



Sap flow characteristics and canopy transpiration of *Alnus alnobetula* within the treeline ecotone of the Central Tyrolean Alps

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Abstract

Throughout two investigation periods, we estimated the canopy transpiration, understory evapotranspiration and total stand water use of *Alnus alnobetula* at three stands within the treeline ecotone of the Central Austrian Alps. Our study included one site at the lower edge of the treeline ecotone and two plots at the tree limit: one north-facing leeward and one south-east facing windward. Canopy transpiration (T_c) was estimated at each site by taking sap flow measurements on six stems and scaling them up to stand canopy level. Understory and soil evapotranspiration (ET_u) were derived using the soil water budget method. Throughout the treeline ecotone, normalized sap flow density was significantly correlated with solar radiation and vapour pressure deficit. By contrast, soil water content had no effect on normalised sap flow density, suggesting that *A. alnobetula* is highly tolerant of the limited soil water availability in the topsoil. Our estimated total stand evapotranspiration ($ET_{tot} = T_c + ET_u$) for the treeline ecotone on Mt. Patscherkofel averaged 4.3 ± 0.6 mm per day, while T_c averaged 3.6 ± 0.5 mm per day. These values considerably exceed the means reported for the growing season of adjacent isolated *Pinus cembra* trees, dwarf shrub communities, and grasslands, and should be taken into account when forecasting the potential effects of shrub encroachment on the water balance of the treeline ecotone.

Keywords Green alder · Shrub expansion · Hydrology · Evapotranspiration

Introduction

During the last decades shrub encroachment occurred across arctic and alpine environments (Hallinger et al. 2010; Myers-Smith et al. 2011; Frost and Epstein 2014). Especially in the European Alps decreasing grazing pressure and land abandonment favoured the expansion of green alder [*Alnus alnobetula* (Ehrh.) K. Koch; former *Alnus viridis* (Chaix) DC.] (Anthelme et al. 2007; Gehrig-Fasel et al. 2007; Boscutti et al. 2013; Bühlmann et al. 2014; Oberhuber et al. 2022). *Alnus alnobetula* is a tall, multi-stemmed, nitrogen-fixing shrub that forms dense thickets with canopy

heights of up to 4 m. Once established, *A. alnobetula* creates a dense canopy and prevents the growth of seedlings and the recruitment of trees across the treeline ecotone (Gehring-Fasel et al. 2007; Hiltbrunner et al. 2014; Wang et al. 2016; Gruber et al. 2022). The expansion of *A. alnobetula* primarily occurs in avalanche gullies and on steep north-facing slopes with high water availability (Holtmeier 2009; Bühlmann et al. 2014). However, *A. alnobetula* is also expanding into sunny sites with shallow soils and limited water availability (Caviezel et al. 2017; Oberhuber et al. 2022; Gruber et al. 2024).

Shrub expansion vigorously influences ecosystem structure (Eldrige et al. 2011, 2012) and biogeochemical cycles including evapotranspiration and runoff. Despite the wealth of information on water loss in grasslands and dwarf shrub communities (Guggenberger 1980; Kronfuss 1977; Wieser 1983; Wieser et al. 2008) and forest trees (Wieser and Leo 2012; Wieser et al. 2014, 2015) in the treeline ecotone of the Central Tyrolean Alps, based on lysimeter and sap flow studies respectively, there is little knowledge about the transpiration of *A. alnobetula* shrub canopies in this area. Yet, there is evidence that compared to montane grasslands

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runoff coefficients and transpiration rates are noticeably higher in shrubland (Tappeiner and Cernusca 1993; Obojes et al. 2014; Van der Bergh et al. 2018). Leaf gas exchange measurements indicated, that under conditions of high sunlight *A. alnobetula* keeps their stomata wide open and shows no midday depression in transpiration due to stomatal closure (Körner et al. 1978a; Van den Bergh et al. 2018).

We hypothesized that evapotranspiration of *A. alnobetula* stands exceeds those from dwarf shrub communities, grasslands and isolated *Pinus cembra* trees within the treeline ecotone of the Central Tyrolean Alps. To test this hypothesis, we measured sap flow density (Q_s) with thermal dissipation probes (Granier 1985) of *A. alnobetula* growing under different site conditions (see below) within the treeline ecotone on Mt. Patscherkofel (Tyrol, Austria) in two consecutive growing seasons. Therefore, our specific aims were (1) to determine the impact of soil water availability and evaporative demand (in terms of radiation and vapour pressure deficit) on shrub water loss of *A. alnobetula*, and (2) to compare the water loss of *Alnus* stands with previously reported evapotranspiration rates from other vegetation types within the treeline ecotone in the Central Tyrolean Alps. The fulfillment of these aims will contribute to a better assessment of the importance of shrubland transpiration for the water balance within the treeline ecotone of the Central Tyrolean Alps in a changing future environment.

Material and methods

Study site and sample stems

The study was carried out within the treeline ecotone on Patscherkofel (Central Tyrolean Alps, Austria; 47°12'37"N, 11°27'07"E) where *Alnus alnobetula* stands generally stretches out between 1950 and 2200 m a.s.l. in north facing avalanche gullies but also in windward south-to south-east facing slopes (Oberhuber et al. 2023; Gruber et al. 2024).

