The pathway of oxygen isotopes from soil to wood (Lötschental, Swiss Alps)

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Introduction

Oxygen isotopes in tree rings are seen as a powerful tool for the reconstruction of past atmospheric conditions such as the isotopic composition of precipitation (Danis et al. 2006; Saurer, Borella & Leuenberger 1997b; Robertson et al. 2001; Anderson et al. 1998), air temperature (Libby et al. 1976; Rebetez, Saurer & Cerubini 2003; Saurer, Cherubini & Siegwolf 2000; Burk & Stuiver 1981; Edwards et al. 2008), precipitation amount (Masson-Delmotte et al. 2005; Treydte et al. 2006, 2007; Reynolds-Henne et al. 2007; Saurer et al. 2008), relative air humidity (Saurer et al. 1997b; Robertson et al. 2001; Ramesh, Bhattacharya & Gopalan 1986; Edwards et al. 2008), or even atmospheric circulation patterns (Miller et al. 2006; Roden & Ehleringer 2007; Welker, Rayback & Henry 2005).

Although the direction of the trees' response to these variables may be robust among species, sites and regions (Treydte et al. 2007; Saurer et al. 2008), uncertainties still exist regarding the spatial and temporal stability of the climate signal (Treydte et al. 2007; Reynolds-Henne et al. 2007). These uncertainties arise from the complex interplay between signals carried in the source water taken up by the roots and those produced by evaporative enrichment and (post-) photosynthetic processes at the leaf level and during downstream metabolism. Therefore, a deeper understanding of the contribution of all potential fractionation and exchange steps occurring on the way through the tree into the tree-ring is a prerequisite for a reliable interpretation of this environmental proxy.

With this study we aim to follow the complete pathway of oxygen isotopes from precipitation to the tree ring over the growing season under varying environmental conditions. We present weekly resolved records of xylem and needle water, phloem sugars and stem wood $\delta^{18}O$ of *Larix decidua* Mill. growing at two different altitudes in the Loetschental/Swiss Alps. These data are related to external variables such as precipitation and soil water $\delta^{18}O$, temperature, relative air humidity and vapour pressure deficit. By following the complete pathway of oxygen isotopes from precipitation to the tree ring over the growing season under varying environmental conditions, we find the source (soil) water $\delta^{18}O$ to be the main controlling factor for tree ring $\delta^{18}O$.

Material and Methods

Our study region is the Loetschental, an inner-alpine dry valley in the Swiss Alps where two sites are located, one at the upper tree line (2100m asl, 46°23'58N, 7°44'34E, SSE) of a south-facing slope and the other at the valley bottom on a rocky hill (1350m asl, 46°23'29N, 7°45'38E, NNW). Hydrological conditions are generally dryer at the valley site which receives less precipitation and thus has lower soil moisture conditions than the upper site. Soil types are similar at both sites with about 60cm depth from the surface to the bedrock and were classified as podzolic cambisols.

At both sites we selected four larch (*Larix decidua*) trees growing in open stands, so that every individual was directly exposed to sun. Development of phenological stages over the vegetation period was recorded by observing bud break, needle maturing, yellowing and fall. Sampling took place weekly from 7 April 2008 (week 15) until 11 November 2008 (week 46) and also diurnally at three sampling dates (Boda et al. 2009). To obtain samples of xylem water, needle water and phloem sugars, we cut three twigs per tree at different heights of the sun exposed crown and separated them into needles, bark and wood. Needle and xylem water was gained by cryogenic vacuum extraction at the Paul Scherrer Insitut (Ehleringer et al. 2000). Phloem sugars were extracted by successive pipetting and drying the solution at 65°C in silver capsules (Boda et al. 2009).

At the end of the vegetation period, we took 10mm tree cores from all sampled trees at breast height to determine cell widths of the actual tree ring. Tree cores were cut into 20µm sections and assigned to the corresponding week of formation by applying a growth model (Gompertz function). This model was generated from the growth rate of four other trees at the same site, for which the amount of cell enlarging, wall thickening and mature cells was determined by taking micro cores on a weekly basis (Rossi, Deslauriers & Morin 2003).

