Water stress limits transpiration and growth of European larch up to the lower subalpine belt in an inner-alpine dry valley

Nikolaus Obojes1, Armin Meurer2, Christian Newesely3, Erich Tasser1, Walter Oberhuber4, Stefan Mayr4 and Ulrike Tappeiner4

1Eurac Research, Viale Druso 1, Bolzano 39100, Italy; 2Institute of Forest Botany and Forest Zoology, Technische Universität Dresden, Dresden 01062, Germany; 3Department of Ecology, University of Innsbruck, Sternwartestrasse 15, Innsbruck 6020, Austria; 4Department of Botany, University of Innsbruck, Sternwartestrasse 15, Innsbruck 6020, Austria

Author for correspondence:
Nikolaus Obojes
Tel: +39 0471 055 306
Email: nikolaus.obojes@eurac.edu

Received: 21 February 2018
Accepted: 2 June 2018

New Phytologist (2018) 220: 460–475
doi: 10.1111/nph.15348

Key words: climate change, dendrometer, elevation transect, radial stem variations, sap flow, tree ring width, tree water status.

Summary

• Climate change will further constrain water availability in dry inner-alpine environments and affect water relations and growth conditions in mountain forests, including the widespread larch forests.
• To estimate the effects of climate conditions on water balance and growth, variation in sap flow and stem radius of European larch was measured for 3 yr along an elevation transect from 1070 to 2250 m above sea level (asl) in an inner-alpine dry valley in South Tyrol/Italy. Additionally, long-term climate–growth relations were derived from tree cores.
• Sap flow and radial growth were reduced in dry periods up to an elevation of 1715 m, leading to maximum annual growth at 2000 m. In a wet year no growth difference between elevations was observed. Long-term tree ring data showed a positive growth response to precipitation up to 1715 m and to temperature only above 2000 m.
• Our results demonstrate that reduced water availability and higher atmospheric demand limit larch at low elevation within dry Alpine regions. This indicates a general upward shift of this species’ elevational amplitude upon climate change, and respective negative effects on future silvicultural use and ecosystem services at lower elevations in the European Alps.

Introduction

Forests are particularly sensitive to climate change because of the long life span of trees, which does not allow for rapid adaptation to environmental change (Lindner et al., 2010; APCC, 2014). Rising atmospheric carbon dioxide (CO2) concentrations, higher temperatures, and changes in precipitation influence the vegetation period, growth, health, and distribution of trees and increase threats such as pest outbreaks, fires, and droughts (EEA, 2012; IPCC, 2014). In recent decades, average temperatures in the Alps increased more rapidly than the global trend, while no general trend in precipitation was observed (Böhm et al., 2001; Beniston, 2005; Rebetez & Reinhard, 2007; Ciccarelli et al., 2008). Rising temperatures will extend the growing season, which might have positive effects on tree growth and forest development. However, higher temperatures will intensify drought stress because of a higher evaporative demand and more rain instead of snowfall will reduce the water supply of trees during the early growing season. In central Europe, this will be especially critical in dry inner-alpine regions (EEA, 2012; Elkin et al., 2013; Gobiet et al., 2014), and also cause changes in tree species composition (Zweifel et al., 2009; Falk et al., 2012; Zimmermann et al., 2013; Fisher et al., 2018).

European larch (Larix decidua Mill.) is one of the most important and valuable forest tree species in central Europe and was planted far beyond its natural abundance in the Alps, the Carpathians, and the Sudeten region (Falk et al., 2012). Often together with Pinus cembra (L.), it forms the forest line community in many regions in the Alps. European larch prefers a rather continental climate with mean annual temperatures up to 13.5°C, dry air with many sunny days, and a minimum yearly precipitation of 450 mm (Wolfslehner et al., 2011; Falk et al., 2012). It avoids nutrient-poor sands and waterlogged soils (Kölling & Zimmermann, 2007). Owing to their deciduous needle-leaves, larches have a shorter growing season to reach similar above-ground production rates as adjacent evergreen conifers. To this end, they have twofold greater photosynthetic rates enabled by higher nitrogen concentration in the foliage, higher specific leaf area owing to less investment in structural tissues, and a more carbon-efficient crown shape and canopy structure (Schulze et al., 1985; Matyssek, 1986; Gower & Richards, 1990).

Climate change is expected to reduce the suitable habitat for larch plantations in lowland Central Europe (Falk et al., 2012). In the Alps, however, larch may benefit from the higher vulnerability of Picea abies (L., Karst), the primary species in the upper montane and subalpine zone, to increased temperatures, drought,
wind fall, and pests (Schmidt, 2009; Wolfslehner et al., 2011; Ganthaler et al., 2014; Hartl-Meier et al., 2014). The present study focuses on the potential future limitation and/or potentials of European larch at alpine stands. We monitored growth and water balance of larch trees growing along an elevation gradient between 1060 and 2250 m above sea level (asl) at the long-term socioecological research (LTSER) site Matsch/Mazia in northern Italy. The site is located in an extremely dry inner-alpine valley and is thus well suited to study hydraulic limitations (Staffler & Karrer, 2001). The large elevation range of European larch in this region is partially a result of the natural substitution of Fagus sylvatica-dominated communities by larch forests (Staffler & Karrer, 2001; Vacik et al., 2010a). Additionally, the anthropogenic promotion of larch in traditional dual-use sylvipastoral systems (Fontana et al., 2014) and reforestation in the late 19th and the 20th century of previously cleared and pastured slopes (Staffler & Karrer, 2005; Vacik et al., 2010b) increased the abundance of larch at lower elevations. The variation in climatic conditions along the elevation gradient in an already dry region allows a ‘space-for-time’ approach (Becker et al., 2007; Körner, 2007b), where comparatively humid and cool conditions at higher elevations represent the present, while dry and warm conditions at lower elevations represent the likely future climate. At multiple sites along the elevation transect, we measured sap flow to monitor transpiration and stem radius fluctuations to determine both tree water status and radial growth. To add a long-term perspective, we also quantified radial growth trends in relation to climatic conditions during the last decades with stem core samples.