The geology in the Mt. Pascherkofel area is dominated by gneisses and schist. The soils are classified as a Haplic Podzol (Neuwinger 1970), a soil type typical for the Central Tyrolean Alps (Wieser 2012). According to a 30-year record (1991–2020) of meteorological data at a weather station on

the top of Mt. Patscherkofel (2252 m a.s.l.) the mean annual air temperature was 0.8 ± 0.7 °C with July (8.9 °C) and February (−6.6 °C) being the warmest and coldest month respectively. The mean annual precipitation was 889 mm with the majority (371 mm) falling during the summer (June–August), while winter (December–February) is the driest season (132 mm). Due to the occurrence of strong southerly Föhn-type winds, snow depths and the duration of a permanent snow cover vary considerably. While on leeward north facing slopes a continuous snow cover with snow depths up to 3 m may persist from late October until May, snow depth on south facing sites is commonly less than 1 m and only small patches of snow persist till mid spring.

Within the study area we selected 18 *A. alnobetula* stems at three study sites (six stems per site) differing in geomorphologic features (Table 1), where *A. alnobetula* was the only canopy constituent and the understory was nil. Our design included one site at the lower edge of the treeline ecotone close to the forest limit (hereafter FL-site) and two plots at the tree limit: a north-exposed leeward site (hereafter TLN-site) and a south exposed windward site (TLS-site). The two sites at the tree limit were only apart 150 m in linear distance and slightly below a wind-exposed east–west ridge. At the time of study (2023–2024) the shrubs were 20–25 years old, the stem diameter 20 cm above ground ranged from 38 to 48 mm, their height ranged from 140 to 350 cm, and the stand density per plot was 6 to 7 stems m^{-2} (Table 1). At each study plot environmental conditions and sap flow density were continuously monitored from June 21 throughout September 9 during the growing seasons of 2023 and 2024, respectively.

Environmental and sap flow density measurements

At each of the tree study plots air temperature (T_{air}), relative humidity (Rh , CS215 Temperature and relative Humidity Sensor), solar radiation (R_s ; SP1110 Pyranometer Sensor), and wind velocity (v ; A100R; all sensors Campbell Scientific, Shepshed, UK) were monitored 2 m above ground in open areas neighbouring the stocks. Additionally, four soil temperature probes (T 107 temperature probe Campbell Scientific Shepshed, UK) and five ML2 Theta Probes (Delta-T

Table 1 Description of the selected study plots and characteristics of *A. alnobetula* stems selected for sap flow measurements within the treeline ecotone on Mt. Patscherkofel and daily maximum sap flow density obtained during the study periods (June 21–September 9) 2023 and 2024

Site	Elevation (m a.s.l.)	Aspect	Slope (°)	Soil depth (cm)	Canopy height (cm)	Age (years)	Stem diameter ^a (mm)	Stand den- sity (stems m^{-2})	Q_{s-max} 2023 ($g\ m^{-2}\ s^{-1}$)	Q_{s-max} 2024 ($g\ m^{-2}\ s^{-1}$)
Forest limit	1940	NNW	35	15–20	350±50	25±6	48±3	6	11.6±1.3	8.0±1.4
Treeline north	2150	N	35	10–15	270±80	20±7	39±2	6	21.7±0.8	18.5±2.4
Treeline south	2140	SE	25	5–10	140±40	21±8	38±1	7	14.1±1.2	10.5±1.1

^aValues are the mean±SE of six stems measured at height of sensor installation

devices Ltd. Bruckwell, UK) were used for monitoring soil temperature (T_{soil}) and soil moisture (θ) in 5 to 10 cm soil depth close within the rooting zone of the stems used for sap flow measurements. Precipitation (P) was obtained from the Geosphere Austria weather station on the summit of Mt. Patscherkofel at 2252 m a.s.l.

Soil water deficit (SWC) was quantified using relative extractable water (REW, a dimensionless quantity) and was assumed to occur when REW dropped below 0.4 (Granier 1987; Breda et al. 1995). We used the θ values observed at a soil depth of 5–10 cm as a proxy for estimating REW, as described by Granier et al. (1999) and Vincke and Thyry (2008)

$$\text{REW} = (W_{\text{act}} - W_{\text{min}}) / (W_{\text{fc}} - W_{\text{min}}) \quad (1)$$

where W_{act} denotes the actual daily soil water content, W_{min} the minimum soil water content observed during the investigation period and W_{fc} the soil water content at field capacity (Granier et al. 2000).

Sap flow density (Q_s) was monitored by means of the heat dissipation approach according to Granier (1985). In each study stem one 10 mm long sensor was installed into the outer xylem. Each sap flow sensor (SFS2 M-M12, UP Umweltanalytische Produkte GmbH, Cottbus, Germany) consisted of two probes. The probes (with a sensor length of 10 mm) were installed vertically, 15 cm apart, on the north-facing side of the stems, approximately 20 cm above the ground. The upper probe included a heater that was continuously supplied with a constant power of 0.15 W (CCS 2 constant current source, UP Umweltanalytische Produkte GmbH, Cottbus, Germany), while the lower unheated probe remained at stem temperature for reference. The sensors were shielded with a thick aluminum-faced foam cover to protect against physical damage, thermal influences from radiation and exposure to rain.

At the FL site, all environmental and Q_s data were transmitted to an AM416 multiplexer and recorded using a Campbell CR1000 data logger (Campbell Scientific, Shepshed, UK). At the TLN and TLS sites, however, only environmental data were stored in a Campbell CR1000 data logger, while Q_s data were recorded using a Delta-T GP2 data logger (Delta-T Devices Ltd., Bruckwell, UK). All the data loggers were programmed to record 30-min averages of measurements taken every minute. Two car batteries (12 VDC, 80 Ah) which were recharged by two 80 W solar panels in combination with a charge controller, provided power for all the electrical equipment at each study plot.

Estimation of canopy transpiration, understory evapotranspiration and total stand water use

For each sensor 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) occurring at times of zero flow according to the calibration equation of Granier (1987) and revalidated by Clearwater et al. (1999) and Köstner et al. (1998):

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

Each night, the difference in temperature (ΔT_m) was determined and used as a reference for the following day. The underlying assumption of zero sap flux during the night was justified, as vapour pressure deficits were generally low, and temperature courses reached equilibrium between both probes during most nights, suggesting complete refilling of the internal water reserves of the stems.