Additionally precipitation (rain collectors) and soil water in 10cm and 60cm depth (tension lysimetry) was sampled weekly following standard procedures to minimize evaporation between sampling periods (Thimonier et al. 2005; O'Driscoll et al. 2005; Boda et al. 2009). Due to rather dry conditions at the lower site, relatively few water samples were collected.

Isotope measurements were carried out at the WSL (Soil and precipitation water; Delta V Advantage mass spectrometer, Gasbench II, Thermo-Finnigan), the PSI (xylem and needle water, wood; Delta Plus XP mass-spectrometer; Thermo-Conversion Elemental Analyser TC/EA, Thermo-Finnigan) and the University of Trier (phloem sugars; Delta V Advantage mass spectrometer, Thermo-Conversion Elemental Analyser TC/EA, Thermo-Finnigan). The overall analytical precision, estimated from periodic standard deviation of commercial standards was ±0.2‰ for water samples, ±0.3‰ for wood samples. All data is referenced to VSMOV and given in ‰ as deviation from the standard.

At both sites air temperature and relative humidity data at 15 minute resolution were measured in the stands using HOBO pro v2 sensors (U23-002) starting at the beginning of the 2008 growing season. For analysis of the seasonal cycle, weekly mean/maximum values were calculated.

Results

Seasonal patterns in δ^{18}O

There is a marked decrease in $\delta^{18}O_{xylem}$ at the beginning of the vegetation period, partly followed by $\delta^{18}O$needles and $\delta^{18}O$phloem. This pattern is surprising and contradicts the trend that would be expected by the influence of isotopically depleted snowmelt water (Robertson et al. 2001; Treydte et al. 2006). Since the water flow through the deciduous Larch trees should be interrupted in winter times, we hypothesize a coupled effect of water storage from previous autumn (Waring, Whitehead & Jarvis 1979; Brandes et al. 2007) and additional enrichment due to evaporation effects in the twigs (Dawson and Ehleringer 1993). This assumption is supported by phenological data, since needles mature and start with full stomatal transpiration roughly when source water and xylem signals become coupled again. Since we hypothesise that this trend is not related to the current year processes of interest, we excluded all early values, before the minimum, from our correlation analysis.
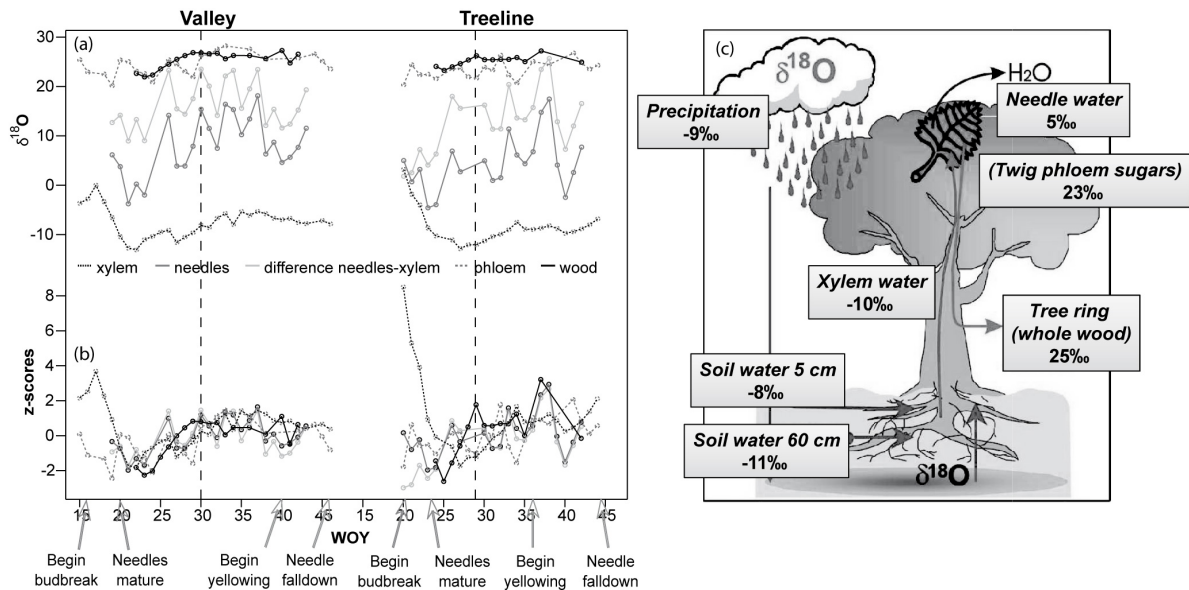
Figure 1: Seasonal $\delta^{18}O$ variations per site and parameter and distribution of mean values within the tree
a) Comparison of absolute values $\delta^{18}O_{xylem}$, $\delta^{18}O_{needles}$, the difference $\delta^{18}O_{xylem}$- $\delta^{18}O_{needles}$ and $\delta^{18}O_{tree-ring}$
b) Normalized data of the same parameters. Dotted lines represent the transition between early and latewood
c) Mean $\delta^{18}O$ of all tissues over the whole growth period 2008 (May-October) at the treeline (2100 m asl)

