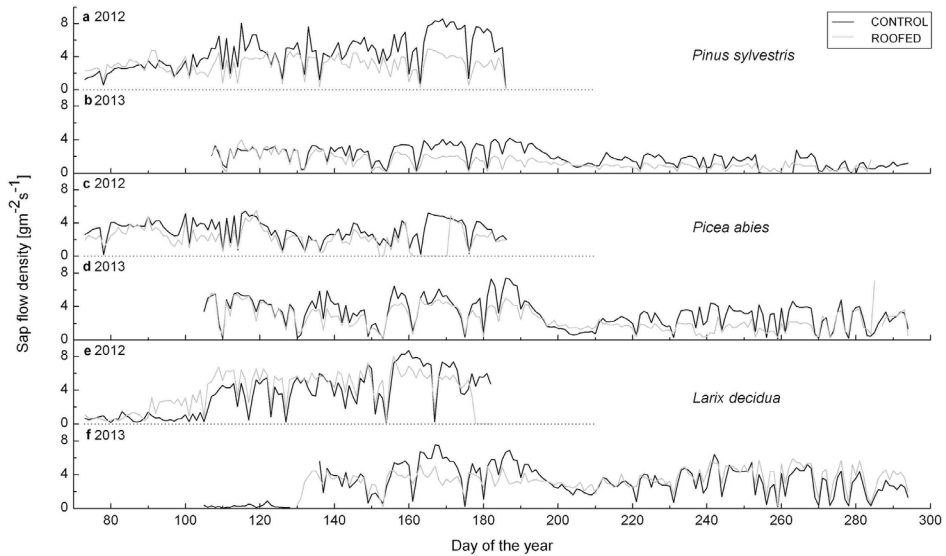


Fig. 4: Seasonal course of daily mean sap flow density in control and roofed *Pinus sylvestris* (left), *Picea abies* (middle), and *Larix decidua* trees (right) from March 13, throughout July 4, 2012 and from April 15, throughout October 21, 2013. Values are the mean \pm SE of one or two to six sensors per treatment in 0-20 mm sapwood depth.

(Fig. 4). Even in roofed *L. decidua* trees Ψ never dropped below a critical level -4.9 MPa. A value which would cause a 50% loss in hydraulic conductance (Beikircher et al., 2010).

Variations in radial patterns of Q_s observed in our study (Table 2) were similar to that found in several studies on conifers, with peak values in the outer sapwood (Cermak et al., 1992; Oren et al., 1998; Lundbald et al., 2001; Nadezhdina et al., 2007; Kucerova et al., 2010). The reversed radial pattern of Q_s observed in roofed *P. sylvestris* trees in the third year of soil water manipulation (2013; Table 2) might have been an effect of water availability as there is evidence that radial patterns of Q_s can be redistributed under conditions of soil water deficit (Cermak and Nadezhdina 1998).

Seasonal patterns of Q_s were similar to those reported previously for the same study site (Leo et al. 2013) and a neighboring *P. sylvestris* stand (Wieser et al., 2014). During the second and third year, withholding water significantly decreased Q_s in *P. sylvestris* and *P. abies* but not in *L. decidua* (Fig. 4, Table 2). Independent of treatment lower shoot water potentials in roofed *P. sylvestris* and *P. abies* trees (Fig. 3) were accompanied by a decline in E (Fig. 5) and a lower canopy conductance related to the same reference levels of D (Leo et al., 2013), emphasizing the influence of plant available water on tree water loss. This soil drought response of *P. sylvestris* and *P. abies* fits to a typical water saving strategy. A water saving strategy has also been observed previously in drought stressed adult field grown *P. sylvestris* trees in Austria (Wieser et al., 2014), the northern Mongolian forest Steppe (Dulamsuren et al., 2009), Siberia

(Sugimoto et al., 2002), Scotland (Perks et al., 2004), Spain (Llores et al., 2008) and in Mediterranean tree species (Epron and Dryer, 1978; Borghetti et al., 1998; Luis et al., 2005; Brito et al., 2014, 2015) and thus significantly reducing tree water loss under periods of high evaporative demand.

The significantly lower Q_s values in roofed *P. sylvestris* and *P. abies* trees observed at our study site suggest that both conifer species behave “isohydric” as they close their stomata relatively early under conditions of low plant water availability and thus stabilize their water relations (Anfodillo et al., 1998; Matyssek et al., 2009). This water saving strategy of *P. sylvestris* and *P. abies* corresponds to the vulnerability of both species to xylem embolism (Beikircher et al., 2010). *Larix decidua* apparently follows an “anisohydric” strategy and maintains high water loss (Anfodillo et al., 1998; Dulamsuren et al., 2009; Matyssek et al., 2009), and hence also a higher CO₂ uptake rate than spruce and pine (Table 3). An anisohydric strategy to withstand high evaporative demand and low soil water availability, however, is not critical until severe soil drought can cause hydraulic collapse before finally leading to xylem cavitation (Breda et al., 2006).

Our our results suggest that *P. sylvestris*, *P. abies*, and *L. decidua* are well adapted to cope with low plant water availability and high evaporative demand. All selected species were undergoing water limitations as measured by decreasing water loss throughout the growing season, which is in accordance with previous findings that soil water availability limits tree growth within the study area (e.g., Schuster and Oberhuber 2013). Low water-holding capacity of the shallow stony soils, which causes fast decrease of soil water availability during rainless periods, makes our study area comparable to other dry inner Alpine environments, where a high vulnerability of *P. abies* and *L. decidua* to drought was determined by Lévesque et al. (2013).

5. Conclusions

In accordance with our hypothesis, a decline in soil water availability leads to a decline in Q_s of *P. sylvestris* and *P. abies*. This fits to a typical water saving strategy with a more pronounced reduction in conductance to water vapor under limited soil water availability. Conversely, *L. decidua* follows a more risky strategy to withstand soil water shortage and high evaporative demand. *P. sylvestris* and *P. abies* responded to low plant water availability in an inner alpine dry forest ecosystem by a water-saving strategy through a more pronounced reduction in conductance to increasing evaporative demand. In this sense, pine and spruce differ from larch, which is characterized by a higher stomatal conductance (Table 3). We conclude from the present study that the water-saving strategy of *P. sylvestris* and *P. abies* may be a selective advantage to tolerate increasing aridity in dry inner alpine valleys. Correspondingly, limited soil water availability might be critical for *L. decidua* if aridity will increase in future. These results should also be taken into consideration when forecasting potential impacts of climate change on future forest management practices in inner alpine dry val-

leys, because the water-saving strategy of *P. sylvestris* and *P. abies* may be a selective advantage as it might enable both species to tolerate increasing aridity as a result of global warming (IPCC 2013). Finally, long term studies are needed as the next step, in order to predict long term shifts in the abundance of the three selected conifer species under predicted climate warming.

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