As *A. alnobetula* wood is diffuse porous and sapwood can hardly be distinguished from heartwood (Schoch et al. 2004), water can be transported across the entire xylem section of the stem (c.f. also Van der Bergh et al. 2018). Furthermore, as there is evidence that sap flow rates estimated in up to 10 cm thick *Alnus* stems agreed well with the water consumption of cut stems derived from potometer measurements (Van der Bergh et al. 2018) we assumed (1) uniform Q_s across the entire stem cross section and (2) that our installation sampled 100% of the whole water flow in *A. alnobetula*. Since at our study sites Q_s of *A. alnobetula* was not correlated with the correspondent stem diameter ($R^2=0.11$; $P=0.51$), canopy transpiration per unit ground surface (T_c ; mm day^{-1}) was determined as follows (c.f. also Zimmermann et al. 2000; Oishi et al. 2010; Wieser et al. 2018):

$$T_c = Q_{s-\text{totmean}} * A_{s-\text{stand}} \quad (3)$$

where $Q_{s-\text{totmean}}$ is the average daily total Q_s of the sample stems and $A_{s-\text{stand}}$ is the cumulative sapwood area per ground face area ($\text{m}^2 \text{m}^{-2}$). A stand specific sapwood area of 96, 33, and 61 $\text{cm}^2 \text{m}^{-2}$ was used for up-scaling T_c at the FL-, the TLN-, and the TLS-site, respectively. Scaling up employing this method can be applied in uniform stands little variation in stem size and a high individual variation in Q_s (Cermak et al. 2004), as it was in our case at our study four sites (Table 1). Furthermore, there is also evidence that the scaling error for estimating stand specific Q_s -mean sums is less than 7% when using 6 sample stems per site (Cermak et al. 2015).

Shrub understory evapotranspiration (ET_u , soil evaporation and understory transpiration) was estimated from soil

moisture content measurements according to the soil water budget approach (Kucerova et al. 2010). Within the treeline ecotone on Mt. Patscherkofel an important amount of precipitation leaches as gravitational water into deeper soil layers after refilling the macropores of the top soil (Neuwinger 1970; Guggenberger 1980; Wieser 2012). Thus, we assumed that ET_u solely absorbed water of the top soil (Waring and Running 1998) and that ET_u is primarily dependent on evaporative demand reaching the shrub-land floor (Granier et al. 1999). Due to precipitation inputs, water movement within the soil profile and the ET_u influence on the soil water content, we eliminated all days with rain and also up to two days following heavy rain events (>25 mm) for estimating ET_u (c.f. also Wieser et al. 2018). As there is evidence that understory vegetation is poorly coupled to the atmosphere (Jarvis and McNaughton 1986; Berbigier et al. 1991) we calculated ET_u as follows:

$$ET_u = -\Delta W \quad (4)$$

where $-\Delta W$ (mm) is the change in water content of the top soil (see Table 1) between two consecutive days. Total stand evapotranspiration (ET_{tot}) was calculated as the sum of T_c and ET_u .

Leaf level gas exchange and water potential measurements

Leaf H_2O gas exchange (transpiration and stomatal conductance) was measured in situ with a portable MiniPam2/porometer (Walz, Effeltrich, Germany), and an M 600 pressure chamber (PMS Instrument Company, Albany, Or, USA) was used for estimating shoot water potential during two sunny days in July 2024 (July 26 and 30). All these measurements were obtained from six stems on the TLS- and the TLN-site, respectively. For each stem we measured repeatedly gas exchange and water potential every two hours between 6 a.m. and 5 p.m. for obtaining diurnal courses of transpiration, leaf conductance and shoot water potential.

Data analysis

In this study, we emphasized the comparison of transpiration characteristics of *A. alnobetula* as affected by differences in geomorphologic features (elevation and aspect) within the treeline ecotone. Because of the large variation in Q_s (Table 1) within individual stems, within study sites (FL, TLN, TLS-site), and investigation periods (2023 and 2024), we used normalized Q_s values for our analysis. This was achieved by converting Q_s values of each stem to a ratio of the maximum daily mean value observed during the measurement periods (Table 1). Consequently, each stem had a

maximum normalized Q_s of 1, and thus allowing a better comparison of Q_s to environmental variables with respect to elevation and aspect (Luis et al. 2005; Du et al. 2011).

Values of environmental data and Q_s were available at 30-min intervals. To avoid the possibility of stem capacitance affecting the analysis of transpiration responses to environmental variable variation, we averaged the diurnal Q_s and environmental data values to obtain daily means (Ewers et al. 1999; Oren et al. 1999). Finally, normalized Q_s data were pooled over all six stems per stand (FL, TLN and TLS-sites) and season (2023 and 2024).

Regression analyses were used to examine how normalized Q_s respond to solar radiation (R_s), vapour pressure deficit (VPD) and soil water content (θ). The relationships between normalized Q_s and R_s , and between normalized Q_s and θ , were derived using linear regression analysis. The relationship between normalized Q_s and VPD, however, was analyzed using the following exponential saturation function:

$$Q_s = (1 - \exp(-a * VPD)) \quad (5)$$

where a is a fitting parameter. All statistical analyses were made with the SPSS Statistics, Version 26 (IBM, New York, NY, USA), while non linear curve fittings were performed using FigP for Windows (Biosoft, Cambridge, UK). Values are the mean of six trees $\pm$ SE.

