

## Measured and modelled source water $\delta^{18}\text{O}$ based on tree-ring cellulose of larch and pine trees from the permafrost zone

Olga V Churakova-Sidorova<sup>(1-2)</sup>,  
Sebastian Lienert<sup>(3-4)</sup>,  
Galina Timofeeva<sup>(2)</sup>,  
Rolf Siegwolf<sup>(2)</sup>,  
John Roden<sup>(5)</sup>,  
Fortunat Joos<sup>(3-4)</sup>,  
Matthias Saurer<sup>(2)</sup>

To identify source water for trees growing on permafrost in Siberia, we applied mechanistic models that quantify physical and biochemical fractionation processes, leading to oxygen isotope variation ( $\delta^{18}\text{O}$ ) in plant organic matter. These models allowed us to investigate the influence of a variety of climatic factors on tree-ring cellulose from two dominant species: *Larix cajanderi* Mayr. from northeastern Yakutia (69° 22' N, 148° 25' E, ~ 250 m a.s.l.) and *Pinus sylvestris* L. from Central Yakutia (62° 14' N, 129° 37' E, ~ 220 m a.s.l.). The climate of the region is highly continental with short growing seasons, low amount of precipitation and these forest ecosystems are growing on permafrost, which in turn impact the water cycle and climate variation in the  $\delta^{18}\text{O}$  of source water. We compared outputs of the Land surface Processes and eXchanges (LPX-Bern v. 1.3), and Roden-Lin-Ehleringer (RLE) models for the common period from 1945 to 2004. Based on our findings, trees from northeastern and central Yakutia may have access to additional thawed permafrost water during dry summer periods. Owing to differences in the soil structure, active thaw soil depth and root systems of trees at two Siberian sites, *Larix cajanderi* Mayr. trees can access water not more than from 50 cm depth, in contrast to *Pinus sylvestris* L. in Central Yakutia which can acquire water from up to 80 cm soil depth. The results enhance our understanding of the growth and survival of the trees in this extreme environment.

**Keywords:** Conifers, Climate, Drought, Permafrost Thaw Depth, Siberia,  $\delta^{18}\text{O}$  of Source Water

### Introduction

Modern climatic changes are leading to significant air temperature increase in the Eurasian subarctic at even faster rates compared to the global average (Overland et al. 2018, Fischer et al. 2018). Siberian forests respond to both the timing and magnitude of changes in soil moisture as well as to soil temperature, permafrost thickness and distribution, which is in turn affected by snow and vegetation cover, soil texture and geothermal heat flux as well as atmospheric dryness (Cable et al. 2014, Boike et al. 2013, Churakova-Sidorova et al. 2019, Kropp et al. 2019). Therefore, the fate of trees growing on permafrost undergoing climatic changes is of great interest, owing to the important role of permafrost in these ecosystems: (i) as additional water source (Sugimoto et al. 2002, Cable et al. 2014, Churakova-Sidorova et al. 2016a, Young-Robertson et al. 2017) for trees during droughts; and (ii) for the large amounts of carbon stored in these soils, which essentially contribute to the global carbon and water budget (Cable et al. 2014).

Increasing temperatures at higher latitudes, especially in areas with low precipitation inputs such as parts of Yakutia (200-250 mm year<sup>-1</sup>), enhance the risks of tree decline and mortality in boreal forests (Sidorova et al. 2010, Boike et al. 2013, Churakova-Sidorova et al. 2016a, Timofeeva 2017).

A number of studies report a pronounced increase of seasonal permafrost thaw depth in western Siberia (Sugimoto et al. 2002, Melnikov et al. 2004, Pavlov et al. 2004, Fyodorov-Davydov et al. 2008). Sugimoto et al. (2002) reported, that the active soil layer depth at the central Yakutia can reach up to 1.4 m making thawed permafrost water available for *Larix gmelinii* Rupr. Moreover, the authors demonstrated that during wet summers in central Yakutia *Larix gmelinii* Rupr. can use rain water, while thawed permafrost water can be used by trees mainly during drought summers. Fyodorov-Davydov et al. (2008) investigated the spatial and temporal trends in active soil layer for northern Yakutia and its relation to landscape and climate variables. The soil layer thaws during June-August and freezes again in autumn, defying the length of the short growing season. The few studies in Siberian regions show significant differences between sites in hydrological and geomorphological characteristics, which should be taken into account. To our knowledge, there are no direct seasonal or long-term measurements of the thawing depth of the active soil layer for northeastern Yakutia, which is the driest forested area in the world. Precipitation and thawed permafrost water are particularly crucial for trees growing in this region with severe temperature limitations and low amounts of precipitation (Arneeth

□ (1) Siberian Federal University, Krasnoyarsk, Svobodnyy pr 79, RU-660041 (Russia); (2) Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111 CH-8903 Birmensdorf (Switzerland); (3) University of Bern, Climate and Environmental Physics, University of Bern, Sidlerstr. 5, CH-3012 Bern (Switzerland); (4) Oeschger Centre for Climate Change Research, University of Bern, Falkenplatz 16, CH-3012 Bern (Switzerland); (5) Southern Oregon University, Biology Department, Ashland, OR 97520 (USA)

@ Olga V Churakova-Sidorova  
(ochurakova@sfu-kras.ru)

Received: Aug 07, 2019 - Accepted: Apr 24, 2020

**Citation:** Churakova-Sidorova OV, Lienert S, Timofeeva G, Siegwolf R, Roden J, Joos F, Saurer M (2020). Measured and modelled source water  $\delta^{18}\text{O}$  based on tree-ring cellulose of larch and pine trees from the permafrost zone. *iForest* 13: 224-229. - doi: 10.3832/ifor3212-013 [online 2020-06-19]

Communicated by: Rossella Guerrieri

et al. 2002, Sidorova et al. 2008, 2010).

