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Artificial Top Soil Drought Hardly Affects Water Use of *Picea abies* and *Larix decidua* Saplings at the Treeline in the Austrian Alps

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Abstract: This study quantified the effect of shallow soil water availability on sap flow density (Q_s) of 4.9 ± 1.5 m tall *Picea abies* and *Larix decidua* saplings at treeline in the Central Tyrolean Alps, Austria. We installed a transparent roof construction around three *P. abies* and three *L. decidua* saplings to prevent precipitation from reaching the soil surface without notably influencing the above ground microclimate. Three additional saplings from each species served as controls in the absence of any manipulation. Roofing significantly reduced soil water availability at a 5–10 cm soil depth, while soil temperature was not affected. Sap flow density (using Granier-type thermal dissipation probes) and environmental parameters were monitored throughout three growing seasons. In both species investigated, three years of rain exclusion did not considerably reduce Q_s. The lack of a significant Q_s-soil water content correlation in *P. abies* and *L. decidua* saplings indicates sufficient water supply, suggesting that whole plant water loss of saplings at treeline primarily depends on evaporative demand. Future work should test whether the observed drought resistance of saplings at the treeline also holds for adult trees.

1. Introduction

Concerns have been raised in regard to high altitude treelines (i.e., the ecotone between the upper limit of the closed continuous forest canopy and the treeless alpine zone above) [1,2], as they may undergo significant alterations due to climate change. During the last century, global surface temperature has increased by about 0.6 ± 0.2 °C, and in the Alps warming has been well above global average [3–5]. Global change models predict a further increase by 1.4–5.8 °C in upcoming decades and an increased occurrence of climate extremes, including more frequent and severe drought [6]. At the treeline in the Central Austrian Alps, the observed temperature increase was apparently most pronounced during spring and summer compared with autumn and winter [7]. Moreover, as shown by the Central Austrian Alps [8], higher temperatures coupled with a decline in relative humidity and thus a considerable increase in evaporative demand may reduce the water supply of adult trees [9]. Although drought effects on tree transpiration have been studied intensively in various climates

worldwide [10] and references therein, the reasons for the intra-annual variability of transpiration and responses to extreme meteorological conditions such as those during the dry summer of 2003 [11–13] still await clarification for conifers at the treeline. Norway spruce (*Picea abies* (L.) Karst.) and European larch (*Larix decidua* Mill.) are the dominant tree species at high elevation sites in the Alps [14].

Reductions in water loss of adult *P. abies* and *L. decidua* trees upon rain exclusion were reported in the literature for a low elevation site in the Austrian Alps [15,16]. In an inner alpine dry valley, rain exclusion throughout three growing seasons considerably reduced the water loss of evergreen *P. abies*, while no effects of rain exclusion were detected in deciduous *L. decidua* [15,16]. At treeline, however, larch may benefit from the higher vulnerability of spruce to increased temperatures and drought [17–19]. The present study focuses on the effect of limited soil water availability in the absence of other soil disturbances on the tree transpiration of *P. abies* and *L. decidua* saplings at treeline. There is evidence that soil water deficits have a stronger impact on reducing tree water loss in adult *P. abies* than in adult *L. decidua* trees [20,21]. As seedling establishment at the treeline is an important issue and because saplings, due to the small size of their root systems, could be particularly vulnerable to reduced soil moisture in the top soil, we tested the hypothesis that (1) a decline in soil water availability in the absence of any other soil disturbance will result in a decline in the water loss of evergreen *P. abies*, while (2) deciduous *L. decidua* will not respond to 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 [20]. Findings are used to explore tree response in a future warmer environment within the treeline ecotone of the Central Austrian Alps.

2. Materials and Methods

2.1. Study Site and Experimental Design

The study was carried out in a south-exposed afforestation at the treeline above Neustift in the Stubai Valley, Tyrol, Austria (1980 m a.s.l.; 47°7′45″ N, 11°18′20″ E), adjacent to the LTER-Master site Stubai. The average annual temperature is 3 °C, the annual precipitation is 1097 mm, and the soil type is a dystric cambisol. The stand formed a sparsely open canopy permitting a dense understory of grass and herbaceous species. During the study period (2016–2018), the saplings were 17 ± 3 years old. The stem diameter 0.3 m above ground (= height of sensor installation; see below) was 7.9 ± 1.5 cm, and the average height was 4.9 ± 1.5 m. Saplings selected for the experiment were separated by a distance of at least 3–5 m.