Results

Environmental conditions

Seasonal patterns of environmental conditions obtained during the study periods (21 June–9 September) 2023 and 2024 are shown in Fig. 1. Averaged over the two investigation periods, daily mean air temperature (T_{air}) decreased with altitude while daily mean vapour pressure deficit (VPD) tended to decline with altitude (Table 2). Solar radiation (R_s) and wind velocity (v) increased with altitude, whereas root zone soil temperature (T_{soil}) decreased with altitude (Table 2). Mean T_{air} and T_{soil} were slightly higher in 2024 than in 2023 (Table 2). At the forest limit, mean VPD was higher in 2024 but lower at both treeline sites as compared to 2023 (Table 2). Mean solar radiation was similar in both investigation periods at the forest limit and considerably higher at both treeline sites in 2024 than in 2023, while wind velocities were similar in both investigation periods (Table 2).

Precipitation (P) varied considerably during the course of this investigation (Fig. 1). Of the 2 years examined, 2023 was the wetter investigation period with a total of 422 mm,

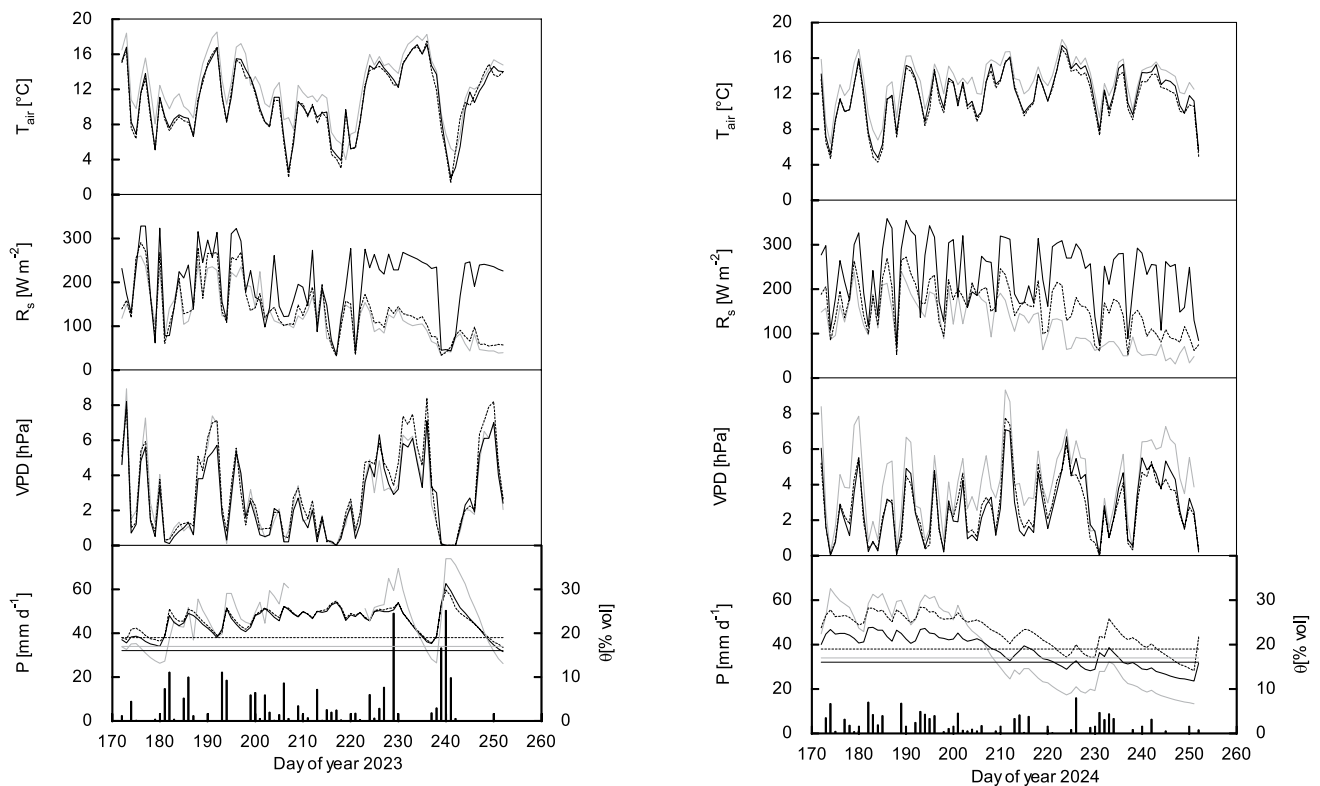


Fig. 1 Seasonal course of daily mean air temperature (T_{air}), daily mean solar radiation (R_s), daily vapour pressure deficit (VPD), daily mean volumetric soil water content in 5–10 cm soil depth (θ), at the forest limit (solid grey line) the treeline south (solid black line) and the

treeline north site (dotted black line), and the daily sum of precipitation (P ; Mt Patscherkofel summit) between 21 June and 9 September 2023 and 2024. The horizontal lines indicate soil water deficit

while throughout the investigation period 2024 the total sum of precipitation amounted only 223 mm. As a result, shallow soil water content (θ) in 5–10 cm soil depth was considerably lower in 2024 than in 2023 (Fig. 1, Table 2). Based on an REW of 0.4 (corresponding to a shallow soil water content of 17, 19, and 16%vol. at FL, the TLN, and the TLS-site, respectively) soil water deficit characterized 17, 13 and 2% of the investigation period 2023 at FL-, the TLN-, and the TLS-site, respectively (Fig. 1). The corresponding values for the investigation period 2024 were 54%, at the FL-, 20% at the TLN-, and 31%, the TLS-site (Fig. 1).