We expected growth limitation by cold temperatures at high elevations but overall increased growth rates in recent decades as a result of increasing temperatures. At medium elevations, we anticipated ideal conditions for larch, with optimal water supply and temperatures allowing high growth rates. At low elevations, the combination of low precipitation and high temperatures should lead to water deficits and respective stomata closure and sap flow reduction during dry periods, and thus to a decrease in growth.

Materials and Methods

Study area

This study was conducted at the LTSER platform ‘Matsch/Mazia’ (LTER_EU_IT_097) in the Vinschgau/Val Venosta region in the province of South Tyrol, Italy. Owing to the sheltering effect of surrounding mountains, the area is one of the driest in the Alps. Long-term radial growth was analyzed at five sites (S1100, S1200, S1700, S2000, S2200) located at elevations between 1060 and 2250 m, while sap-flow and dendrometer measurements were conducted between 2012 and 2014 at the three mid-elevation sites. Soil texture was sandy loam at the three lower sites and loam at the two highest site. Soils were rather shallow with depths of c. 30 cm, except for S1700 which had slightly deeper soil. While larch is the most abundant tree species above 1500 m, it is rather rare at lower elevations, which were reforested 50–100 yr ago mainly with Pinus nigra (Arn.) Trees from all size classes with a diameter at breast height larger than 20 cm were selected at each site (see Table 1).

Microclimate

Long-term average yearly precipitation for Matsch/Mazia (1570 m) is 528 mm, and average yearly temperature is 6.6°C (source: Hydrographic Office, Autonomous Province of South Tyrol). The lower parts of the valley are warmer and drier; at a nearby grassland elevational transect, lapse rates of 0.54 K per 100 m and 12 mm per 100 m for temperature and precipitation, respectively, were measured (Della Chiesa et al., 2014). The area has a continental alpine precipitation regime, characterized by low total annual precipitation with convective rainfall events in summer and cold winters with weak Atlantic frontal systems and little precipitation (Hydrographic Office, Autonomous Province of South Tyrol). Frequent dry northerly wind increases the evaporative demand (Vacik et al., 2010a).

From spring 2012, air temperature and humidity at a height of 1.5 m and soil water content (SWC using capacitance sensors (ECH2O by ONSET, Bourne, MA, USA) and soil-specific calibration) at depths of 5, 20 and 50 cm were measured at sites S1200, S1700 and S2000 (sensors and logger by ONSET). Averages of SWC from the tree depths were used for further analysis. To avoid the influence of forest canopy structure, precipitation and solar radiation were measured at a height of 2 m in open grassland sites at each elevation (sensors and logger by ONSET and Campbell Scientific, Logan, UT, USA). Vapor pressure deficit (VPD) was calculated from air temperature and humidity, and potential evapotranspiration (PET) was determined according to Allen et al. (1998). Minor data gaps were filled using the R-package missforest (Stehkoven & Bühlmann, 2012).

Long-term temperature and precipitation data dating back to 1857 were available from the climate station Marienberg/Monte Maria (1310 m), located 5 km from S1100 (Auer et al., 2007). Assuming a linear trend, annual mean temperature increased by 0.11°C per decade since the start of measurements in 1857, from an average 5.4°C (1861–1870) to 6.7°C (2001–2010). This rate increased to 0.41°C per decade recently (1981–2010). A slight decrease of precipitation by 3.2 mm per decade (1857–2015) was not statistically significant.

Sap flow

Sap flow was measured at breast height (1.3 m) at six trees per site with tissue heat balance (THB) sensors, described by Čermák et al. (2004). We used version P4.2 at S1200 and EMS51 at S1700 and S2000, both by EMS (Brno, Czech Republic). At S1200, at S2000 in 2012, and at S1700 in early 2013, we had two sensors per tree on the north and south sides of the trunk. As a result of technical problems, only one sensor on the north side of the trunk was installed during the rest of the measuring period at S1700 and S2000. In contrast to other methods (e.g. heat dissipation and the heat pulse method), THB sensors are independent of sap wood depth as the electrodes cover the whole sap wood and measurement is integrated over their complete length.
Table 1  Site and tree properties of the five measuring sites

| Site Location | Elevation belt | Aspect | Elevation (m asl) | Ratio of bark cover (%) | Elevation belt | Aspect | Elevation (m asl) | Ratio of bark cover (%) | Elevation belt | Aspect | Elevation (m asl) | Ratio of bark cover (%) | Elevation belt | Aspect | Elevation (m asl) | Ratio of bark cover (%) | Elevation belt | Aspect | Elevation (m asl) | Ratio of bark cover (%) |
|---------------|----------------|--------|------------------|------------------------|----------------|--------|------------------|------------------------|----------------|--------|------------------|------------------------|----------------|--------|------------------|------------------------|----------------|--------|------------------|------------------------|----------------|--------|------------------|------------------------|
| S1100 | N 46° 30’ 78” | 1070 | NWW | 46° 30’ | 1070 | 1070 | 1070 | 1070 | 1070 | 1070 | 1070 | 1070 | 1070 | 1070 | 1070 | 1070 | 1070 | 1070 | 1070 | 1070 | 1070 | 1070 | 1070 |
| S1200 | N 46° 30’ 66” | 1160 | NWW | 46° 30’ | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 |
| S1700 | N 46° 30’ 68” | 1160 | NWW | 46° 30’ | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 | 1160 |
| S2000 | N 46° 30’ 72” | 1260 | NWW | 46° 30’ | 1260 | 1260 | 1260 | 1260 | 1260 | 1260 | 1260 | 1260 | 1260 | 1260 | 1260 | 1260 | 1260 | 1260 | 1260 | 1260 | 1260 | 1260 | 1260 |
| S2200 | N 46° 30’ 88” | 1360 | NWW | 46° 30’ | 1360 | 1360 | 1360 | 1360 | 1360 | 1360 | 1360 | 1360 | 1360 | 1360 | 1360 | 1360 | 1360 | 1360 | 1360 | 1360 | 1360 | 1360 | 1360 |

Calculation of tree water deficit and radial growth from dendrometer records

Stem circumference variation was measured slightly above breast height (1.8 m) at four trees per site at a resolution of 1 mm and an interval of 10 min with DRL26 band-type dendrometers by EMS Brno. To reduce the influence of hygroscopic shrinking and swelling of the bark on dendrometer records (DMR) and to ensure close contact with the stem, the dead outermost layers of the bark (periderm) were removed (Zweifel & Hasler, 2001; Gruber et al., 2009). For further data processing, stem circumference was transformed to stem radius and hourly averages were calculated.