Rain exclusion was achieved by roofing the forest floor according to the approach of [15,16]. A 1.2 mm thick rip-stop film fixed 30 cm above ground prevented precipitation fro reaching the soil surface by draining off rainfall downhill outside the roof without notably influencing the above ground microclimate. The sides were open for allowing air circulation, and the area covered around each individual tree was approximately 4 × 4 m (≈16 m²); (see Figure S1). The roofs were installed underneath the canopy around the stems of six individual saplings (three of *P. abies* and three of *L. decidua*; hereafter "rain exclusion" treatment). An identical number of *P. abies* and *L. decidua* saplings served as controls in the absence of any soil water manipulation ("control" treatment). Rain exclusion operated in 2016 from 16 August to 3 October and continued throughout the snow free period during 18 May–13 September 2017 and 23 May–13 September 2018.

2.2. Environmental Sap Flow Density Measurements and Stem Radial Increment

Air temperature (T_{air}) and relative humidity (RH; Vaisala HMP45AC, Helsinki, Finland), photosynthetic active radiation (PHAR; Delta T BF5H; Cambridge, UK), and precipitation (P; Young 52202, Traverse City, MI, USA) were monitored at 2 m above ground in an open area neighboring the saplings. These data were recorded with a CR1000 data logger (Campbell Scientific, Shepshed, UK) programmed to record 30 min averages of measurements taken by 1 min intervals. In order to

determine seasonal differences in shallow soil water content (SWC) and soil temperature (T_s) between the control and the rain exclusion plots, three soil moisture sensors (Theta Probe Type ML2x, Delta-T, Cambridge, UK) and three soil temperature probes (HOBO Pendant; ONSET, Pocasset, MA, USA) were installed at 5–10 cm and 10 cm soil depths, respectively. Close to three saplings per treatment were used for sap flow measurements. The soil moisture sensors were connected to a DL6 data logger (Delta-T, Cambridge, UK), while the soil temperature probes were equipped with internal storages. The measuring interval for soil moisture and soil temperature was set to 30 min, and the mean SWC (vol %) and T_s of the control and the rain exclusion plots, respectively, were calculated by averaging all measurements per treatment.

Sap flow density (Q_s) through the trunks of the selected study saplings was monitored with thermal dissipation sensors [22] 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) 15 cm apart vertically on the north facing side of the stems, 0.3 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 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. The temperature difference between the upper heated probe and the lower reference probe was recorded every 30 min. Power for the sap-flow systems was provided by a car battery (12 VDC, 90 Ah), which was recharged by means of an 80 W solar panel and a charge controller.

For each sensor, Q_s (g m^{-2} 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 determined by [23]

$$Q_s = 119 \times [(\Delta T_m - \Delta T)/\Delta T]^{1.231}. \tag{1}$$

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

After the 2018 growing season, two radii per tree were taken at the height of the sap-flow sensors using a borer with a 5 mm diameter increment. Cores were dried in the laboratory, mounted on a holder, and the surface was prepared with a razor blade. For contrast enhancement of tree-ring boundaries, white chalk powder was rubbed into the pores. Ring widths were measured to the nearest 1 µm using a reflecting microscope (Olympus SZ61, Tokyo, Japan) and the software package TSAP WIN Scientific (UGT-Müncheberg, Müncheberg, Germany).

2.3. Data Analysis

All the analyses were performed using the SPSS 16 software package (SPSS Inc. Chicago, IL, USA), and curve fits were performed using FigP for Windows (BIOSOFT, Cambridge, UK). Differences in the overall mean SWC and T_s between the control and the rain exclusion treatment before roof closure and during the periods of rain exclusion in 2016, 2017, and 2018, respectively, were analyzed by a one-way ANOVA. Due to the small sample sizes [24], differences in Q_s and stem radial growth between controls and the rain exclusion treatment were evaluated by a Mann–Whitney U-test using the exact probabilities for small sample sizes, and a probability level of $p < 0.1$ was considered statistically significant [24].