Based on isotopic differences between precipitation and permafrost, variations of stable oxygen isotopes ( $\delta^{18}\text{O}$ ) may help to reveal water relations in deep-rooted plants (Saurer et al. 2016). Oxygen isotopes in plant organic matter are influenced by variations in the isotopic composition of the water source, which is closely related to the precipitation and soil water (after modification by evaporation at the soil surface and due to the shallow active layer depth).

In this study, we aim to determine the source water of *Larix cajanderi* Mayr. and *Pinus sylvestris* L. trees from the Siberian subarctic using measured and modeled  $\delta^{18}\text{O}$  variation in annual tree-ring cellulose at two contrasting study sites (northeastern and central Yakutia).

## Materials and Methods

### Study sites

Both study sites are located in the broad permafrost zone in northeastern Siberia: in northeastern Yakutia (NE – 69° 22' N, 148° 25' E, ~ 250 m a.s.l.) and Central Yakutia (CE – 62° 14' N, 129° 37' E, ~ 220 m a.s.l.) in Russia.

The mean winter temperatures (December-February) averaged for the period from 1948 to 2004 are -36 °C and -38 °C and in summer (June-July) +12 °C and +19 °C for NE and CE, respectively. However, minimum temperature range during winter can vary between -38 °C and -46 °C, while maximum day time summer temperatures range from +27 °C to +42 °C. *Larix cajanderi* Mayr. and *Pinus sylvestris* L. trees are the dominant tree species in NE and CE respectively. The growing period is rather short for trees at both sites and lasts around 60 days (Abaimov et al. 1997).

Low precipitation inputs are typical for both regions (200-250 mm year<sup>-1</sup>) and most of the precipitation falls in summer. The main difference between the two sites are soil conditions. *Larix cajanderi* Mayr. trees in NE are mainly growing on stones, rocks and mixtures of clay (Sidorova et al. 2008), while *Pinus sylvestris* L. in CE are growing on mixtures of sand and clay soils (Nikolaev 2003). The root system is also different between these species as they adapt to site-specific edaphic conditions. *Larix cajanderi* Mayr. roots are shallower than those of *Pinus sylvestris* L., which tend to be slightly deeper and more extensive in spread.

### Local climate data

To assess the drivers of  $\delta^{18}\text{O}$  variation in tree-ring cellulose for measured and modeled datasets, we used daily maximum and minimum temperature, daily precipitation and daily relative humidity data from the Chokurdach weather station (70° 30' N, 148° 08' E, ~ 250-300 m a.s.l.) located close to the north-eastern site (NE) for the period from 1948 to 2004. For Central Yakutia

(CE) we used data from the weather station in Yakutsk (62° 02' N, 129° 44' E, ~ 220 m a.s.l.) for the period from 1966 to 2004.

### Annual $\delta^{18}\text{O}$ in tree-ring cellulose chronologies

As a reference, we used  $\delta^{18}\text{O}$  values of *Larix cajanderi* Mayr. cellulose chronologies, which were constructed based on individually analysed annual tree rings from four trees from the NE site (Sidorova et al. 2008) for the period from 1880 to 2004 and from five trees for the period from 1900 to 2013 from the CE sites (Timofeeva 2017). These measured  $\delta^{18}\text{O}$  chronologies were used for comparative analyses with the LPX-Bern modeled data of the source water,  $\delta^{18}\text{O}$  of cellulose, and thaw depths for the common period (from 1901 to 2004) for both sites.

Cellulose samples from both study sites (NE and CE) were measured at the Stable Isotope Research Facility of the Paul Scherrer Institute (Villigen, Switzerland). For measurements of the oxygen isotope ratios from NE, cellulose samples were pyrolysed to CO at 1080 °C (Saurer et al. 1998) in the continuous flow mode with an elemental analyzer (Carlo Erba EA-1110<sup>®</sup>, Milan, Italy) linked to an isotope-ratio mass spectrometer (Delta 5<sup>®</sup>, Finnigan MAT, Bremen, Germany). The CE samples were pyrolyzed using PYRO-cube<sup>®</sup> at 1420 °C (Elementar, Hanau, Germany) and analyzed with a Delta Plus XL<sup>®</sup> Mass spectrometer (Thermo Finnigan, Bremen, Germany). An earlier study showed that both systems yielded similar precisions ( $\pm 0.2\%$ ) and the values from the two instruments were highly correlated (better than the measurement precisions – Weigt et al. 2015). The isotopic values were expressed in the  $\delta$  notation relative to the international standard (eqn. 1):

$$\delta_{\text{sample}} (\text{‰}) = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \cdot 1000 \quad (1)$$

where  $R_{\text{sample}}$  is the molar fraction of  $^{18}\text{O}/^{16}\text{O}$  ratio of the sample and  $R_{\text{standard}}$  of the Vienna Standard Mean Ocean Water for oxygen.