At the valley site, a mean inter-series correlation of r=0.58 (p<0.05) between the tree parameters points to a common signal contained, with highest dependency of needle water on xylem water variations (r=0.67, p<0.01). If the source water trend is removed from the needle water ($\Delta^{18}O_{needles}$), any accordance to the other tree internal parameters disappears, indicating little influence of the leaf water enrichment on phloem and tree-ring values. Normalized records (Fig. 1b) indicate that these correlations are mainly created by a common long-term trend rather than by short-term variations. At the treeline, such a common trend is less obvious. There, $\Delta^{18}O_{needles}$ shows even a negative correlation to $\delta^{18}O_{xylem}$ (r=-0.53, p<0,05), which seems to be induced by the strongly decreasing trend of $\delta^{18}O_{xylem}$ in the beginning of the vegetation period, coincidently with an increasing trend of needle water enrichment. The strong common signal at the valley site suggests a fast and continuous transfer, in contrast to more diffuse patterns at the treeline. A reason could be that low temperatures partly decelerate the tree metabolism and therefore lead to stronger but not uniform time lags. Figure 1c visualizes the change in the mean growing season $\delta^{18}O$ values along the whole $\delta^{18}O$ pathway for the tree-line, where also continuous records of soil water $\delta^{18}O$ are available.

Signal transfer

At our sites in the Loetschental, short-term $\delta^{18}O_{soil}$ variations are only partly explained by precipitation variations whereas both contain similar long-term trends, particularly in the first half of the growing season (Fig. 2a). This overall increase can easily be explained by a successive transition from snowmelt to liquid precipitation and increasing temperatures, which is metachronous between the two sites. Later in the season, soil water seems to show a delayed response, particularly to one negative $\delta^{18}O_{ppt}$ peak in week 34 at the tree-line, which also could result from a snowfall event that dominated the water sample of this week. With our sampling intervals, however, we were not able to appropriately estimate these time lags in more detail.
$\delta^{18}O_{xylem}$ consistently lies between the values of both soil layers, suggesting a predominant use of surface water under shallow soil conditions. Additionally, a certain residence time of xylem water in

the tracheids (Brandes et al. 2007), and the occurrence of considerable time shifts between water at the trunk basis and in the crown in coniferous species (2.5 - 21 days; Meinzer et al. 2006) can modify the absolute level of xylem values.

At the treeline, where soil water was available on approximately a weekly basis, $\delta^{18}O_{xylem}$ nicely follows seasonal trends in $\delta^{18}O_{soil}$ (Fig. 2a). Unfortunately, this clear dependency of xylem water on soil water variations at the treeline cannot be fully confirmed at the valley site, due to large gaps in the soil water records.