Because of the large variation in Q_s within saplings (spruce and larch), treatment (control vs. rain exclusion), and year (2016, 2017, and 2018), we used normalized Q_s data in this study. This was achieved by converting Q_s values of each tree to a ratio of the maximum daily mean value observed during each measurement period (Table 1). Subsequently, each tree had a normalized Q_s of 1, which allowed for a better comparison of Q_s to environmental variables between control and rain exclusion saplings.

Table 1. Maximum sap flow density (Q_{Smax}; g m^{-2} s^{-1}) of *Picea abies* and *Larix decidua* saplings in control and rain exclusion plots obtained during the study periods 2016, 2017, and 2018. Data are medians ± half total range of three saplings per treatment. No significant effects of rain exclusion were found.

Treatment	*Picea abies*			*Larix decidua*		
	2016	2017	2018	2016	2017	2018
control	3.8 ± 1.7	7.3 ± 1.0	7.5 ± 5.9	11.2 ± 4.8	9.5 ± 1.0	9.0 ± 1.3
rain exclusion	6.2 ± 1.6	10.6 ± 0.7	12.8 ± 1.9	11.8 ± 3.8	10.0 ± 1.9	9.3 ± 2.4

Normalized Q_s was also used to calculate relative canopy conductance. Canopy conductance related to ground surface area (g_c) can be calculated from whole tree transpiration rate per unit of ground surface area (T) and ambient vapor pressure deficit (VPD) according to [25]

$$g_c = \gamma\lambda\, T/\rho c_p \text{VPD}, \tag{2}$$

where γ is the psychometric constant (kPa K^{-1}), λ is the latent heat of water vaporisation (J kg^{-1}), ρ is the density of the air (kg m^{-3}), c_p is the specific heat of air at constant pressure (J kg^{-1} K^{-1}), and VPD is the vapor pressure deficit (kPa) calculated from T_{air} and RH. As we used normalized Q_s values in this study, we calculated a simplified relative g_c as the ratio of normalized Q_s and VPD.

Values of Q_s and of environmental variables were available at a 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 [24], we averaged diurnal values of Q_s and environmental parameters to daily means. Finally, for each species (spruce and larch), the data set was pooled over all the saplings per treatment.

Regression analyses were performed to analyze the response of normalized Q_s values to soil water content (SWC), photosynthetic active radiation (PHAR), and vapor pressure deficit (VPD), as these environmental factors have often been found to be most closely related to Q_s in the conifers under study [18,26,27]. While correlation of normalized Q_s with SWC and PHAR was obtained by linear regression analysis, the relationship between normalized Q_s and VPD was analyzed using the following exponential saturation function:

$$Q_s = (1 - exp(-a \times \text{VPD})) \tag{3}$$

where *a* is a fitting parameter.

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

$$g_c = g_{cmax} \times (1/(1 + (\text{VPD}/a))) \tag{4}$$

where g_{cmax} is the maximum canopy conductance observed during the study period, and *a* is a fitting parameter.

2.4. Environmental Conditions

Table 2 provides an overview of the microclimatic conditions during the growing seasons (1 May–31 October) of 2016, 2017, and 2018 at the study site. Daily mean photosynthetic active radiation (PHAR) averaged 247 µmol m^{-2} s^{-1} in 2016, 331 µmol m^{-2} s^{-1} in 2017, and 349 µmol m^{-2} s^{-1} in 2018.

Daily mean air temperature (T_{air}) was 9.4 °C in 2016 and in 2017, and 10.9 °C in 2018. The corresponding values for daily mean vapor pressure deficit (VPD) were 2.4, 2.7, and 2.8 hPa in 2016, 2017, and 2018, respectively. Precipitation (P) during the growing seasons 2016, 2017, and 2018 amounted to 830, 1171, and 563 mm, respectively. Roofing excluded 136–962 mm of the incoming P during the growing season (Table 2).