Sap flow density and influencing factors

To further elucidate response patterns of Q_s to environmental factors with respect to study site, daily mean normalized Q_s patterns obtained at forest limit and the two treeline sites, respectively, were correlated with the corresponding soil water content (θ) in 5–10 cm soil depth as well as with solar radiation (R_s), and vapour pressure deficit (VPD) values obtained at the three study plots 2 m above ground.

Examined at a daily timescale we obtained no effect of shallow soil water content, and hence also of soil water deficit on Q_s (Fig. 2) while the correlations between normalized

Q_s and the both atmospheric factors reflected positive relationships (Figs. 3, 4). We obtained linear correlations between normalized Q_s and R_s at R^2 levels of 0.52, 0.46, and 0.72 at the FL, the TLN and the TLS-site, respectively (Fig. 3).

With respect to VPD, normalized Q_s increased sharply at low VPD and tended to saturate at mean daily VPD values > 7 hPa (Fig. 4). Nevertheless, conditions with such high daily mean VPD values were infrequent during our two study periods (c.f. Figs. 1, 2). Even so, daily mean VPD explained (Fig. 4) 64, 39, and 74% of the variation in Q_s at the FL, the TLN and the TLS-site, respectively (Fig. 4).

Diurnal and seasonal courses

Diurnal and seasonal of water fluxes generally followed diurnal trends in evaporative demand (Figs. 5, 6). Overall, diurnal courses of Q_s obtained with heat dissipation approach matched our leaf level transpiration measurements as shown for the TLN and the TLS-site in Fig. 5. On both days investigated, Q_s and leaf transpiration generally followed diurnal trends in evaporative demand (Fig. 5). Our porometer measurements also showed high leaf conductance values up to $300 \text{ mmol m}^{-2} \text{ s}^{-1}$ and no midday depression in water

Table 2 Seasonal mean values of air temperature (T_{air} , °C), vapour pressure deficit (VPD, hPa), solar radiation (R_s , W m⁻²), wind velocity (v ; m s⁻¹), soil temperature (T_{soil} , °C) and soil moisture (θ , %vol.) in 5 to 10 cm soil depth of the rooting zone near the stems used for sap flow measurements obtained during the investigation periods (June 21 throughout September 9) 2023 and 2024 at the forest limit (FL-site), the treeline north (TLN-site), and the treeline south (TLS-site)

Site	June 21–September 9 2023						June 21–September 9 2024					
	T_{air}	VPD	R_s	v	T_{soil}	θ	T_{air}	VPD	R_s	v	T_{soil}	θ
FL-site	12.7	3.1	125	0.6	11.1	22.7	13.5	4.1	121	0.6	12.2	18.2
TLN-site	10.4	3.2	134	1.2	9.3	22.8	11.7	2.7	159	0.9	11.0	21.2
TLS-site	10.7	2.9	197	0.8	9.4	20.6	12.1	2.8	234	0.9	11.1	16.9

All values are based on daily means

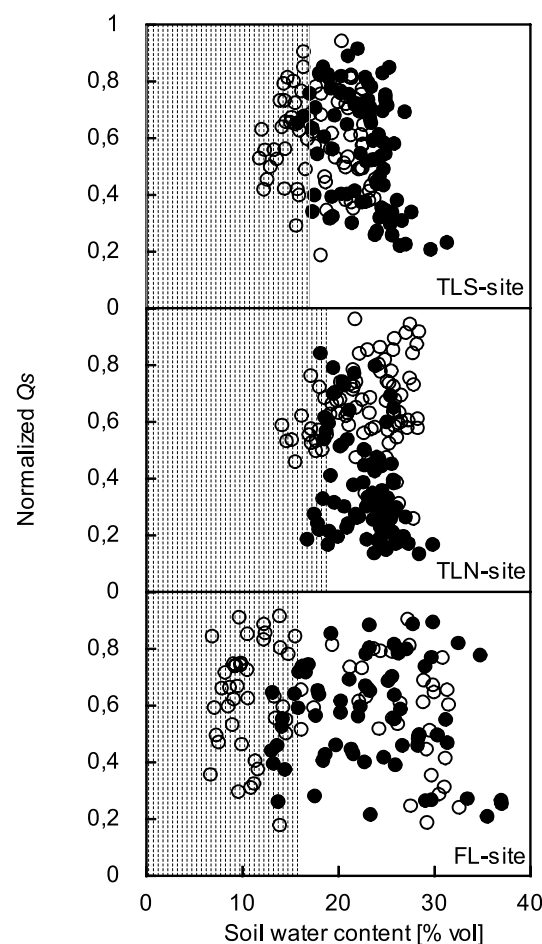


Fig. 2 Normalized mean daily sap flow density in relation to soil water content in 5–10 cm soil depth during the investigation periods 2023 (closed symbols) and 2024 (open symbols) at the forest limit (FL-site), the treeline north (TLN-site) and the treeline south site (TLS-site). The dashed areas indicate soil water deficit

loss due to stomatal narrowing in spite of low leaf water potentials lower than 15 hPa (Fig. 5). Canopy transpiration related to ground surface area (T_c) varied between 0.9 and 7.3 mm day⁻¹ at the FL-site, between 1.3 and 5.5 mm day⁻¹ at the TLN-site, and between 1.5 and 6.4 mm day⁻¹ at the TLS-site, respectively (Fig. 6).