### Estimation of the $\delta^{18}\text{O}$ of source water using RLE model

Roden-Lin-Ehleringer (RLE) model was applied to determinate the  $\delta^{18}\text{O}$  of source water over time. For snowmelt and thawed permafrost water as well as rainwater we employed ranges between -28 and -25‰ and -6 to -11‰, respectively (Kurita et al. 2005, Prokushkin, personal communication). An earlier study by Saurer et al. (2016) showed that soil water is a mixture of precipitation and thawed permafrost water, and that evaporation plays a minor role in this region. Barometric pressure was obtained as an estimate of 95 kPa from elevation tables in Percy et al. (1989). Fan et al. (2018) reported that values for stomatal conductance in leaves of *Salix boganidensis* from lowland Indigirka

site in the northwestern Yakutia could range between 0.4 and 0.6 mol m<sup>-2</sup> s<sup>-1</sup>. Streit et al. (2014) reported that the stomatal conductance of *Larix decidua* needles was higher compared to *Pinus mugo* and varied from 0.2 to 0.6 mol m<sup>-2</sup> s<sup>-1</sup> during July at the high-elevated site in Stillberg, Davos (2180 m a.s.l.), Switzerland. To our knowledge, there are no direct measurements for *Larix cajanderi* Mayr. or *Pinus sylvestris* for Yakutia. For stomatal conductance we used value of 0.3 mol m<sup>-2</sup> s<sup>-1</sup>, assuming a low stomatal conductance for conifer needles from a northern tree line in the cold Yakutia region.

The  $\delta^{18}\text{O}$  of xylem cellulose ( $\delta^{18}\text{O}_{\text{cx}}$ ) was predicted as a function of both the isotopic ratio of the substrate sucrose and of the medium water at the site of cellulose synthesis, root, or xylem as part of the tree-ring (Roden et al. 2000). The  $\delta^{18}\text{O}$  in tree-ring cellulose is calculated as (eqn. 2):

$$\delta^{18}\text{O}_{\text{cx}} = f_0 \cdot (\delta^{18}\text{O}_{\text{wx}} + \epsilon_0) + (1 + f_0) \cdot (\delta^{18}\text{O}_{\text{lw}} + \epsilon_0) \quad (2)$$

where  $f_0$  is the fraction of exchange with leaf water ( $\delta^{18}\text{O}_{\text{wx}}$ ) and estimated to be 0.42 for oxygen from the best fit relationship derived from controlled experiments (Roden et al. 2000). The subscript cx is xylem cellulose, wx is xylem water and lw is leaf water at the site of sucrose synthesis. The parameter  $\epsilon_0$  is a biochemical fractionation associated with the water-carbonyl oxygen interactions (27 ‰ - Sternberg & DeNiro 1983, Luo & Sternberg 1992).

We modeled leaf water as (eqn. 3):

$$\delta^{18}\text{O}_{\text{lw}} = \delta^{18}\text{O}_{\text{source}} + \epsilon_e + \epsilon_k + (\delta^{18}\text{O}_{\text{vapor}} - \delta^{18}\text{O}_{\text{source}} - \epsilon_k) \cdot e_a / e_i \quad (3)$$

where  $\delta^{18}\text{O}_{\text{lw}}$  is the isotope ratio at the site of evaporation,  $\delta^{18}\text{O}_{\text{source}}$  is a mixture of soil and precipitation water used by trees,  $\epsilon_e = 1.0096$ , which is the temperature dependent equilibrium fractionation due to the phase change from liquid water to vapour (Majoube 1971),  $\epsilon_k = 1.0285$ , which is the kinetic fractionation (Merlivat 1978) due to diffusion of vapour into unsaturated air,  $\delta^{18}\text{O}_{\text{vapor}}$  is the isotopic composition of atmospheric water vapour, and  $e_a/e_i$  the ratio of the ambient to the leaf internal vapour pressure (kPa – Craig & Gordon 1965, Dongmann et al. 1974).

The RLE model can predict source water  $\delta^{18}\text{O}$  values for both the NE and CE study sites by the following equation (eqn. 4):

$$\delta^{18}\text{O}_{\text{source water}} (\text{‰}) = f_0 \cdot (\delta^{18}\text{O}_{\text{stemwater}} + \epsilon_{\text{oh}}) + (1 - f_0) \cdot (\delta^{18}\text{O}_{\text{lwm}} + \epsilon_{\text{oa}}) \quad (4)$$

where  $f_0 = 0.42$ , which is fraction of exchange with medium water;  $\epsilon_{\text{oh}}$  and  $\epsilon_{\text{oa}} = 27$ , which is heterotrophic and autotrophic fractionation factor during cellulose synthesis;  $\delta^{18}\text{O}_{\text{lwm}}$  is the modeled leaf water (Yakir & DeNiro 1990).

