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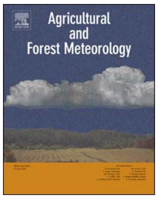

Long-term trends in leaf level gas exchange mirror tree-ring derived intrinsic water-use efficiency of *Pinus cembra* at treeline during the last century

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Dedicated to our teacher and colleague Prof. W. Tranquillini, who passed away in September 2016.

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ABSTRACT

The ability of treeline conifers in the Central European Alps to cope with recent climate warming and increasing CO_2 concentration is still poorly understood. We determined basal area increment (BAI) and tree ring stable carbon isotope ratios ($\delta^{13}C$) of *Pinus cembra* trees from 1925 through 2013. Stable isotope ratios and BAI were compared with leaf level gas exchange measurements carried out *in situ* between 1934 and 2012, and thus, provided new insights into long-term trends of tree-ring derived intrinsic water-use efficiency (iWUE). Mature *P. cembra* trees at treeline responded to increasing C_a and air temperature with a parallel increase in maximum net CO_2 uptake rate at ambient CO_2 ($A_{\max}$) and tree-ring-derived intercellular CO_2 partial pressure (C_i). $A_{\max}$ tripled and was positively correlated to BAI and C_i. The latter increased in parallel with ambient CO_2 concentration and stomatal conductance. In contrast to the instantaneous gas exchange parameters, $\delta^{13}C$ derived iWUE informs about the long-term changes in the carbon water relations. These data showed three changes in the iWUE chronosequences, which could be identified with different long term gas exchange patterns: (1) from stomatal controlled functioning from 1925 to 1981, to a situation where (2) both net CO_2 fixation (A) and leaf conductance for water vapour (g_w), responded to the environment from 1982 to 1997, and (3) back to a stomata controlled pattern over iWUE from 1998 onwards. This temporal pattern was also mirrored in leaf level gas exchange assessments, suggesting a parallel increase of A and g_w of *P. cembra* at treeline during the last nine decades.

1. Introduction

People have raised concern about treeline associated forest ecosystems, as they may undergo significant alterations due to increasing atmospheric CO_2 concentrations and climate warming (Holtmeier and Broll, 2007; Wieser et al., 2009). Warming experiments and free-air CO_2 enrichment carried out at treeline in the Austrian and Swiss Alps indicate that ecosystem warming (Wieser et al., 2015) and increasing atmospheric CO_2 concentrations (Dawes et al., 2013; Streit et al., 2014) increased net CO_2 uptake rate of pine and larch. Transpiration (E) and leaf conductance to water vapour (g_w) were insensitive to changes in CO_2 concentration (Streit et al., 2014), while ecosystem warming increased g_w and hence also E in *Pinus cembra* at treeline (Wieser et al., 2015) in the Swiss and Austrian Alps, respectively, and in conifers in boreal forest ecosystems (Bergh and Linder, 1999; Kellomäki and Wang, 1998; Marchin et al., 2016; Van Herk et al., 2011).

At time scales of decades and longer, environmental parameters (temperature, air humidity, water availability, and ambient CO_2) also influence net CO_2 uptake rate, which is reflected in the carbon isotope ratio ($\delta 13C$) of wood in tree rings (Churakova et al., 2016). $\delta 13C$ in plant organic matter is related to the ratio between net CO_2 fixation (A) versus leaf conductance for water vapour (g_w), which is defined as the intrinsic water-use efficiency (iWUE = A/g_w), independent of VPD. Therefore, iWUE is not identical to the instantaneous WUE of photosynthesis (pWUE = A/E), which is the ratio A to E. In addition to g_w, pWUE depends also on evaporative demand, as E is determined by the product of g_w and leaf to air vapour pressure deficit (LAVPD = $e_i - e_a$; where e_i and e_a stand for the intercellular and the ambient vapour pressure respectively), or more precisely Δw, i.e. pressure corrected LAVPD. In contrast iWUE does not consider the evaporative demand

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but only accounts for the internal (C_i) versus the ambient (C_a) CO_2 concentration ratio (C_i/C_a). Furthermore iWUE is an integrative measure representing the carbon water relation for the whole vegetation period, including periods with high and very low assimilation rates, at low light, low temperature and dry conditions. This distinction is important, because the two parameters cover different time scales: iWUE (A/g_w) can be traced back for as many tree rings as analyzed (centuries), while pWUE (A/E), yields instantaneous information (Cernusak et al., 2013; and further references therein). This discrepancy between the isotope (Saurer et al., 2014) and instantaneous gas exchange approach is a clear result of the different time scales, as the isotopic iWUE integrates low light, low temperature and dry conditions over the whole vegetation period, whereas gas exchange derived pWUE predominantly reflects optimal conditions (near light saturation, temperatures in the range of the plants optimum photosynthetic rate and usually sufficient water supply).

The aim of this paper is to compare long-term trends in leaf-level gas exchange with tree-ring width, stable carbon isotope ratios ($\delta^{13}C$) extracted from tree-rings, and $\delta^{13}C$ derived iWUE of *P. cembra* trees growing at the treeline in the Central Tyrolean Alps, and its response to environmental changes over the past 89 years (1925–2013). As precipitation during the growing season is abundant and occurs every third to fourth day on average in this region (Wieser, 2012) soil water availability can be ruled out as a limiting factor (Matyssek et al., 2009; Mayr, 2007; Tranquillini 1979), thereby leaving other environmental influences such as temperature to be the predominant control for tree growth (Oberhuber et al., 2008). The results are expected to contribute to an increased understanding and appreciation of the importance of instantaneous gas exchange measurements and environmental conditions for the interpretation of iWUE inferred from $\delta^{13}C$ in high mountain regions where soil water limitation is absent.