At both sites, needle water evaporative enrichment, with the xylem water trend eliminated, strongly reflects high and low frequency variations of meteorological variables (Fig. 2c), particularly relative air humidity (rH) and vapour pressure deficit (VPD). These effects can be easily explained by variations of the evaporative demand (Farquhar et al. 2007).
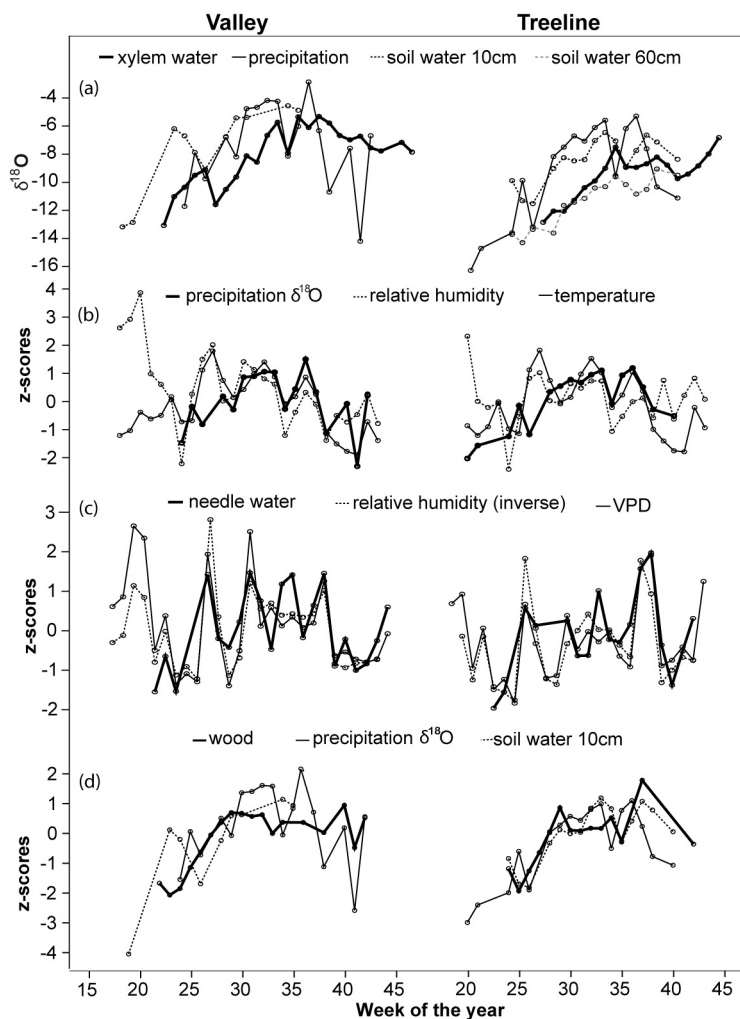

Figure 2: Seasonal $\delta^{18}O$ variations per site and parameter

Interestingly, daily maximum temperatures correlate with $\Delta^{18}O_{needles}$ at the valley site (r=0.65, p<0.01), but not at the tree-line. Only in the valley the soil water signal carried in the xylem is significantly fingerprinted in $\delta^{18}O_{needles}$ (r=0.60, p<0.01).

Unexpectedly, phloem sugars do not show any correlations to $\Delta^{18}O_{needles}$ despite strong seasonal variations at both sites. The mean offset between phloem sugars and xylem water of 31.7‰ (compared to 18.8‰ between phloem and needles) points to a substantial proportion of either twig assimilated sugars (Barnard et al. 2007) or a mixing of day sucrose with sugars from transitory

starch breakdown during night. At least in the valley, $\delta^{18}O_{phloem}$ correlates with $\delta^{18}O_{xylem}$, $\delta^{18}O_{needles}$ and $\delta^{18}O_{tree-ring}$.