### Simulating $\delta^{18}\text{O}$ in LPX Bern

The Land surface Processes and eXchanges (LPX-Bern v. 1.3) model (Keller et al. 2017) is a dynamic global vegetation model and features a process-based representation of the coupled terrestrial nitrogen, carbon and water cycle. Here only a natural vegetation, consisting of ten Plant Functional Types (PFTs) competing for resources and confined by bioclimatic limits, is considered. The  $\delta^{18}\text{O}$  isotope enabled version of the LPX-Bern model is introduced and discussed in detail by Keel et al. (2016), which helps to reduce uncertainties in the interpretation of raw measured  $\delta^{18}\text{O}$  chronologies for investigating different temporal scales of the oxygen isotope patterns in tree rings. The  $\delta^{18}\text{O}_{\text{cell}}$  (stem cellulose isotopic composition) was calculated based on the eqn. 4.

The  $\delta^{18}\text{O}_{\text{lw}}$  is calculated according to eqn. 3, but modified by including the Péclet effect (Farquhar & Lloyd 1993) using the modeled rate of transpiration (eqn. 5):

$$\delta^{18}\text{O}_{\text{lw Péclet}} = \delta^{18}\text{O}_{\text{source}} + (\delta^{18}\text{O}_{\text{lw}} - \delta^{18}\text{O}_{\text{source}}) \cdot (1 - e^{-P})/P \quad (5)$$

where  $P = EL/CD$ ;  $L$  is mixing path length (m);  $E$  is the rate of transpiration ( $\text{mol m}^{-2} \text{s}^{-1}$ );  $C$  is the concentration of water  $5.55 \cdot 10^4 \text{ mol m}^{-3}$ ;  $D$  is the diffusivity of  $\text{H}_2^{18}\text{O}$  in water  $2.66 \cdot 10^{-9} \text{ m}^2 \text{ s}^{-1}$ ;  $P$  is the Péclet number (Ikeda 1983);  $\delta^{18}\text{O}_{\text{lw Péclet}}$  is the Péclet corrected leaf water enrichment;  $\delta^{18}\text{O}_{\text{lw}}$  from the eqn. 3 is the enrichment of the leaf water at the surface of evaporation.

In this study, the model runs for both study sites with a single grid cell configuration from 1901 to 2004. Monthly temperature, precipitation, cloud cover and number of wet days data are extracted from the  $0.5^\circ$  latitude/longitude grid cells closest to the study cells locations of the global CRU-TS3.22 climate dataset (Harris et al. 2014). Internally, the meteorological data are interpolated to a daily time-step, except for precipitation, where a stochastic weather generator is applied to compute daily precipitation according to Gerten et al. (2004). The temperature and precipitation data correspond well ( $r = 0.96$ ;  $p < 0.05$ ) with the local weather stations (see above) from 1966 to 2004. Similarly, nitrogen deposition is supplied to the model (Lamarque et al. 2013). Furthermore, the oxygen module requires input values for the  $\delta^{18}\text{O}$  of soil water and water vapor, as well as relative humidity data, which are extracted from global transient isotope-enabled simulations of the coupled atmosphere-land surface model ECHAM5-JSBACH (Haese et al. 2013). Since the simulation only spans the period 1960-2012, earlier years are approximated by the values of the year 1960. Identical atmospheric  $\text{CO}_2$  concentrations are prescribed to both study sites from a global reconstruction (Etheridge et al. 1998, Francey et al. 1999, MacFarling Meure et al. 2006).

The LPX-Bern  $\delta^{18}\text{O}$  simulations are useful for investigating different temporal scales of the oxygen isotope patterns in tree-ring, which help to reduce uncertainties in the interpretation of raw measured  $\delta^{18}\text{O}$  chronologies.

### Climatological and statistical analyses

Pearson correlation coefficients were calculated between local weather station data and the CRU-TS3.22 climate dataset were calculated (Harris et al. 2014). Statistical calculations were performed in licensed version of the software Statistica® v. 13.3 (StatSoft, Tulsa, OK, USA).