Irreversible growth- and reversible water status-related stem radius changes were determined according to Zweifel et al. (2005), with modifications by Ehrenberger et al. (2012), by attributing the measured stem radius variations to changes in stem growth and short-term daily fluctuations in water status. The growth line (GRO) was defined by a moving maximum of the current and previous dendrometer readings. Daily deviations from this GRO were considered a relative measure of drought-related tree water deficits (TWD). This assumes that radial stem growth is restricted to periods of stem water saturation, while stem radius variation below a previous stem radius maximum is induced by changing tree water status (Oberhuber et al., 2015a; Zweifel, 2016; Zweifel et al., 2016).

To simplify the comparison of yearly growth between sites and years, growth curves of each tree were modeled using Gompertz equations (Zeide, 1993; Kahm et al., 2010) with the R-package COFECHA (Kahm et al., 2010); the corresponding parameters maximum amplitude of growth (A), maximum growth rate (μ), start of growth (λ), and inflection point (Ip) were compared between sites and years.

Dendroecological techniques

To compare intra-annual growth measured with dendrometers to long-term growth trends, core samples of 0.5 cm diameter were taken in August 2014 at each site. Two cores of each tree were taken at breast height parallel to the slope to avoid sampling of reaction wood and growth irregularities. In the laboratory, the samples were mounted on a holder and the surface smoothed with a razor blade (Pilcher, 1990). Early-wood, late-wood, and total ring widths were measured with a resolution of 1 μm using a digital measuring table (LINTAB 4; Rinntech, Heidelberg, Germany) and the tree-ring program TSAP-Win (Rinntech, Heidelberg, Germany). Accurate dating was verified using the program COFECHA (Holmes, 1994), which identifies segments within each tree ring series that may have measurement errors or
erroneous cross-dating. To improve the climate signal, residual chronologies were calculated by removing low-frequency variability related to tree aging and forest stand development, by fitting a negative exponential curve or a linear regression line to the tree ring series and then applying a cubic smoothing spline with a frequency-response cutoff set at two-thirds of the length of each series with the program ARSTAN (Cook & Holmes, 1984). Dimensionless indices were formed by dividing the observed ring width value by the predicted ring width value. Residual chronologies were derived using ARMA models, with a robust mean value function applied to discount the effects of statistical outliers (Holmes, 1994). Because of its smaller dependence on tree age, basal area increment (BAI, calculated according to Biondi & Qeadan (2008) as $\text{BAI}_i = \pi R_i^2 - \pi R_{i-1}^2$, with $R_i$ the stem radius at the end and $R_{i-1}$ the stem radius at the beginning of the annual increment) is considered a better indicator for radial growth than tree ring width (Fritts, 1976; Schuster & Oberhuber, 2013a).

Upscaling

Current and future growth conditions of larch were scaled up to the Alpine and surrounding region based on the yearly climatic water deficit and a minimum yearly average temperature of $-2.5^\circ$C defining the lower temperature limit of larch (Körting, 2007). Climatic water deficit was defined as precipitation minus potential evaporation. The latter was calculated based on the Thornthwaite method (Thornthwaite & Mather, 1951; Begueria et al., 2007). Climatic water deficit was calculated based on the effects of statistical outliers (Holmes, 1994). Because of its smaller dependence on tree age, basal area increment (BAI, calculated according to Biondi & Qeadan (2008) as $\text{BAI}_i = \pi R_i^2 - \pi R_{i-1}^2$, with $R_i$ the stem radius at the end and $R_{i-1}$ the stem radius at the beginning of the annual increment) is considered a better indicator for radial growth than tree ring width (Fritts, 1976; Schuster & Oberhuber, 2013a).

Statistical analysis

We used daily values for intra-annual correlation analysis to reduce the size of the dataset and to avoid the problem of stem capacitance affecting correlations with climate conditions (Oren et al., 1998; Ewers et al., 1999; Luís et al., 2005; Matheny et al., 2015). Relations of site means of daily sums of sap flow, daily radius change (DRC), and daily maximum TWD vs climate parameters were calculated using general additive mixed models (GAMM), employing the R packages mgcv (Wood, 2006) and nlme (Pinheiro et al., 2017). We followed the protocol by Zuur et al. (2009) to account for autocorrelation of the data, heterogeneity of residuals, and nonlinear effects between explanatory and response variables. As explanatory variables, we used the daily sum of PET summarizing air temperature and humidity, radiation and wind speed and representing water demand as well as daily means of SWC and/or daily sums of precipitation describing water availability. In a second step we used VPD and radiation as explanatory variables instead of PET in addition to precipitation and SWC. Possible interactions with measuring sites as well as lag effects (1 and 3 d) in the relation between the explanatory and the response variable were tested and accounted for in case they improved the model. Sap flow was correlated with climatic conditions for the period when neither development nor coloring and cessation of larch needles reduced daily maxima at any site (Julian day (DOY) 150–250) (Zimmermann et al., 2000; Luis et al., 2005; Wieser & Leo, 2012). According to Deslauriers et al. (2007) we used only data from the main period of stem growth to estimate the effect of climatic conditions on daily growth rates. As main growth periods, we defined periods with continuously increasing DMR, high daily growth rates, and a minimum daily TWD close to 0, which differed between years and sites (Table 2). To estimate the influence of water demand (PET) and water supply (SWC, precipitation) on tree water statuses-related stem radius variations, we also set up models for DRC and TWD for late summer (DOY 225–275), when yearly stem growth was mostly completed.