$\delta^{18}O_{tree-ring}$ at the tree-line is predominantly controlled by $\delta^{18}O_{soil\_10}$, explaining 72% of the variance. Particularly the increasing trend in the first half of the vegetation period is well matched (Fig. 2d). The correlation to $\delta^{18}O_{ppt}$ is lower, although still significant, and of similar strength as at the valley site (valley: r=0.58, treeline: r=0.59; p<0.05). At the valley site $\delta^{18}O_{soil}$ is not significantly correlated with $\delta^{18}O_{tree-ring}$ because of the soil water data gaps. Whereas short-term variations are weakly reflected and seem to be damped, the seasonal trend, also kept in soil water $\delta^{18}O$, nevertheless is mirrored. Additionally, there are correlations with $\delta^{18}O_{xylem}$, $\delta^{18}O_{needles}$ and $\delta^{18}O_{phloem}$ at the valley site and with $\delta^{18}O_{needles}$ at the tree-line. Interestingly, at both sites, any correlations to external variables (rH, VPD and T) that were found to dominate the needle water variations are insignificant and did also not improve when splitting the records in early and late wood, and calculating the correlations to external variables for both periods separately.

The fact that $\Delta^{18}O_{needles}$ is not correlated to $\delta^{18}O_{tree-ring}$ means that seasonal source water variations clearly dominate over physiological processes at the leaf level. During wood synthesis, part of the oxygen atoms exchange with xylem water, reducing the influence of needle water enrichment and retrieving some of the source water signal. This exchange was reported to be about 42% for cellulose (Sternberg et al. 1986; Sternberg et al. 2003; Roden et al. 2000). Based on Barbour et al. (2007), we calculated an exchange of whole wood of 40% at the valley and 21% at the tree-line, the latter value being much lower than it would have been expected for cellulose. This could be related to a different proportion of oxygen atoms exposed to exchange with medium water in whole wood compared to cellulose. This points to a stronger contribution of downstream metabolic processes than at the treeline.

Overall, our findings indicate that $\delta^{18}O_{tree-ring}$ predominantly records the source water information, which partly relays on xylem water preserved in the needles and partly on a post-photosynthetic exchange with medium water. Needle water enrichment and fractionation effects during assimilate production seem to be of lower relevance for the isotope signal in the wood. Consequently, the strength of the atmospheric signal recorded in the source water is most crucial for the application of $\delta^{18}O_{tree-ring}$ for climate reconstruction. $\delta^{18}O_{soil}$ in the Loetschental reflects the precipitation trend at both sites, albeit damped and with a certain time lag. Therefore, $\delta^{18}O_{ppt}$ is indirectly represented in $\delta^{18}O_{tree-ring}$ by explaining at least 33% to 34% of the variance. Since roughly half of the seasonal variation in $\delta^{18}O_{ppt}$ itself is explained by local weekly maximum temperature (58% at the valley site, 46% at the tree-line), being in the range of results of longer-term, inter-annual studies in Switzerland (Rebetez et al. 2003), the lack of correlation between seasonal $\delta^{18}O_{tree-ring}$ and temperature could be enhanced again on inter-annual scales, considering the integrating character of the tree ring.

Conclusions

We investigated the seasonal pathway of oxygen isotopes from precipitation through several tree tissues into the tree ring at two altitudes in the Loetschental to estimate the influence of the source water and the stomatal signal under different ecological conditions.

Most interestingly variations in $\delta^{18}O_{tree-ring}$ at our sites are clearly dominated by the source water signal. This includes recent precipitation water and further water pools within the soil, from the beginning of cell development in spring. Although variations in needle water enrichment are strongly controlled by weather conditions during the whole growing period, they are not significantly fingerprinted in the tree ring and therefore are seen to be of low relevance in contributing to the overall tree ring $\delta^{18}O$ signal. This finding suggests low relevance of needle water enrichment and fractionation effects during assimilate production for wood synthesis.

The impact of plant physiological parameters seems to be independent of altitude and moisture conditions. However, we can state that cool conditions lead to a more diffuse short-term pattern of the oxygen isotope transfer within the tree, due to lower metabolism rate and resulting time lags in the response to meteorological and physiological impacts.

Overall, our findings have direct implications on future sampling strategies for climate reconstructions based on tree ring $\delta^{18}O$: They clearly suggest that the strongest climate signal should be recorded at sites, where soils are most frequently supplied with precipitation water during the growing period, namely in temperate regions under humid precipitation conditions with precipitation maximum in summer. This suggestion is supported by results from a European tree ring isotope network containing the strongest climate signal at temperate sites in the United Kingdom and Northern France (Treydte et al. 2007).

Acknowledgements

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