## Results

### Modeled and measured $\delta^{18}\text{O}$ tree-ring cellulose data

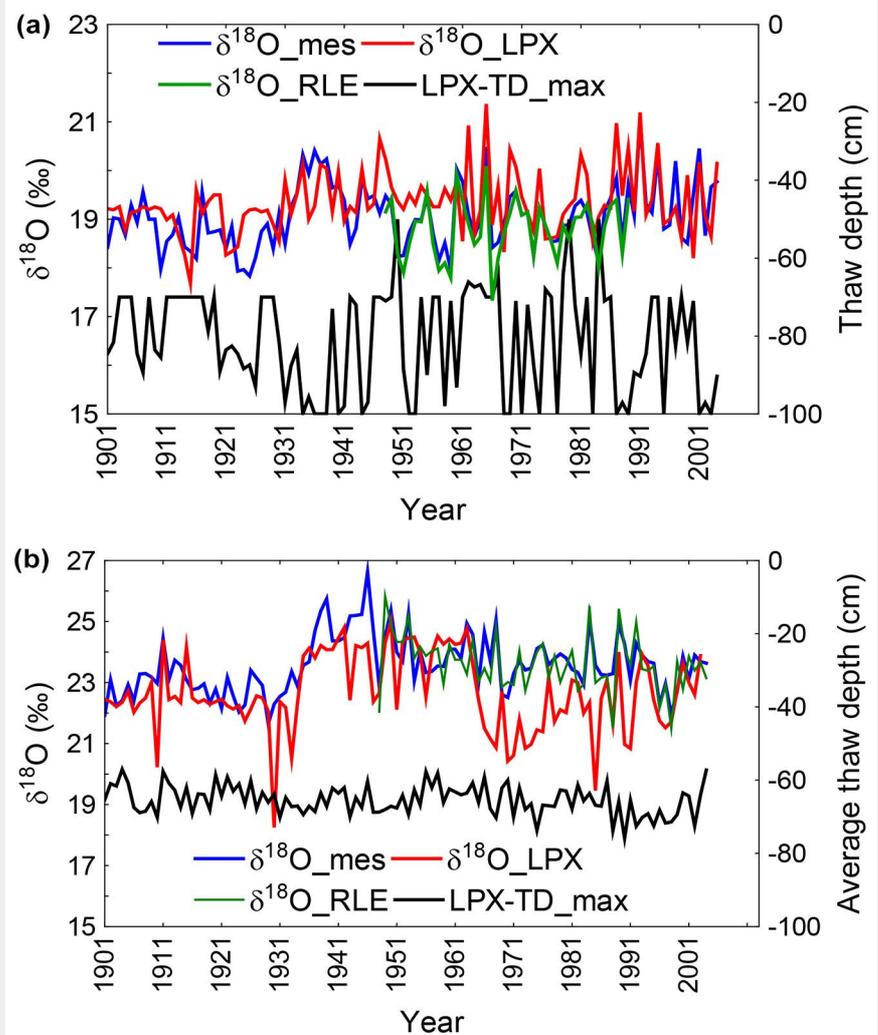
Using the LPX-Bern (Keel et al. 2016) and RLE (Rodén et al. 2000) models, we obtained modeled  $\delta^{18}\text{O}$  tree-ring cellulose values for the NE (Fig. 1a) and CE (Fig. 1b)

study sites in Yakutia.

Modeled LPX-Bern thaw soil depth varied much stronger for the NE site (in the range from 50-100 cm) compared to the modeled soil depth at the CE site (50-70 cm). Modeled values and data for  $\delta^{18}\text{O}$  in cellulose agree in so far that the tree-ring cellulose is more depleted in the heavier  $^{18}\text{O}$  isotope at the NE site than at the CE.

Measured  $\delta^{18}\text{O}$  data from the NE and CE are significantly correlated with RLE ( $r = 0.92$  and  $r = 0.74$ ,  $p < 0.05$ ) and LPX-Bern ( $r = 0.59$  and  $r = 0.46$ ,  $p < 0.05$ ), respectively for both studied regions. On average the offset between modeled RLE and measured  $\delta^{18}\text{O}$  data for both NE and CE is low (less than 1‰).

The LPX-Bern modeled thaw depth (maximum values) correlates significantly ( $r = -0.29$ ,  $p < 0.05$ ) with measured NE  $\delta^{18}\text{O}$  data only. The  $\delta^{18}\text{O}$  measured data from the NE and CE correlated significantly between each other ( $r = 0.20$ ,  $p < 0.05$ ) for the common period from 1901 to 2004, although



**Fig. 1** - The  $\delta^{18}\text{O}$  in tree-ring cellulose measured and modeled using LPX-Bern and RLE models. Modeled thaw depth as output parameter of the LPX model is presented for the (a) northeastern (NE) and (b) Central (CE) sites in Yakutia. Maximal seasonal thaw depth (LPX-TD\_max) simulated by LPX-Bern model is presented in black lines for both sites (a, b).