Long-term climate–growth relations were tested with response functions using the packages dplyr (Bunn et al., 2016) and treeclim (Zang & Biondi, 2015) in R, a form of principal components regression, which accounts for the collinearity in monthly climate predictors (Fritts et al., 1971; Briffa & Cook, 1990). Static and moving response functions were used to correlate site master chronologies of residuals resulting from ARMA modelling of the ring series (Holmes, 1994) to monthly mean temperature and total precipitation at a statistical significance of $P<0.05$, using a bootstrap procedure with $N=1000$ (Zang & Biondi, 2015).

All statistical analyses were performed using R (R Core Team, 2016); data manipulation was facilitated using the packages plyr (Wickham, 2011) and zoo (Zeileis & Grothendieck, 2005). Figures were generated using ggplot2 (Wickham, 2009) and egg (Baptiste, 2017).

Results

Microclimate

Yearly mean temperatures from 2012 to 2014 were more than 1°C higher than the 30 yr (1981–2010) average at the Marienberg station (Fig. 1a). Below-average temperatures were only observed in winter 2013 and in July and August 2014. Precipitation corresponded to the long-term average in 2012 and 2013. By contrast, precipitation in 2014 was >100 mm higher than the

| Year | $\text{S}1200$ | $\text{S}1700$ | $\text{S}2000$ |
|------|--------------|--------------|--------------|
| 2012 | 155–175      | 155–190      | 175–200      |
| 2013 | 120–140      | 175–190      | 170–200      |
| 2014 | 120–190      | 165–190      | 165–190      |
long-term average, with c. 2.5 times more snowfall from December to March than in the previous 2 yr (see Supporting Information Table S1a,b) and a rainy July and August (Fig. 1f). Temperature (Fig. 1a) and VPD (Fig. 1b) decreased more (yearly average of 3.7°C in total and 0.67°C per 100 m elevation difference) between S1200 and S1700 than between S1700 and S2000 (1.1 K in total and 0.39 K per 100 m). Precipitation increased with elevation by 8–19 mm per 100 m between S1200 and S1700 and by 22–30 mm per 100 m between S1700 and S2000 (the lowest elevational trend occurred in 2014). Mean global radiation was lowest at S1700 (Fig. 1c) as a result of increased shading by surrounding mountains. As a consequence, PET was highest at S1200 and lowest at S1700 (Fig. 1d). SWC also increased with elevation, with a stronger increase from S1700 to S2000 (Fig. 1e). At S2000 and S1700, snowmelt in March to April led to high SWC at the start of the growing season. Growing season means of temperature, VPD, solar radiation, and PET were lower in 2014 than in the two previous years across all sites, while mean SWC and total precipitation were higher, mainly as a result of a cool and rainy July and August.

Sap flow, intra-annual radial growth, and TWD

Daily sums of sap flow (averaged per site) generally increased early during the growing season, reached a maximum in late May to early June and decreased rapidly again in early autumn. Compared with S1200 and S1700, sap flow started to increase c. 20 d and reached its maximum c. 10 d later at S2000 in 2014 (Fig. 2a; sap flow data for spring 2012 and 2013 are partly missing as a result of sensor/logger malfunction). Sap flow decreased rapidly at all sites around DOY 270–280, corresponding to a substantial decrease of air temperature in 2013 and to a 2 wk dry period in 2014. Single days with low values, related to rainy weather conditions, were observed at all sites and more frequently in 2014 than

Fig. 1 (a) Daily mean air temperature ($T_{air}$), (b) vapor pressure deficit (VPD), (c) daily sums of global radiation ($r_s$), (d) potential evapotranspiration (PET), (e) daily mean soil water content (SWC), and (f) accumulated daily precipitation sums ($P_{acc}$) at the study sites S1200, S1700 and S2000 for the years 2012–2014. (a, e) These panels include 30 yr averages (1980–2010, ±SD indicated by the gray area) from the nearby climate station Marienberg (1310 m). DOY, day of year.
in 2013. Maximum daily sums of sap flow were about the same at S1700 and S2000, but only half at S1200. While sap flow under fair-weather conditions stayed rather constant between DOY 170 and DOY 260 at all sites in 2014, it decreased strongly and lastingly after DOY 200 at S1200 and S1700 in 2013 and after DOY 170 at S1200 in 2012. At S2000, no lasting decrease in sap flow was observed.

Dendrometer records and the estimated GRO curves showed a stronger yearly growth at S2000 than at the two lower sites in 2012 and 2013 (Fig. 2b, c). Growth at S1200 and S1700 ceased well before DOY 200, and stem radius shrank for several days during dry periods in these two summers. Correspondingly, TWD increased to > 200 μm, starting as early as DOY 175 at S1200 and S1700 in 2012 and 2013 (Fig. 2d). Such high TWD was reached at S2000 only after DOY 250 in autumn 2013. By contrast, yearly growth in 2014 exceeded the level of S2000 at S1700 and reached it at S1200. Hardly any decrease of DMR was observed at any site in 2014 until after DOY 240 and, correspondingly, TWD increased to values higher than 100 μm only in late summer/autumn.

Fitting Gompertz equations to the GRO curves confirmed higher annual increments at S2000 than at S1200 and S1700 in 2012 and 2013, while they were almost equal in 2014 (Fig. 3a). Maximum growth rates were constantly high at S2000 and lowest at S1200, although mean values in 2012 and 2014 were twice as high as in 2013 and extremely inconsistent at S1700, with values as low as at S1200 in 2013 and > S2000 in 2000 (Fig. 3b). The start of growth and the inflection point of the growth curves were always clearly earliest at S1200 and similar at S1700 and S2000 (Fig. 3c,d).