Seasonal water fluxes of *Alnus alnobetula* stands compared to previously reported evapotranspiration from other treeline associated vegetation types

Cumulative total stand water use of (ET_{tot}) estimated for an entire investigation period varied between 330 and 403 mm in 2023 and between 294 and 377 mm in 2024 (Table 3) and was composed of the following fluxes: 294 to 403 mm from canopy transpiration (T_c) and 35 to 83 mm from understorey evapotranspiration (ET_u) (Table 3). Accordingly, the

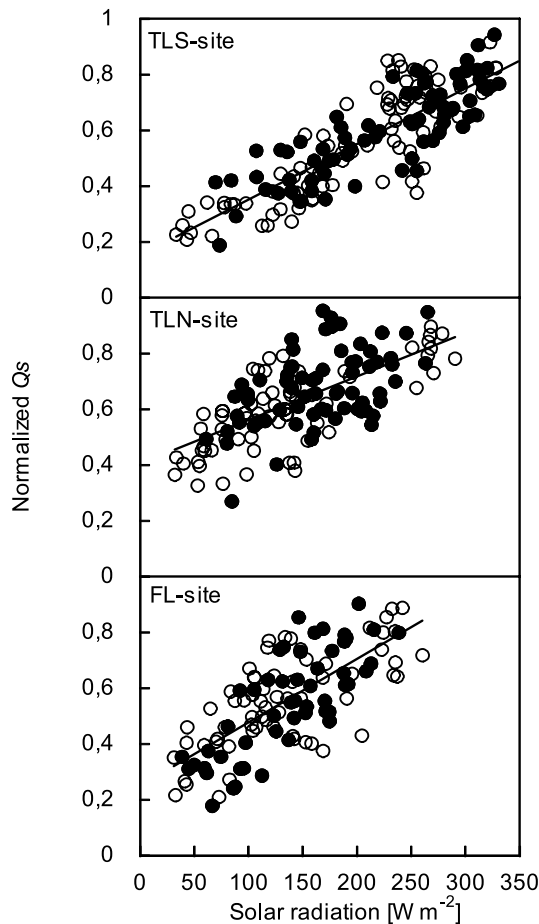


Fig. 3 Normalized mean daily sap flow density as a function of solar radiation during the investigation periods 2023 (closed symbols) and 2024 (open symbols) at the forest limit (FL-site), the treeline north (TLN-site) and the treeline south site (TLS-site). Points were fit by linear regression analysis: forest limit; $y=0.0022x+0.25$, $R^2=0.52$; treeline north: $y=0.0026x+0.43$, $R^2=0.46$; treeline south: $y=0.0020x+0.15$, $R^2=0.72$; all P values <0.001

contribution of T_c to ET_{tot} varied between 78 and 86%, and the contribution of ET_u to ET_{tot} was 14 to 22% (Table 3).

Even so, averaged over both investigation periods daily mean T_c varied between 3.5 and 3.7 mm day⁻¹ (Table 4). Daily mean ET_{tot} varied between 4.3 and 4.4 mm day⁻¹ (Table 4). These values considerably exceeded daily mean values obtained for a *Pinus cembra* forest 50 m below the treeline, isolated *Pinus cembra* trees, dwarf shrub communities, grasslands and pastures within the treeline ecotone of the Central Tyrolean Alps (Table 4).

Discussion

The present study focused on seasonal variations in water loss in *A. alnobetula* stands within the treeline ecotone of the Central Austrian Alps. Here, topsoil water availability

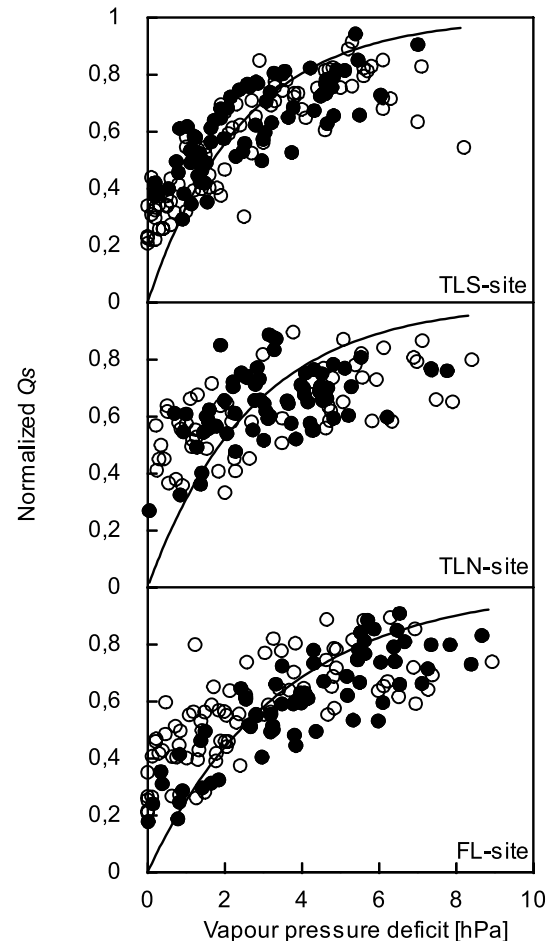


Fig. 4 Normalized mean daily sap flow density as a function of vapour pressure deficit during the investigation periods 2023 (closed symbols) and 2024 (open symbols) at the forest limit (FL-site), the treeline north (TLN-site), and the treeline south site (TLS-site). Points were fit by exponential saturation functions: forest limit; $y=1-\exp(-0.29*x)$, $R^2=0.64$; treeline north: $y=1-\exp(-0.25*x)$, $R^2=0.39$; treeline south: $y=1-\exp(-0.41*x)$, $R^2=0.74$; all P values <0.001

may be limited during dry periods due to low water-holding capacity (unpublished observations by the author). Even during a 43-day period at the end of the investigation period 2024 (DOY 209–252) when shallow soil water content at the FL-site was continuously below 17 vol% (Fig. 1), we hardly detected a significant effect on daily canopy transpiration (Fig. 2). This finding suggests that *A. alnobetula* has a high tolerance to limited soil water availability in the topsoil. It is therefore possible that roots penetrating below the shallow soil layer into the debris of the parent material can access deeper water pools, maintaining favourable water status when the topsoil is exhausted (Dawson 1996; Villa-Salvador et al. 1997; Sarris et al. 2013). Access to deep soil water reserves has also been reported in a Canary Island pine forest at the treeline in Tenerife (Brito et al. 2015) and in a mixed broadleaf deciduous forest in North Carolina (Oishi et al. 2010). Furthermore, evidence suggests that the