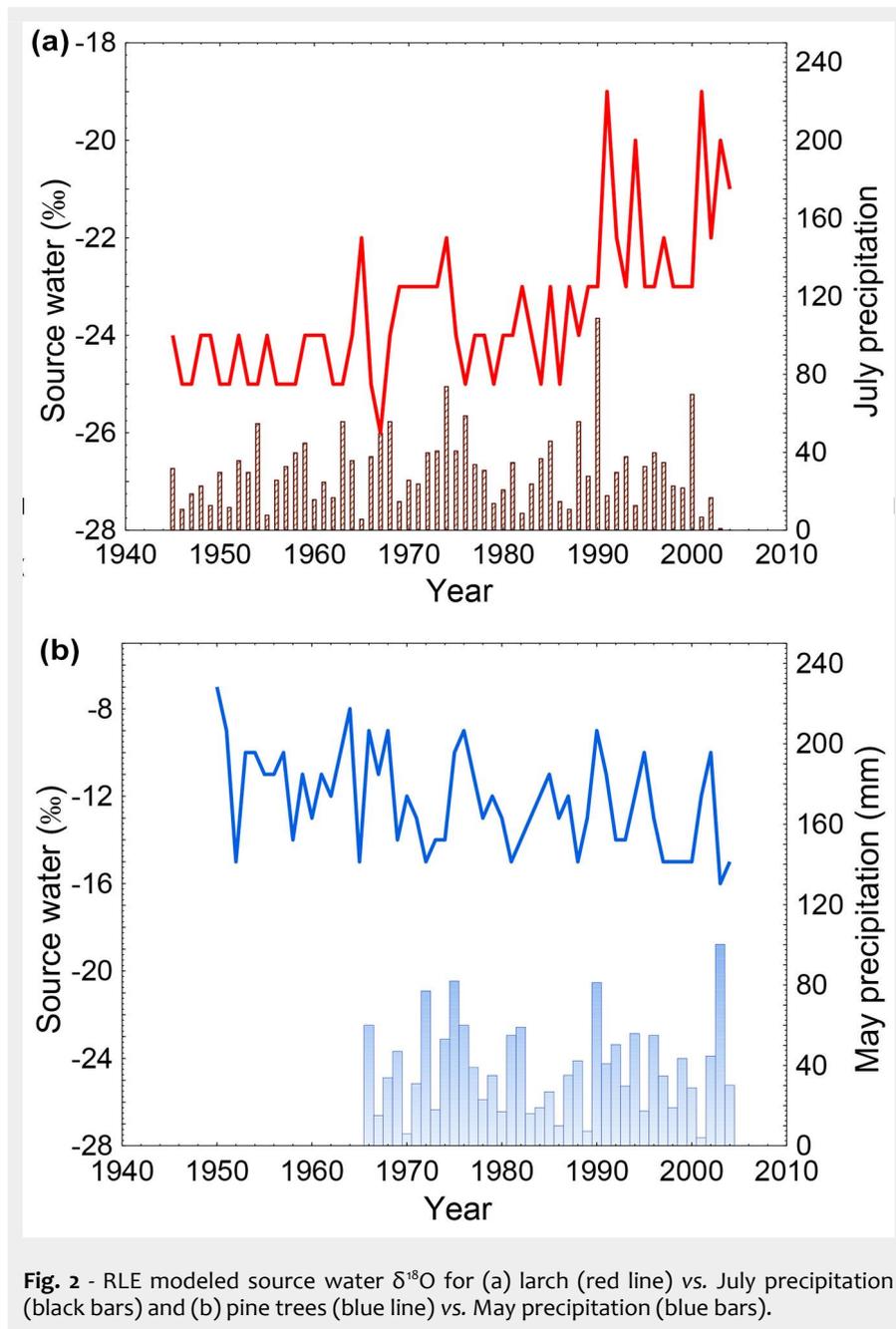


Fig. 2 - RLE modeled source water  $\delta^{18}O$  for (a) larch (red line) vs. July precipitation (black bars) and (b) pine trees (blue line) vs. May precipitation (blue bars).

the distance between the two sites is about 860 km. Modeled data for thaw permafrost soil depth at NE and CE also correlate significantly ( $r = 0.39$ ,  $p < 0.05$ ).

#### Modeling of source water

The  $\delta^{18}O$  leaf water in the RLE is calculated based on the isotopic composition of leaf water at the site of evaporation, which is not the same as bulk leaf water due to the contribution of unevaporative vein water and tissues (Yakir et al. 1993) and the “Péclet effect” (see Farquhar & Lloyd 1993 which describe the convective / diffusive mixing between evaporatively enriched and un-enriched source water from the xylem).

A strong increase in estimated isotopic composition of the source water after the 1990s for NE was revealed, while an overall declining trend for CE was found (Fig. 2).

Correlation coefficients between source water  $\delta^{18}O$  and July precipitation were significant at NE ( $r = -0.27$ ,  $p < 0.05$ ) and for May precipitation ( $r = -0.28$ ,  $p < 0.05$ ) at the CE site. However, the negative correlation with July precipitation was weak.

A decrease in July precipitation at the NE site was detected after the year 2000, which is consistent with the modeled  $\delta^{18}O$  source water values.

#### Discussion and conclusion

Simulations of thawing depth and  $\delta^{18}O$  values in tree-ring cellulose, using the output of the RLE model as a proxy for source water over time, indicate that thawed permafrost water is available for trees from NE in addition to precipitation water. Based on this analysis we conclude that thawed permafrost water could be an important water source for trees, especially

for periods when the amount of precipitation is lower than the evaporative water loss. Our model simulation is in line with earlier findings by Sugimoto et al. (2002) for the central part of Yakutia, confirming that trees from the CE could use thawed permafrost water during dry events. Yet the question remains whether *Larix cajanderi* Mayr. from the NE site can utilize thawed permafrost water. There was also an indication of source water enrichment ( $^{18}O$ ) increased over time. This could be caused by rising temperatures resulting in higher evapotranspiration due to higher vapor pressure deficit (VPD) during drought conditions (Yuan et al. 2019), but may also be the result of a diminishing influence of thawed permafrost water, which has a more negative isotope ratio than rain water (Saurer et al. 2016).