---

**Fig. 2** (a) Site average (± SE) of the daily sum of sap flow per tree, (b) radial stem variation (daily mean DMR), (c) potential growth (daily maximum GRO), and (d) daily minimum tree water deficit (TWD) at the study sites S1200, S1700 and S2000 for the growing seasons 2012–2014. DOY, day of year.
The best statistical model relating sap flow to microclimate showed site-specific relationships of sap flow with PET and SWC (Table 3; Figs S1, S2). Sap flow increased strongly at low values of PET and SWC and levelled off at higher values; differences between sites were small for PET and larger for SWC. No significant correlation occurred between sap flow and SWC at S2000. During the growth period, the best models displayed nonsite-specific relationships of DRC and TWD with PET and precipitation with a 1 d time lag (Table 3). DRC decreased initially with PET but increased again at higher values and increased nonlinearly with precipitation (Fig. S1c,d). TWD increased linearly with PET and decreased with precipitation at low and high values, while increasing in between (Fig. S1e,f). For the late summer period with no growth and DRC and TWD only depending on tree water status, the relationship of DRC with PET showed a far smaller increase of DRC at high values of PET than in the growth period (Fig. S2a). The DRC–precipitation relationship was site-specific with the slope decreasing with elevation (Fig. S2b). TWD during late summer increased linearly and non-site-specifically with PET (Fig. S2c), decreased with precipitation (Fig. S2d) and decreased nonlinearly and site-specifically with SWC (Fig. S2e). Using VPD and solar radiation instead of PET to characterize water demand resulted in models with mostly slightly higher variance explained (higher adjusted $r^2$; Table S2; Figs S3, S4). Both VPD and radiation had significant influence on sap flow, DRC and TWD. Variance explained by the GAMM models was high for the sap flow and late summer models and substantially lower for the growth period models; autocorrelation was strongest for the TWD models.

**Long-term climate–growth relationship**

Mean ring width was highest at the S1200 and S2000 sites and lowest at S2200 and S1100, with generally high standard deviations (see Table 4). Mean sensitivity, an indicator of relative change between consecutive rings (Fritts, 1976), decreased with elevation from 0.51 at S1100 to 0.17 at S2000, but increased again to 0.34 at the forest line (S2200). First-order autocorrelation, describing the correlation of tree ring width with the previous year, was highest at S1200 and S1700. Rather high signal-to-noise ratios and expressed population signal values clearly above the commonly accepted threshold of 0.85 at all sites indicate strong, coherent stand-level climate signals (Cook et al., 1990; Speer, 2010).

The substantial increase of air temperatures, especially since 1980, caused different growth responses along the elevation transect (Fig. 4a–c). Basal area increment (BAI) was consistently low at S1100 since the 1920s, with comparatively high values in the more humid late 1970s. At S1200, growth rates decreased rapidly after extremely high initial values and were the second lowest of
Table 3 Results of generalized additive mixed models to relate sap flow, daily radius change (DRC), and tree water deficit (TWD) to potential evaporation (PET), precipitation (P), and soil water content (SWC)

| DOY   | Sap flow | DRC | TWD   |
|-------|----------|-----|-------|
| 150–250 (2013 + 2014 only) | Growth period (see Table 2) | 225–275 | Growth period (see Table 2) |
| N     | 561      | 278 | 458   |
| Adjusted $R^2$ | 0.87      | 0.37 | 0.60  |
| Phi   | 0.54     | 0.61 | 0.53  |

| Linear estimate | Smoother-edf | Sig. | P-value |
|-----------------|--------------|------|---------|
| Intercept       | 38.65        | < 0.001 |        |
| PET             | 4.18         | < 0.001 | 3.59   | < 0.001 |
| s(PET): S1200   | 5.31         | < 0.001 |       |
| s(PET): S1700   | 5.34         | < 0.001 |       |
| s(PET): S2000   | 4.79         | < 0.001 |       |
| P_lag1          | 3.82         | < 0.001 |       |
| P last 3        |              |       | -0.68  | < 0.001 |
| s(P_lag1): S1200|              |       | 1.74   | < 0.001 |
| s(P_lag1): S1700|              |       | 2.94   | < 0.001 |
| s(P_lag1): S2000|              |       | 1.58   | < 0.001 |
| s(SWC_lag1): S1200|             |       | 3.46   | < 0.001 |
| s(SWC_lag1): S1700|             |       | 4.85   | < 0.001 |
| s(SWC_lag1): S2000|             |       | 0.0001 | n.s.    |

DOY, time period included in the model; $N$, number of observations (measuring days); adj. $R^2$, variance explained; phi, a measure of autocorrelation. For linear relations the estimate of intercept and slope (‘linear-estimate’), for nonlinear smoothers the estimated degrees of freedom (describing the shape of the smoother, ‘smoother-edf’). are displayed. ‘_lag1’ following the climate variables indicates when using a 1 d lag period provided better results, ‘P last 3’ is the sum of precipitation of the current and the two previous days. In case site-specific relationships were found, the edf-value is given for each site.
all sites since the 1990s. At S1700, growth increased strongly from the 1960s until the 1990s, but decreased rapidly afterwards. Growth rate at S2000 was consistently high since the 1930s. After some fluctuations around a constant average from the 1900s to the 1960s, growth increased strongly at S2200 since the 1970s and was highest in the last 20 yr. Fig. 4(d) depicts the residual chronologies after removing long-term trends used for calculating climate–growth relations. Contrasting growth trends of S2000 and S2200 compared with the lower-elevation sites observed, especially in recent decades, indicate an opposing influence of climatic factors.