Table 2. Mean daily photosynthetic active radiation (PHAR), air temperature (T_{air}), vapor pressure deficit (VPD), and sum of precipitation (P) during the growing season (1 May–31 October) as well as the amount of precipitation excluded by roofing the forest floor in 2016, 2017, and 2018.

Year	PHAR (μmol m^{-2} s^{-1})	T_{air} (°C)	VPD (hPa)	P (mm)	Rainout Period	P Excluded (mm)	% P Excluded
2016	247	9.4	2.4	830	16 August–3 October	137	16
2017	331	9.4	2.7	1171	18 May–13 September	962	82
2018	349	10.9	2.8	563	23 May–23 September	512	91

Before rain exclusion (DOY 228 in 2016 and DOY 144 in 2017), daily mean soil water content (SWC) at a 5–10 cm soil depth did not differ significantly ($p = 0.51$) between control and rain exclusion plots (Figure 1). Due to frequent precipitation over the three investigation periods (Figure 1), daily mean SWC at a 5–10 cm soil depth of the control plots varied between 11 vol % (14 August 2018) and 43 vol % (29 August 2016) (Figure 1) averaging 35 vol % in 2016, 32 vol % in 2017 and, 30 vol % in 2018 (Table 3), indicating that control saplings did not suffer from shallow soil drought. As expected, rain exclusion caused SWC at a 5–10 cm soil depth to decline continuously throughout the end of rainout periods (Figure 1). Roofing caused SWC to be on average 21, 45, and 20% below the corresponding control levels in 2016, 2017, and 2018, respectively (all $p < 0.001$, Table 3).
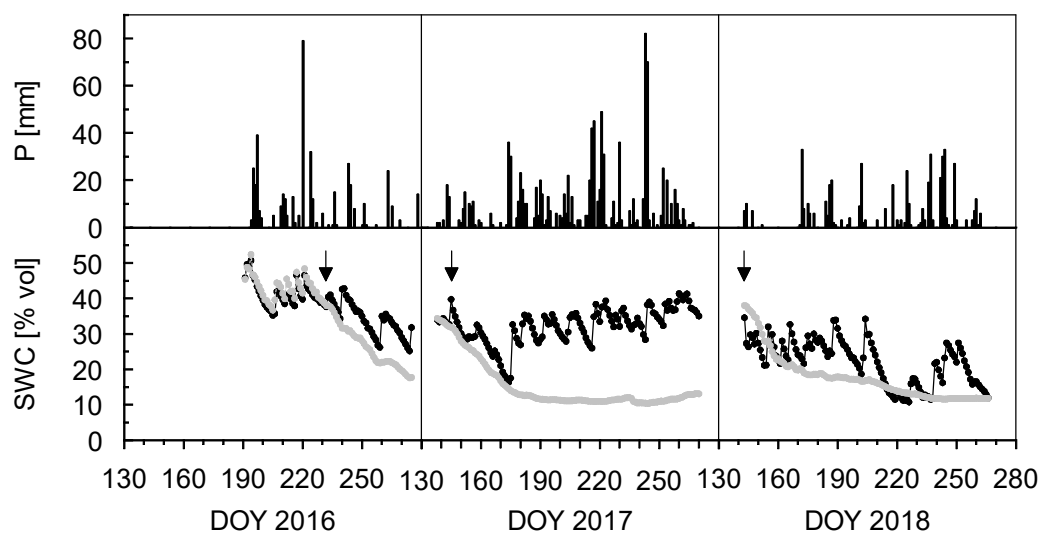
Figure 1. Seasonal course of daily sum of precipitation (P) and daily mean soil water content (SWC) at 5–10 cm soil depth in control (black) and rain exclusion plots (grey) from 10 July–2 October 2016, 18 May–27 September 2017, and 23 May–23 September 2018. SWC data are the mean of three sensors per treatment. Arrows indicate the start of rain exclusion.

Roofing, however, did not considerably influence soil temperature at a 10 cm soil depth. Average soil temperature at a 10 cm soil depth over 2016, 2017, and 2018 did not differ significantly ($p > 0.48$ each) between control (11.9 °C) and rain exclusion plots (11.8 °C; Table 3).