Precipitation or snowmelt can be stored in soils or lost as run off, depending on permafrost depth. Source water for *Pinus sylvestris* L. trees from the CE site did not indicate a strong increase of thawed permafrost use as an additional water source as it was found at the NE. Opposite to the NE, trees from the CE have limited water availability caused by drought conditions in this area.

Our study showed that trees from NE and CE might have access to additional thawed permafrost water during dry summer periods, which is in line with the study by Sugimoto et al. 2002. Due to differences in the soil structure, active thaw soil depth and root systems of trees at two Siberian sites, *Larix cajanderi* Mayr. trees cannot access water deeper than 50 cm, while *Pinus sylvestris* L. in Central Yakutia can access water as deep as 80 cm. This is opposite to the finding of Sugimoto et al. (2002), who showed possible water access up to 1.4 m. These differences can be explained by different soil structures (sand in central Yakutia and rocks in northeastern Yakutia) as well as with species-specific rooting distributions, resulting in different rooting depths. Thus, trees have different access to water sources depending on their root distribution, i.e., surface rooting system (*Larix cajanderi* Mayr.) vs. roots proliferated to deeper soil layers (*Pinus sylvestris* L. – Sidorova et al. 2008, Körner 2012, Churakova-Sidorova et al. 2016b, Saurer et al. 2016, Kropp et al. 2019).

We could show that the application of different oxygen isotope models (Keel et al. 2016, Roden et al. 2000) helps to reveal the impact of important hydro-climatic factors such as the interplay between water sources; e.g., precipitation, soil moisture and frozen soil water and soil thawing depth, influencing tree-growth and physiology in an ecosystem under permafrost conditions. The discrepancies between modeled and measured data are in part due to different parameterizations, but more so due to different model designs for different scales, from whole plant to ecosystems. So far, direct seasonal measurement

for the thawed permafrost depth or measurement for stomatal conductance at the remote study site, like NE are rare due to the harsh climatic conditions leading to costly and complex fieldwork at this region. Therefore, the modeling approach can be a powerful tool for the investigation of the influence of a variety of climatic factors on Siberian forest ecosystem water relations that impact on isotope fractionations in tree-ring cellulose from remote Siberian sites.

Furthermore, we must keep in mind that the heterogeneous soil structure will result in a great variation of  $\delta^{18}\text{O}$  values of the xylem water, especially with regard to time gaps between the isotopic signals of precipitation and what we find in xylem water. Depending on the depth of the active soil layer (where trees can access water) and its structure, these time gaps can be considerable (Allen et al. 2019). Such structural variations are difficult to take into account in any modeling approach. Further studies on adjustments and harmonization between LPX-Bern and RLE models and their parameterization based on a wider pool of measured data will provide the basis to enhance the relevance of these models to a powerful analytical tool. Although each model has its strengths and weaknesses, making use of their complementarity and strengths facilitates the enhancement of our understanding of the source water availability and its complexity for trees in these boreal ecosystems under permafrost dynamics. For instance, the use of a process-based model, such as the LPX-Bern (Keel et al. 2016), allows investigating  $\delta^{18}\text{O}$  signals in tree rings as a proxy for hydrological and climate dynamics on a regional or global scale. Furthermore, factorial simulations (where each parameter is modified specifically) are a potential avenue to further improve our understanding of the linkage between the vegetation cover, climatic drivers and permafrost dynamics.

### Acknowledgments

This work was supported by the Russian Science Foundation (RSF) (19-14188000 28), EU-FP7 Marie Curie Fellowship (EU-ISOTREC 235122, 909122). FJ and SL acknowledge support by the Swiss National Science Foundation (# 200020\_172476). We thank Martin Werner for providing the soil water and humidity  $\delta^{18}\text{O}$  data from the ECHAM5-JSBACH model.

### Author Contributions

OCh did the measurements and data interpretations for the NE Yakutia, and applied the RLE model to both studied sites. GT performed the experiments at the CE Yakutia site. SL modeled  $\delta^{18}\text{O}$  and thaw depth for both NE and CE sites. All authors significantly contributed to the writing of the manuscript.

### Conflicts of Interest

The authors declare no conflict of interest.