Response functions revealed that tree ring width was directly correlated with spring and early summer precipitation at the three lower elevation sites (Figs 5, S5). At S1100 and S1200, precipitation in January (snowfall) and in the previous late August and September also had a positive effect on radial growth. S1700 showed a positive T-response for May and the previous October and a negative one for the previous December. At the two higher-

Table 4 Chronology statistics of selected stands along an elevation gradient

| Site  | Trees a (n) | Age b (yr) | Mean ring width (µm) | MS c | Autocorr c | SNR c | EPS c | OIC c |
|-------|-------------|------------|----------------------|------|------------|-------|-------|-------|
| S1100 | 10/7        | 120.6 ± 3.6 | 1080 ± 930          | 0.51 | 0.14       | 21.87 | 0.96  | 0.84  |
| S1200 | 15/15       | 45.5 ± 3.0  | 2630 ± 1860         | 0.39 | 0.27       | 30.33 | 0.97  | 0.79  |
| S1700 | 15/15       | 109.1 ± 4.3 | 1480 ± 720          | 0.26 | 0.44       | 24.81 | 0.96  | 0.73  |
| S2000 | 15/13       | 74.2 ± 17.3 | 2190 ± 870          | 0.17 | 0.34       | 14.44 | 0.94  | 0.63  |
| S2200 | 10/7        | 92.4 ± 56.3 | 1350 ± 480          | 0.34 | 0.22       | 9.08  | 0.90  | 0.57  |

Trees, number of trees sampled/included in the site chronology; MS, mean sensitivity; Autocorr, first-order autocorrelation; SNR, signal-to-noise ratio; EPS, expressed population signal; OIC, overall interseries correlation. Age and mean ring width are site averages ± SD (for trees included in the site chronology).

aEach tree was cored twice at opposite sides and parallel to the contour line.
bCambial age at c. 1.3 m above ground.
cCalculated before prewhitening, that is, removing of serial autocorrelation.

Fig. 4 (a) Time course of mean annual air temperature (T), (b) total precipitation (P) at the Marienberg climate station (1310 m) and (c) site averages of basal area increment (BAI), (d) ring width index (RWI; describing the residual chronologies after removing long-term trends and used for calculating climate–growth relations) and (e) sampling depth n, at the five measuring sites from 1890 to 2013 (as trees were cored in summer 2014). Thin lines show yearly data; thick lines are 25 yr (for T, P and BAI) and 5 yr (for RWI) smoothers; gray areas in (a) and (b) display 95% confidence regions.
elevation sites, April temperature and, for S2000, also previous July 'temperature' were indirectly correlated with tree ring width, while current July and previous September temperatures had a positive influence at S2200. Precipitation had no significant influence on tree ring width at S2000 and S2200. A moving-response function revealed that the positive influence of the previous August and September precipitation, current May precipitation (S1100 and S1200) and June precipitation (S1200, S1700, and S2000), and the negative response on February and March precipitation (S2000 and S2200) were increasing in recent decades. By contrast, the positive growth response on January precipitation (S1100 and S1200), previous September temperature (at S2000 and S2200) and current May temperature (at S1700 and S2000) decreased recently (Fig. 5, S6).

Extremely warm and dry summers, such as in 1976 or 2003, influenced growth negatively at S1100, S1200 and S1700, while trees at the two higher elevations hardly reacted or even showed an increase of growth (S2200 in 1976). By contrast, colder and humid summers, such as in 1975, led to positive growth reactions at the three lower sites and a negative one at the forest line (Fig. 4; Table S3).

Estimation of current and future growth conditions of larch in the Alpine region

Upscaling the results of our transect sites to the Alpine range and its surroundings (Fig. 6) indicated good growing conditions for most of the Alps (except for some southern valley floors and lower areas in the southwest) and its northern foothills. The scenario with increased temperature and reduced precipitation displayed a major increase of areas with severe, drought-induced growth restrictions in most major valleys and lowlands in the Alpine range and its foothills. By contrast, at higher elevations in the central Alps, areas with favorable growth conditions will increase.

Discussion

By measuring sap flow, stem radius variation, and tree ring widths of larch along an elevation gradient, we covered climate conditions ranging from the dry edge of this species' distribution at low elevation to the rather cool and humid environment at the
forest line (Körner, 2007a,b; King et al., 2013). We expected growth limitations by water shortage at low elevation and by low temperatures at the forest line and near-optimal conditions in between. By contrast, we observed intra-annual and long-term growth limitations up to an elevation of 1700 m, while growth rates at 2000 m hardly responded to variations in temperature or precipitation. Remarkably, highest growth rates during the last 10 yr occurred at the forest line at 2300 m, which indicates an ongoing shift of favorable growth conditions to higher elevations in inner-alpine environments. With a geographic information system-based upscaling, we demonstrated that the elevation gradient mirrored future conditions of larger regions in and around the Alps. While areas with severe growth restrictions as a result of limited water availability (corresponding to our low-elevation sites) are currently restricted to some valleys within the Alps and their foothills, they will increase strongly by the end of the century. Increasing temperatures and decreasing precipitation (EEA, 2012; Elkin et al., 2013; APCC, 2014) will then cause increased drought stress.

Sap flow
European larch is considered an anisohydric tree species, which does not show restrictive stomata regulation (Anfodillo et al., 1998; Leo et al., 2014). It compensates for a short growing season (as a result of its deciduous needle leaves) by maintaining its photosynthetic activity also during drier conditions (Lévesque et al., 2013). Consequently, Anfodillo et al. (1998) observed a strong coupling of sap flow with VPD (i.e. evaporative demand) in larch and no reduction in sap flow during short summer droughts (i.e.
a minor reduction of water supply). Accordingly, at S2000, sap flow was strongly influenced by day-to-day weather conditions, but did not show any lasting reduction during summer. By contrast, we observed a reduction of sap flow when dry periods reduced (initially high) SWC substantially in the summer of 2012 and 2013 at S1200, but also at S1715 (i.e. upper montane/low subalpine belt; Fig. 2a). Leo et al. (2014) found a similar reduction of sap flow in larch in a rain exclusion experiment, where daily sap flow decreased by 25% in sheltered compared with control trees. The shelter prevented a refilling of soil water reservoirs after a long drought in April diminished the effects of snowmelt. In our study, drought-induced reductions in sap flow were only absent in 2014, which was a humid year with >100 mm more annual precipitation than the 30 yr average.