Table 3. Seasonal mean soil water content (vol %) at a 5–10 cm soil depth and soil temperature (°C) at a 10 cm soil depth in control and rain exclusion plots for the periods 16 August–3 October 2016, 18 May–13 September 2017, and 23 May–23 September 2018. Values are the mean ± SE of three sensors per treatment. Significant differences ($p < 0.1$) between control and rain exclusion plots are marked in bold and italics.

Treatment	Soil Water Content			Soil Temperature		
	2016	2017	2018	2016	2017	2018
control	*34.6 ± 2.8*	*32.3 ± 4.0*	*29.9 ± 3.8*	11.9 ± 0.7	11.6 ± 1.0	12.0 ± 0.9
rain exclusion	*27.9 ± 4.2*	*15.3 ± 3.0*	*15.7 ± 3.2*	11.9 ± 0.7	11.5 ± 1.0	12.0 ± 0.8

3. Results

3.1. Diameter Growth

In 2015, the year preceding the rain exclusion experiment, stem radial increment did not differ significantly between control and the rain exclusion *P. abies* and *L. decidua* saplings, respectively (Table 4). Rain exclusion had no effect on diameter growth in both species investigated (Table 4). Even after three years of treatment annual stem radial increment of *P. abies* and *L. decidua* saplings did not differ significantly between control and rain exclusion saplings (Table 4).

Table 4. Stem radial growth (mm) at the height of sensor installation of *Picea abies* and *Larix decidua* saplings in the year preceding the experiment (2015) and at the end of the study periods 2016, 2017, and 2018. Data are medians ± half total range of three saplings per treatment. No significant effects of rain exclusion were found.
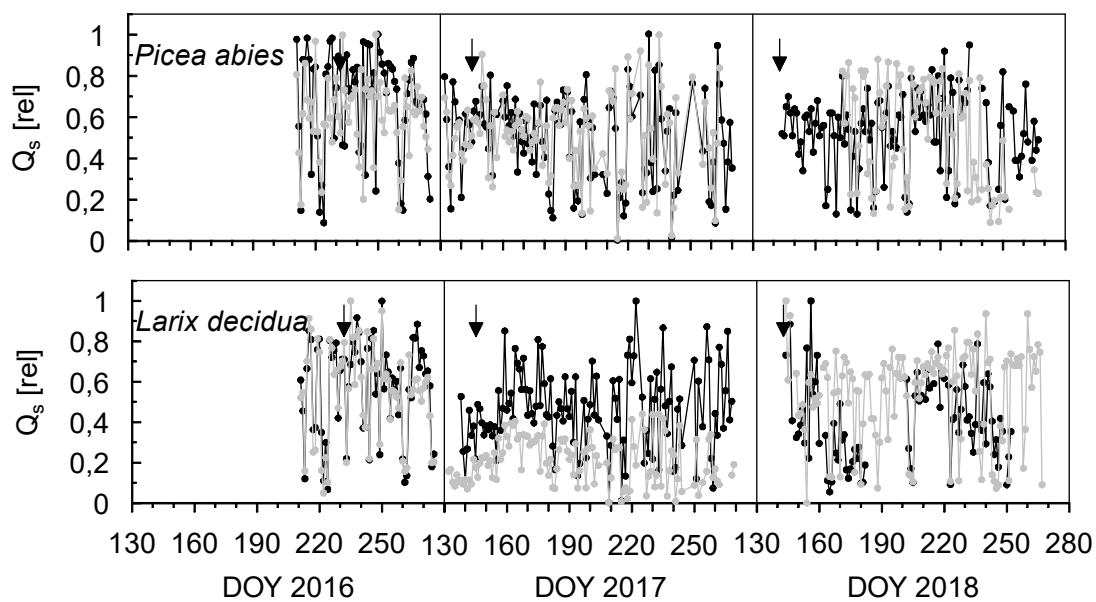
Tree	*Picea abies*				*Larix decidua*			
	2015	2016	2017	2018	2015	2016	2017	2018
control	3.9 ± 1.0	3.9 ± 1.2	3.8 ± 1.1	5.3 ± 1.5	2.1 ± 0.2	1.8 ± 0.1	2.4 ± 0.2	2.1 ± 1.6
rain exclusion	3.3 ± 0.5	3.0 ± 0.1	2.6 ± 0.4	3.2 ± 0.4	2.8 ± 0.1	2.4 ± 1.1	2.9 ± 1.4	4.4 ± 18