2. Material and methods

2.1. Study site and climate data

The study site is located at 2000 m a.s.l on Mt. Patscherkofel (47°12′37′ N, 11°27′07′ E), south of Innsbruck, Austria at the lower edge of the treeline ecotone. According to the World Base for Soil resources (FAO 2006), the soil at the study site is a haplic podzol, a typical soil type of the treeline ecotone in the Central Tyrolean Alps formed on gneisses and schist (Neuwinger, 1972). The water holding capacity of the top soil (to 65 cm depth) at saturation (−0.001 MPa) averages 0.60 $m^3\ m^{-3}$.

The study site is characterized by a cool subalpine climate with the possibility of frost during the whole year, and a continuous snow cover from October until May. Environmental parameters for the period 1963–2010 were obtained from a weather station nearby (Klimahaus Research Station and Alpengarten; 1950 m a.s.l., approx. distance 300 m). During this period (1963–2010) mean annual air temperature (T_{air}) was 2.4 °C, mean annual relative humidity (RH) was 77%, and the mean annual precipitation (P) was 864 mm, with the majority falling during the growing season (May throughout October). Due to ample P throughout the growing season, soil water potential seldom dropped below −0.01 MPa, (≈ soil water contents above 0.35 $m^3\ m^{-3}$), including the hot and dry summer of 2003 (Wieser, 2012).

A longer climate data series for the Mt. Patscherkofel region reaching back to 1866 (Böhm et al., 2001) is available from the Austrian Zentralanstalt für Meteorologie und Geodynamik (ZAMG) climate station in Innsbruck (582 m a.s.l.) approximately 6 km north-west from the field site. Climate data from Innsbruck were highly correlated with those from our treeline site. Within the overlapping time interval (1963–2010) mean annual total P was without any significant difference ($y = 0.995x$; $r^2 = 0.71$ $P < 0.001$) between the treeline site (864 mm) and Innsbruck (867 mm). Mean annual T_{air} decreased with elevation ($y = 0.97\,x - 7.1$, $r^2 = 0.77$, $P < 0.001$), according to a temperature laps rate of 0.55 K per 100 m of elevation. Our estimated laps rate of 0.55 K per 100 m of elevation matches the mean year round laps rate of 0.55 K per 100 published for the European Alps (Baumgartner, 1980; Franz 1979). Mean annual RH was at average 8% higher at treeline (77%) as compared to the Innsbruck station (69%). Given such agreement, the existing time series (1962–2011) of P, T_{air}, and RH was extended to the early end to 1925 and at the recent end to 2013 through linear regressions with the database from the Innsbruck climate station.

In this study we focus on *P. cembra* L., which is the dominant and widespread tree species at treeline in the Central Eastern Alps and accounts for 84% of the tree population within the study area at Mt. Patscherkofel. *Larix decidua* Mill. (9%) and *Picea abies* L. Karst (7%) are scattered at some locations. The trees grow either as isolated trees or in groups of four to five.

2.2. Sampling and dendrochronological procedure

We used dendrochronological methods to assess changes in stem radial growth. In fall 2013 we sampled 10 dominant *P. cembra* trees. The distance between solitary trees and between groups is 20–30 m. In 2013 the selected study trees were 125 ± 4 years old, and their stem diameter at breast height (DBH) averaged 37 ± 3.2 cm. The stem height averaged 12 ± 1.3 m. Two sample cores per tree (S and W exposure) were extracted with a 5-mm-diameter increment borer at breast height. In the laboratory the cores were non-permanently mounted on a holder, dried for contrast enhancement of tree ring boundaries, and the surface was prepared with a razor blade (Pilcher, 1990). Using a reflecting microscope (Olympus SZ61) and the software package TSAP WIN Scientific, ring widths were measured to the nearest 1 µm. For each sample tree the ring widths of both cores were averaged, and residual chronologies were calculated using the ARSTAN software (Cook, 1987; Holmes, 1994) through estimation of the Expressed Population Signal (EPS; Wigley et al., 1984).

To overcome the problem that ring width decreases with tree maturation, ring width was converted to basal stem area increment (BAI) according to:

$$BAI = 3.14\ (R_n^{\ 2} - R_{n\text{-}1}^2) \tag{1}$$

where R is stem radius inside tree bark and n is the year of tree ring formation (Fritts, 1976). Finally BAI of each year were averaged over the ten sample trees.

2.3. Stable isotope analysis, ^{13}C discrimination, and intrinsic water-use efficiency

For carbon isotope analysis we selected these six trees out of the 10 trees used for BAI estimation, which had the strongest correlation to the site-specific tree-ring chronology, no missing rings, and regular ring boundaries. We performed the $\delta^{13}C$ analyses on the same cores as used for BAI assessment, and only sampled the most recent 89 years (1925–2013) of ring formation in order to avoid juvenile age effects on the tree ring isotope signatures (Heaton, 1999; but see McDowel et al., 2011). Annual rings (early wood plus late wood) were cut from each core at the ring boundaries using a scalpel and a reflecting microscope (Wild 308700). In *P. cembra* $\delta^{13}C$ signatures of bulk wood and cellulose have been shown to yield highly correlated signals, and on average $\delta^{13}C$ in bulk wood was lower by 1.0‰ than in cellulose (Wieser et al., 2016). Therefore, due to the ease of processing, we used bulk wood samples for our $\delta^{13}C$ analysis.

For analyzing $\delta^{13}C$, 2.0 ± 0.02 mg of homogenized samples were packed into tin capsules (3.5 × 5 mm, IVA Analysentechnik e. K., Meerbush, Germany) and combusted to CO_2 in an elemental analyzer (Eurovector EA3000) connected to an isotope ratio mass spectrometer (Isoprime, Elementar, Hanau, Germany). The isotope abundance was