The observed saturation of the sap flow–PET and sap flow–VPD relationships (Figs S1, S3) corresponds to findings by Leo et al. (2014), Anfodillo et al. (1998), and Badalotti et al. (2000). While the relationship between sap flow and radiation is described as linear in the literature (Matyssek et al., 2010), we found saturation at a solar radiation of 15 (at S1200) to 25 MJ m–2 d–1 (at S2000), which is an effect of open stand structure (Larcher, 2003). Leo et al. (2014) found a stronger reaction of sap flow to radiation in unsheltered (and therefore less water-limited) conditions as we found the strongest response at our most humid site, S2000. The lack of a significant sap flow–SWC correlation at S2000 indicates sufficient water supply at high elevation, while sap flow at the two lower sites was limited by soil water availability. The different shape of the sap flow–SWC relationship at the two lower sites is a result of generally higher SWC and sap flow at S1700 compared with S1200.

Stem radius variations, TWDs, and intra-astral growth

Lower annual increments measured at S1200 and S1700 in 2012 and 2013 were mainly caused by an earlier termination of the growth period around DOY 190, while radial growth continued until c. DOY 225 at S2000 in 2012 and 2013 and at all sites in the more humid year 2014 (Fig. 2). The cessation of growth at S1200 and S1700 coincided with a reduction in SWC and sap flow and was followed by periods of further reduction in stem radius (DMR) and high TWD, which were interrupted by occasional rainfall. Together, this provides strong evidence for the dependence of radial growth on water availability at S1200 and S1700 (Bréda et al., 2006). Higher TWD values after DOY 240, which were also measured at S2000 in 2013 and 2014, did not affect either growth of the current year (the growing season was already finished) or growth of the following year. In larch, an early cessation of radial growth as a result of limited water availability has also been observed by Oberhuber et al. (2014) and, similarly, in P. abies and Pinus sylvestris (Pichler & Oberhuber, 2007; Levančič et al., 2009; Thabeet et al., 2009), while Moser et al. (2010) found hardly any effect of elevation on the end of the larch growing season under nonwater-limited conditions. Maximum growth rates at S2000 appeared to be less influenced by variations in temperature and precipitation than at S1200 and S1700 (Fig. 3b). The initial low growth rates in 2013, especially at S1700, were probably caused by low temperatures in May, while decreasing growth rates at S1200 and S1700 in June 2012 and 2013 were presumably a consequence of water limitation. Temperature appeared to be the main reason for growth patterns observed in the early growing season when water supply was adequate as a result of snowmelt and spring precipitation (Fig. 3c): warmer spring temperatures at S1200 led to a considerably earlier increase in growth rate, while spring temperatures and the start of radial growth at S1700 and S2000 were similar. Moser et al. (2010) found a delay of 3–4 d per 100 m elevation in the onset of radial growth in larch.

We observed no difference between sites in the correlations of daily stem radius changes (DRC) and TWD vs PET (or VPD and radiation) and precipitation during the growth period (Table 3; Figs S1c–f, S3d–i). The lack of elevational differences indicates a sufficient water supply during the main growing season at all study sites. By contrast, water limitations of various extent during late summer induced site-specific correlations of DRC–precipitation and TWD–SWC (Table 3; Figs S2, S4). The correlation of DRC and TWD to precipitation (mostly of previous days) shows the sensitive response of stem radius to rainfall events. The lack of a correlation of DRC–SWC, even during dry late summer, indicates a buffering of hydraulics by stem water reservoirs (Schulze et al., 1985; Oberhuber et al., 2015b) and/or uptake of water from deeper soil layers and cracks (Valentini et al., 1994; Brooks et al., 2010). Soil moisture in the uppermost soil layers thus may not sufficiently reflect the water supply of trees (Ören & Pataki, 2001; Zweifel et al., 2006). We found a decrease of DRC with PET (for most of the range of PET) and a linear decrease of DRC with VPD at all sites, similar to Oberhuber et al. (2014). The strong correlation of DRC as well as sap flow with PET and its principal driving force VPD indicates a close coupling of transpiration, sap flow, and diurnal stem shrinkage (Steppe et al., 2006). Decreasing TWD at high PET/VPD might be a critical adjustment considering increasing temperatures as a result of climate change.

Long-term effects of climatic conditions on tree growth

Long-term climate–growth relations from tree ring width series corresponded well to short-term sap flow and dendrometer records. They displayed a dependence of growth on precipitation up to an elevation of >1700 m and a decrease of yearly growth at low elevation with increasing temperatures in recent decades. Positive growth responses to precipitation, negative responses to temperature, and/or limited growth rates at lower elevation (1400 m) were also reported for larch, P. sylvestris, P. abies, and Abies alba in other dry alpine areas (Affolter et al., 2010; Eilmann & Rügili, 2012; King et al., 2013; Lévesque et al., 2013, 2016a; Schuster & Oberhuber, 2013a; Swidrak et al., 2013). While we observed positive temperature responses of larch growth only at our highest elevations (S2000 and S2200), they were also found below, providing sufficient water supply (e.g., see Hartl-Meier et al., 2014). In a multispecies overview for Europe, Babst et al. (2013) found negative temperature and positive precipitation correlations to be typical for lower elevations in inner-Alpine dry
valleys. They observed temperature responses above and precipitation responses below a threshold, decreasing from the forest line at 2250 m at 42°N to 1000 m at 49°N and further to sea level at 60°N. Accordingly, a precipitation response should be expected at elevations below 1500 m in our research area (latitude 46°N). However, we actually observed a precipitation response up to 1700 m and a temperature response only above 2000 m, which is an effect of the particularly dry climatic conditions at the study site.