### 3.2. Sap Flow Density and Influencing Factors

Before (DOY 228 in 2016 and DOY 144 in 2017) as well as during rain exclusion, normalized Q_s did not differ considerably between *P. abies* and *L. decidua* saplings in control and rain exclusion plots (Figure 2). In *P. abies* saplings exposed to rain exclusion, flow rates were 92% in 2016, 84% in 2017, and 103% in 2018 when compared to control *P. abies* saplings (all $p > 0.19$). The corresponding values for *L. decidua* saplings exposed to rain exclusion were 92, 107, and 101%, in 2016, 2017, and 2018, respectively (all $p > 0.32$).

Three years of rain exclusion did not significantly modify the response of Q_s to SWC at a 5–10 cm soil depth and evaporative demand in terms of PHAR and VPD. On a daily timescale Q_s and SWC were unrelated (Figure 3). Even when SWC at a 5–10 cm soil depth in the rain exclusion plots dropped below 15 vol %, normalized Q_s of spruce and larch saplings reached values up to 100% (Figure 3, exemplified for 2017) of their corresponding maximum values (see Table 1). With respect to PHAR and VPD, these results generally reflected positive correlations between Q_s and both environmental factors. We obtained linear correlations between normalized Q_s and PHAR (Figure 2, all $p < 0.001$). With respect to VPD, Q_s increased sharply at low VPD and tended to saturate at daily mean VPD values > 4 hPa in *P. abies* and > 7 hPa in *L. decidua* saplings growing in control and rain exclusion plots, respectively ($p < 0.001$ each). In contrast to normalized Q_s, normalized canopy conductance (g_c) declined with increasing VPD, a commonly observed relationship, which was not affected by the rainout treatment in *P. abies* and in *L. decidua* (Figure 4, $p < 0.001$ each).