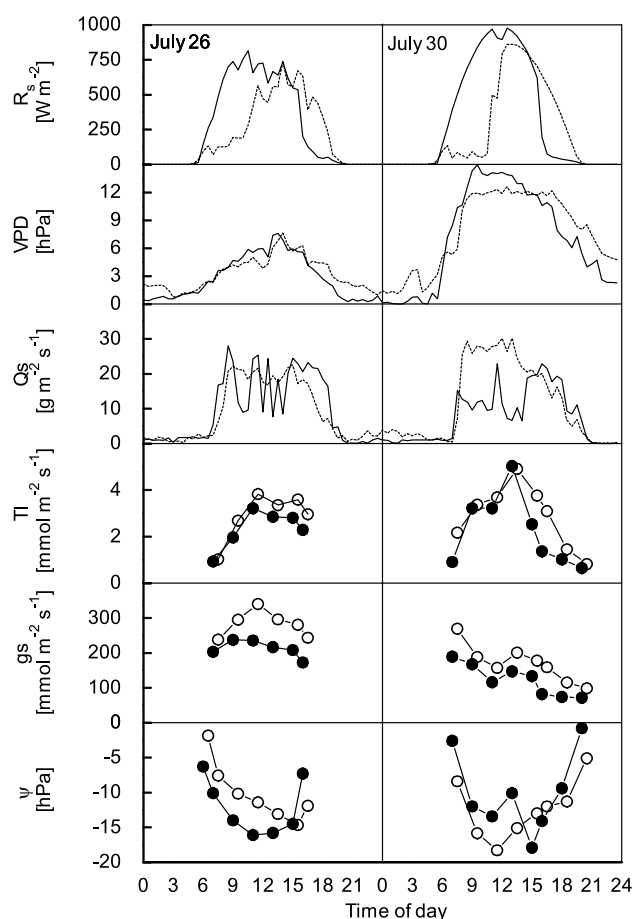


Fig. 5 Diurnal course of solar radiation (R_s), vapour pressure deficit (VPD), sap flow density (Q_s), leaf transpiration (T_l), stomatal conductance (g_s), and leaf water potential (ψ) of *Alnus alnobetula* obtained at the treeline south (solid line and closed symbols) and the treeline north site (dotted lines and open symbols) on July 26 (left), and July 30 (right) 2024

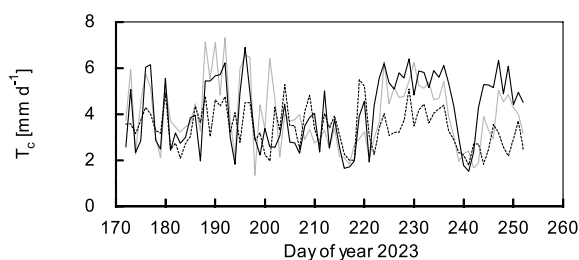


Table 4 Daily mean growing season canopy transpiration (T_c) and cumulative total stand water use (ET_{tot}) of various vegetation types within the treeline ecotone of the Central Tyrolean Alps

Vegetation type	T_c (mm day ⁻¹)	ET_{tot} (mm day ⁻¹)	References
<i>Alnus alnobetula</i>	3.5–3.7	4.3–4.4	This study
Uppermost closed forest	2.6		Matyssek et al. (2009)
Trees at treeline	1.7–2.2		Wieser and Leo (2012), Wieser et al. (2014)
Krummholz	1.6		Wieser et al. (2014)
Dwarf shrubs		1.9–2.5	Guggenberger (1980), Kronfuss (1997)
Grassland and pastures		1.9–2.4	Wieser (1983), Wieser et al. (2008)

distribution of roots is not necessarily closely correlated with their contribution to the total water uptake of woody plants (Bishop et al. 1998; Wattenbach et al. 2005).

Our observed significant linear increase of daily mean normalized Q_s with increasing R_s (Fig. 3) reflects the energy demand for evapotranspiration (Campbell and Norman 1998) and indicates that limitations in transpiration due to stomatal narrowing during periods of high evaporative demand play a minor role in *A. alnobetula* (Fig. 5) as also obtained by others (Körner et al. 1978a; Van der Bergh et al. 2018). This is corroborated by the fact that the slope of the relationship between normalized daily mean Q_s and VPD decreased only at very high VPD (Fig. 4), as also observed by Van der Bergh et al. (2018).

Our estimated ET_{tot} obtained within the treeline ecotone of Mt. Patscherkofel averaged 352 ± 46 mm, and was composed of the following fluxes: $83 \pm 4\%$ from T_c and $17 \pm 4\%$ from ET_u (Table 3). These values obtained for each layer evapotranspiration are comparable to T_c (83–78%) and ET_u

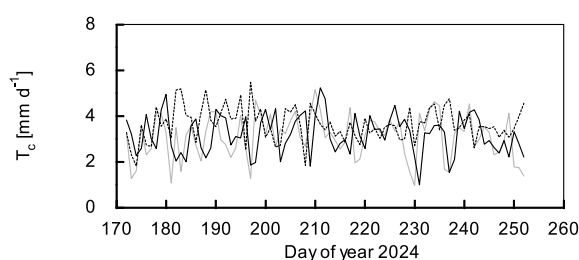


Fig. 6 Seasonal course of shrub transpiration scaled to ground surface area (T_c) at the forest limit (solid grey line), the treeline south (solid black line) and the treeline north site (dotted black line), between 21 June and 9 September 2023 and 2024. Values are the mean of six trees