Additional information provided by long-term tree ring records compared with high-resolution, but short-term dendrometer measurements, are the carry-over effects of late summer and autumn conditions on tree ring width of the following year (Lévesque et al., 2013; Schuster & Oberhuber, 2013b), the multi-year effects of extreme events, and long-term trends in growth and climate–growth relations. A growth reduction lasting several years (as observed after the dry summers of 2003 and 2004 at S1100, S1200, and S1700) was also found for larch by Eilmann & Rigling (2012) after the end of irrigation at a reforestation site in the Valais. Positive and increasing growth responses of high-elevation forests to rising temperatures, as observed at S2000 and S2200, are regularly found not only in larch, but also in P. abies, P. cembra, and Pinus uncinata (Carrer et al., 1998; Rolland et al., 1998; Frank & Esper, 2005; Carrer & Urbinati, 2006). As atmospheric CO₂ and N-fertilization effects and forest management effects do not explain the decadal fluctuations and regional patterns, Rolland et al. (1998) attributed the increase of radial growth in high-elevation forests to climate change. At low elevation, the increasing precipitation sensitivity of radial growth in recent decades might be caused by rising temperatures, although an increase of water competition in denser stands with larger trees should also be considered (Schuster & Oberhuber, 2013a). Regular outbreaks of Larch budmoth (Zeiraphera diniana) were found to reduce tree ring width and disturb climate–growth relations of larch (Weber, 1997; Esper et al., 2007; Baltensweiler et al., 2008; Büntgen et al., 2009; Battipaglia et al., 2014; Saulnier et al., 2017). Following the methods suggested by Büntgen et al. (2009) and Saulnier et al. (2017), we found evidence of larch budmoth outbreaks at S1700, S2000, and S2200 (in the years 1923, 1947, 1957, 1968, 1975 and 1984) but not at the lower-elevation sites; excluding those years did not improve climate–growth correlations.

Conclusion

Our data confirm that climate change leads to increasing growth rates of trees at elevations close to the forest line. In the densely populated and managed Alps, a possible expansion of larch to higher elevations will, however, depend not only on climatic conditions, but also on the further management or abandonment of alpine pastures and meadows (Tasser et al., 2017). Also, more competitive species such as P. abies might move upwards and invade larch–P. cembra forests (Wolfslehner et al., 2011). While growth limitations of larch upon drought were reported in the literature mostly based on long-term tree ring data, we could demonstrate short-term reductions of sap flow and found stem growth limitations up to the lower subalpine belt and thus at higher-than-expected elevations. With increasing temperatures and decreasing precipitation, these limitations will probably apply not only to inner alpine dry valleys, but also to a larger geographical range in the future. For forestry purposes, decreasing growth rates might limit the future forest-economical suitability of larch for large areas of the Alps. However, we also found that humid years, such as 2014, led to high growth rates even at low elevations, indicating that larch will still play an important role as a stabilizing tree species in mixed forests over the coming decades.

Acknowledgements

This research was financially supported by the Austrian Federal Ministry of Science, Research and Economy, with the HRSM-cooperation project KLIMAGRO. S.M., W.O. and U.T. are members of the research focus ‘Alpine Space—Man and Environment’ at the University of Innsbruck. Open Access publication costs were covered by the Department of Innovation, Research and University of the Autonomous Province of Bozen/Bolzano. The LTSER platform Matsch/Mazia belongs to the national and international long-term ecological research networks (LTER-Italy, LTER Europe and ILTER).

Author contributions

N.O., C.N., E.T., W.O., S.M. and U.T. planned and designed the research. N.O. and A.M. conducted field measurements and data analysis, E.T. and N.O. performed the upscaling. N.O. wrote the manuscript. C.N., E.T., W.O., S.M. and U.T. edited the manuscript.

ORCID

Nikolaus Obojes http://orcid.org/0000-0002-6718-2756

References

Affolter P, Büntgen U, Esper J, Rigling A, Weber P, Luterbacher J, Frank D. 2010. Inner Alpine conifer response to 20th century drought swings. European Journal of Forest Research 129: 289–298.
Allen RG, Pereira LS, Raes D, Smith M. 1998. Crop evapotranspiration – guidelines for computing crop water requirements – FAO Irrigation and drainage paper 56. Rome, Italy: FAO – Food and Agriculture Organization of the United Nations.
Anfodillo T, Rento S, Carraro V, Furlanetto L, Urbinati C, Carrer M, Anfodillo T. 1998. Tree water relations and climatic variations at the alpine timberline: seasonal changes of sap flux and xylem water potential in Larix decidua Miller, Picea abies (L.) Karst. and Pinus cembra L. Annals of Forest Science 55: 159–172.
APCC. 2014. Österreichischer Sachstandsbericht Klimawandel 2014 (AARI4). Austrian Panel on Climate Change (APCC), ed. Vienna, Austria: Verlag der Österreichischen Akademie der Wissenschaften.
Auer I, Böhml R, Jurkovic A, Lipa W, Orlik A, Potzmann R, Schönö W, Ungersböck M, Matulla C, Brißk k et al. 2007. HISTALP—historical instrumental climatological surface time series of the Greater Alpine Region. International Journal of Climatology 27: 17–46.

New Phytologist (2018) 220: 460–475
www.newphytologist.com
Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Regression lines and smoothers for the general additive mixed models between sap flow, daily radius change as well as tree water deficits and potential evaporation as well as water availability expressed by precipitation and/or soil water content.

Fig. S2 Regression lines and smoothers for the late summer period (DOY 225–275) for the general additive mixed models between daily radius change as well as tree water deficits and potential evaporation as well as water availability expressed by precipitation and/or soil water content.

Fig. S3 Regression lines and smoothers for the general additive mixed models between sap flow, daily radius change as well as tree water deficits and vapor pressure deficit, global radiation, precipitation, and soil water content.

Fig. S4 Regression lines and smoothers for the general additive mixed models between daily radius change as well as tree water deficits and vapor pressure deficit, global radiation, precipitation, and soil water content for the late summer period (DOY 225–275).

Fig. S5 Static response function analysis between residual chronologies and monthly mean temperature and total precipitation.

Fig. S6 Moving 25 yr response function analysis between residual chronologies and monthly mean temperature and total precipitation.

Table S1 Precipitation and snow cover for the three winter seasons preceding the sap flow/dendrometer measuring seasons as well as long-term (1980–2010) averages; winter precipitation (November to March) for 2011/2012, 2012/2013, and 2013/2014 as well as long-term (1980–2010) averages and standard deviation at the climate station Marienberg/Monte Maria

Table S2 Results of generalized additive mixed models to relate sap flow, daily radius change, and tree water deficits to vapor pressure deficit, global radiation, precipitation, and soil water content.

Table S3 Growth reactions of trees to selected pointer years

Please note: Wiley Blackwell are not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the New Phytologist Central Office.