Figure 2. Seasonal course of daily mean normalized sap flow density (Q_s) of *Picea abies* and *Larix decidua* saplings in the control (black) and rain exclusion plots (grey) from 10 July–2 October 2016, 18 May–27 September 2017, and 23 May–23 September 2018. Data are the mean of three saplings per treatment. Arrows indicate the start of rain exclusion.
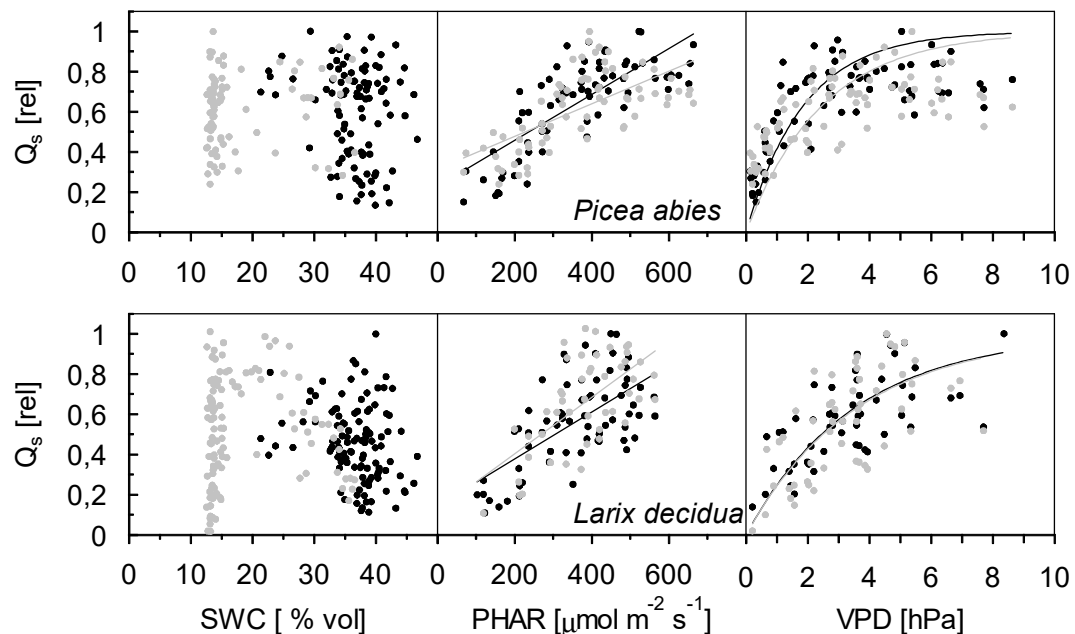
Figure 3. Daily mean normalized sap flow density (Q_s) of *Picea abies* and *Larix decidua* saplings in the control (black) and the rain exclusion treatment (grey) in relation to soil water content at a 5–10 cm soil depth (SWC, **left**), photosynthetic active radiation (PHAR, **middle**), and vapor pressure deficit (VPD, **right**) obtained in 2017. Points are mean values of three saplings per treatment. Points were fit by linear and exponential saturation functions for PHAR and VPD, respectively. *Picea abies*: PHAR: control: y = 0.001×PHAR + 0.23, R^2 = 0.61; rain exclusion: y = 0.0008×PHAR + 0.32, R^2 = 0.42; VPD: control: y = 1× (1−exp (−0.54×VPD)), R^2 = 0.69; rain exclusion: y = 1*(1−exp(−0.39×VPD)), R^2 = 0.54. *Larix decidua*: PHAR: control: y = 0.001×PHAR + 0.14, R^2 = 0.41; rain exclusion: y = 0.002×PHAR + 0.09, R^2 = 0.41; VPD: control: y = 1× (1−exp(−0.28×VPD)), R^2 = 0.48; rain exclusion: y = 1× (1−exp(−0.28×VPD)), R^2 = 0.46. All *P* < 0.001.
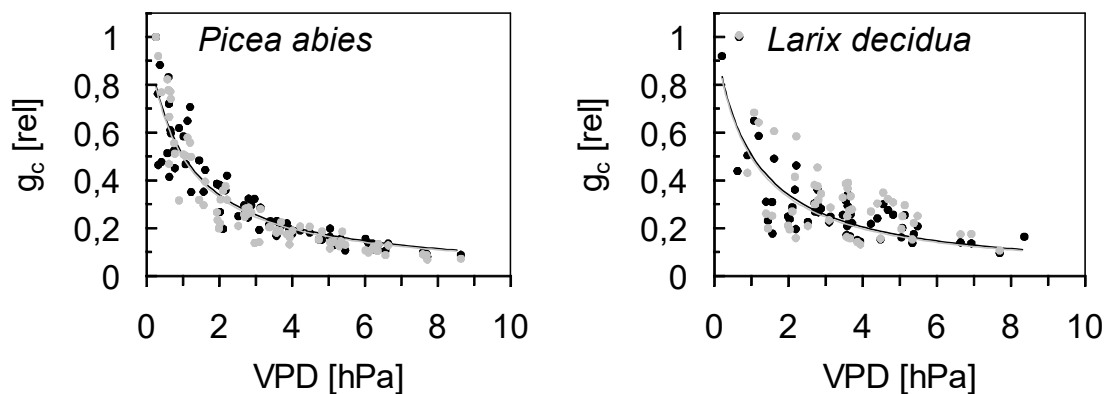
Figure 4. Daily mean normalized canopy conductance (g_c) of *Picea abies* and *Larix decidua* saplings in the control (black) and rain exclusion treatment (grey) in relation to vapor pressure deficit obtained in 2017. Points are mean values of three saplings per treatment. Points were fit by Lohammer type equation: *Picea abies*: control: y = 1/(1 + (VPD/0.93)), R^2 = 0.83; rain exclusion: y = 1/(1 + (VPD/0.98), R^2 = 0.91 *Larix decidua*: control: y = 1/(1 + (VPD/0.94)), R^2 = 0.67; rain exclusion: y = 1/(1 + (VPD/0.94)), R^2 = 0.43. All p < 0.001.