Table 3 Canopy transpiration (T_c , mm day⁻¹), understory evapotranspiration (ET_u , mm day⁻¹), and cumulative total stand water use (ET_{tot}) obtained during the investigation periods (June 21 throughout September 9) 2023 and 2024

Site	2023			2024			Average		
	T_c	ET_u	ET_{tot}	T_c	ET_u	ET_{tot}	T_c	ET_u	ET_{tot}
Forest limit	327	76	403	250	62	312	289	69	358
Treeline north	279	51	330	294	83	377	287	67	354
Treeline south	343	55	398	259	35	294	301	45	346

(17–22%) values reported for an *A. alnobetula* stand at 1675 m a.s.l. in the Swiss Alps (Van der Berg et al. 2018).

Our study clearly indicates that water vapour loss within the treeline ecotone strongly depends on vegetation type (Table 4). Even so, the data presented in Table 4 represent daily means across all weather conditions. Sap flow-based daily mean canopy transpiration (T_c) of *A. alnobetula* stands (3.5–3.7 mm day⁻¹) was 28 to 56% higher than the values reported for a *Pinus cembra* forest 50 m below the treeline (2.6 mm day⁻¹, Matyssek et al. 2009) and the numbers reported for isolated *Pinus cembra* trees (1.7–2.2 mm day⁻¹, Wieser and Leo 2012; Wieser et al. 2014), and Krummholz (1.6 mm day⁻¹; Wieser et al. 2014) within the treeline ecotone of Mt. Patscherkofel. Our estimated daily mean *A. alnobetula* ET_{tot} of 4.3–4.4 mm day⁻¹ also exceeded the value of 1.5–1.9 and 1.9–2.4 mm day⁻¹ obtained by lysimeter measurements for treeline associated dwarf shrub communities (Guggenberger 1980; Kronfuss 1977) and grasslands (Wieser 1983; Wieser et al. 2008) within the treeline ecotone of the Central Tyrolean Alps by 40–56%.

The considerably higher T_c and ET_{tot} water vapour losses observed in *A. alnobetula* as compared to *Pinus cembra* trees and low stature vegetation result from three facts: (1) strong winds to which *A. alnobetula* stands and isolated *Pinus cembra* trees above the forest limit are particularly exposed considerably increases transpiration of *A. alnobetula*, while water loss of *Pinus cembra* tends to decline with increasing wind velocity (Tranquillini 1969); (2) in contrast the water saving strategy of *Pinus cembra* (Wieser et al. 2014) and herbaceous plants (Körner and Mayr 1981) anisohydric *A. alnobetula* displays no midday depression in water loss due to stomatal narrowing with respect to increasing evaporative demand (Fig. 5), and (3) compared to low stature vegetation up to 350 cm tall *A. alnobetula* stands are better coupled to the atmosphere (Jarvis and McNaughton 1986; Berbigier et al. 1991) which favours the water vapour transfer from the foliage to the free atmosphere due to an enhancement of the leaf boundary layer conductance. These findings strongly suggest that further shrub encroachment at high altitude may be expected to cause a substantial increase in water vapour loss and hence also create a considerable reduction of total runoff, and reduced fresh water transport to regions further downslope (Viviroli et al. 2007).

Nevertheless, in our study we did not take into account vegetation type specific differences in rainfall interception (i.e. the difference between above- and below canopy precipitation). In a subalpine *A. alnobetula* stand in the Central Austrian Alps at 1800 m a.s.l. interception approached 11% of total growing season P (Körner et al. 1978b), which is considerably below the value of about 18% reported for treeline associated open forest stands (Aulitzky et al. 1982; Matyssek et al. 2009) but within the range of 7–12%

reported for grassland ecosystems with in the treeline ecotone of the Austrian Alps (Wieser 1983; Körner et al. 1980; Wieser et al. 2018). Yet, although independent of land cover type, the quantity of interception losses strongly depends on leaf area and rainfall intensity (Wieser 1983; Aulitzky et al. 1982), differences in rainfall interception with respect to vegetation type may be neglected within the treeline ecotone (c.f. also Van der Bergh et al. 2018).

Conclusions

In conclusion, our results support our hypothesis that evapotranspiration of *A. alnobetula* stands exceeds those from dwarf shrub communities, grasslands and isolated *Pinus cembra* trees within the treeline ecotone of the Central Tyrolean Alps. Moreover, our measurements suggest that *A. alnobetula* is well adapted to cope with low soil water availability and high evaporative demand within the treeline ecotone, probably due to an increase in axial parenchyma due to limited soil water availability (Gruber et al. 2024) confirming the role of xylem parenchyma with respect to water relations. The observation that within the treeline ecotone on Mt. Patscherkofel ground surface area scaled evapotranspiration of *A. alnobetula* stands is noticeably higher than the water use of adjacent low-stature vegetation and insulated trees should hence be taken into account when forecasting potential effects of climate and land use change on the water balance of the treeline ecotone at high altitude (Van der Berg et al. 2018) and latitude (Black et al. 2021). Although *A. alnobetula* is well adapted to cope with top soil water deficit, further research should also focus on root distribution and identification of water sources used for evapotranspiration (c.f. also Wieser et al. 2018 and further references therein). Finally, it should also be taken into account that future shrub encroachment may reduce biodiversity, inhibit tree seedling establishment, enhance the risk of landslides and limit avalanche protection (Tasser et al. 2003; Bühlmann et al. 2014; Caviezel et al. 2017).

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Declarations

Conflict of interest The authors declare no competing interests.

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