4. Discussion

Our experimental approach was appropriate to manipulate shallow soil water availability, enabling the clarification of tree water loss in two co-occurring conifers in situ under a wide range of environmental conditions at the treeline. Moreover, differences in soil temperature between control and rain exclusion plots stayed within the typical variations at the study site, which confirmed the employed roofing system to prevent any change in soil temperature.

The lack of a significant Q_s–SWC correlation in *P. abies* and *L. decidua* saplings at our study site (Figure 3) indicates sufficient water supply as also observed in adult *P. abies* and *L. decidua* trees at treeline during periods of reduced soil water availability [9,20,28]. Even when SWC at a 5–10 cm soil depth in rain exclusion plots dropped to values below 15 vol %, Q_s of spruce and larch saplings reached values up to 100% of their corresponding maximum values. These findings suggest that, at treeline where VPD is generally considerably lower than at low elevation sites [29–32], whole tree water loss primarily depends on evaporative demand [9,20,27,33,34]. Furthermore, at treeline, small young trees are less coupled to the atmosphere and experience different environmental conditions as compared to adult trees [35], suggesting a smaller effect of increasing evaporative demand on Q_s in saplings as compared to tall trees, which are well coupled to the atmosphere.

Our findings suggest a great tolerance of saplings of both tree species to limited top soil SWC at the treeline. One possible assumption to explain this observation is that roots which extend below the subsoil can maintain a favorable water status, tap water from deeper pools when the upper layers are exhausted. It seems to be possible that, even if only a few fine roots are present in deeper and wet soil layers, these can contribute significantly to water uptake, as is known for forests in dry environments [36–40].

Our data also indicate that a decline in shallow soil water availability hardly affected water loss of *P. abies* and *L. decidua* saplings at treeline in the Central Austrian Alps, falsifying hypothesis (1) and confirming hypothesis (2). In this sense, *P. abies* saplings at treeline differ from adult *P. abies* trees that follow a water-saving strategy [20,21,27]. While reductions in water loss of *P. abies* and *L. decidua* upon rain exclusion were reported in the literature for a low elevation site in the Austrian Alps [15,16], we did not find reductions in Q_s of *P. abies* and *L. decidua* saplings, probably because high air humidity dampens evapotranspiration at high elevation [41]. Nevertheless, reduced soil water availability upon warming may endanger treeline saplings through water imbalances, in particular at their upper distribution limit, where tree habitat becomes stunted and deformed to "krummholz" in the "kampfzone" [32,33,42]. This latter zone already today is affected by temporal soil drought

at wind-exposed ridges and leeward sun-exposed slopes with thin soil layers [14,27]. Finally, while there is ample evidence of upward shifts of treelines caused by climate warming [1,43–46] as well as non-climatic factors (REFs) [47], and further references therein], such as soil conditions [32,33,42] and couple effects of climate and land use change [2,21], it has been uncertain whether and to what extent such shifts can be limited by an increased occurrence of droughts. Our results indicate that, at the treeline, saplings of spruce and larch do not reduce transpirational water losses and growth under drought, suggesting that upward shifts of the treeline will likely not be limited by drier conditions in a warmer world.

5. Conclusions

Although our study suggests comparatively small effects of dry periods on Q_s at the treeline, it remains to be tested whether more severe drought events, likely to occur in the coming decades, have any effects on the Q_s of mature trees with higher water demand, especially during periods of high VPD. There is also evidence that, on a global scale, adult trees suffer from severe drought events [48]. Moreover, saplings differ in their response to drought from adult trees [49] due to ontogenetic changes in foliar gas exchange parameters [50]. It therefore remains to be investigated whether the surprisingly high drought resistance of saplings of the two conifer species at the treeline also holds for mature trees. Such studies, ideally based on long-term experiments manipulating both precipitation and evaporative demand, would also be important for understanding drought effects on forest regeneration under climate warming, as there is evidence that adult trees can enhance the survival and growth of saplings in a future warmer environment [51].

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