### References

- Allen ST, Kirchner JW, Braun S, Siegwolf RTW, Goldsmith GR (2019). Seasonal origins of soil water used by trees. *Hydrology and Earth System Sciences* 23: 1199-1210. - doi: [10.5194/hess-23-1199-2019](https://doi.org/10.5194/hess-23-1199-2019)
- Arneth A, Lloyd J, Santruckova H (2002). Response of central Siberian Scots pine to soil water deficit and long-term trends in atmospheric  $\text{CO}_2$  concentration. *Global Biogeochemical Cycles* 16 (1): 5-15. - doi: [10.1029/2000GB001374](https://doi.org/10.1029/2000GB001374)
- Abaimov AP, Bondarev AI, Ziryanova OA, Shitova CA (1997). Polar forests of Krasnoyarsk region. Nauka, Novosibirsk, Russia, pp. 207.
- Boike J, Kattenstroth B, Abramova K, Bornemann N, Cherverova A, Fedorova I, Fröb K, Grigoriev M, Grüber M, Kutzbach L, Langer M, Minke M, Muster S, Piel K, Pfeiffer E-M, Stoff G, Westermann S, Wischniewski K, Wille C, Hubberten H-W (2013). Baseline characteristics of climate, permafrost and land cover from a new permafrost observatory in the Lena River Delta, Siberia (1998-2011). *Biogeosciences* 10: 2105-2128. - doi: [10.5194/bg-10-2105-2013](https://doi.org/10.5194/bg-10-2105-2013)
- Cable JM, Ogle K, Bolton Bentley RWLP, Romanovsky V, Iwata H, Harazono Y, Welker J (2014). Permafrost thaw affects boreal deciduous plant transpiration through increased soil water, deeper thaw and warmer soil. *Ecology* 95 (3): 982-997. - doi: [10.1002/eco.v7.3](https://doi.org/10.1002/eco.v7.3)
- Churakova-Sidorova OV, Shashkin AV, Siegwolf R, Spahn R, Launois T, Saurer M, Bryukhanova MV, Benkova AV, Kupzova AV, Vaganov EA, Peylin P, Masson-Delmotte V, Roden J (2016a). Application of eco-physiological models to the climatic interpretation of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  measured in Siberian larch tree rings. *Dendrochronologia* 39: 51-59. - doi: [10.1016/j.dendro.2015.12.008](https://doi.org/10.1016/j.dendro.2015.12.008)
- Churakova-Sidorova OV, Saurer M, Bryukhanova M, Siegwolf R, Bigler C (2016b). Site-specific water-use strategies of mountain pine and larch to cope with recent climate change. *Tree Physiology* 36: 942-953. - doi: [10.1093/treephys/tpw060](https://doi.org/10.1093/treephys/tpw060)
- Churakova-Sidorova OV, Fonti MV, Saurer M, Guillet S, Corona S, Fonti P, Myglan VS, Kirdyanov AV, Naumova OV, Ovchinnikov DV, Shashkin AV, Panyushkina IP, Büntgen U, Hughes MK, Vaganov EA, Siegwolf RTW, Stoffel M (2019). Siberian tree-ring and stable isotope proxies as indicators of temperature and moisture changes after major stratospheric volcanic eruptions. *Climate of the Past* 15: 685-700. - doi: [10.5194/cp-2018-70](https://doi.org/10.5194/cp-2018-70)
- Craig H, Gordon LI (1965). Deuterium and oxygen-18 variations in the ocean and marine atmosphere. In: "Stable Isotopes in Oceanographic Studies and Paleotemperatures" (Tongiorgi E, Lishi FV eds). Pisa, Italy, pp. 9-130.
- Dongmann G, Nürnberg HW, Förstel H, Wagener K (1974). On the enrichment of  $\text{H}_2^{18}\text{O}$  in the leaves of transpiring plants. *Radiation and Environmental Biophysics* 11: 41-52. - doi: [10.1007/BF01323099](https://doi.org/10.1007/BF01323099)
- Etheridge DM, Steele LP, Langenfelds RL, Francey RJ, Barnola JM, Morgan VI (1998). Historical  $\text{CO}_2$  records from the Law Dome DE08, DE08-2, and DSS ice cores. In: "Trends: a Compendium of Data on Global Change". Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, TX, USA, web site. [online] URL: <http://cdiac.ornl.gov/trends/co2/lawdome.html>
- Fan R, Morozumi T, Maximov TC, Sugimoto A (2018). Effect of floods on the  $\delta^{13}\text{C}$  values in plant leaves: a study of willows in Northeastern Siberia. *PeerJ* 6: e5374. - doi: [10.7717/peerj.5374](https://doi.org/10.7717/peerj.5374)
- Farquhar GD, Lloyd J (1993). Carbon and oxygen isotope effects in the exchange of carbon dioxide between terrestrial plants and the atmosphere. In: "Stable Isotopes and Plant Carbon-water Relations" (Ehleringer JR, Hall AE, Farquhar GD eds). Academic Press, San Diego, CA, USA, pp. 47-70. - doi: [10.1016/B978-0-08-091801-3.50011-8](https://doi.org/10.1016/B978-0-08-091801-3.50011-8)
- Fischer HK, Meissner J, Mix AC, Abram NJ, Austermann J, Brovkin V, Capron E, Colombaoli D, Daniau A-L, Dyez KA, Felis T, Finkelstein SA, Jaccard SL, McClymont EL, Rovere A, Sutter J, Wolff EW, Affolter S, Bakker P, Ballesteros-Cánovas JA, Barbante C, Caley T, Carlson AE, Churakova Sidorova OV, Cortese G, Cumming BF, Davis BAS, De Vernal A, Emile-Geay J, Fritz SC, Gierz P, Gottschalk J, Holloway MD, Joos F, Kucera M, Loutre MF, Lunt DJ, Marcisz K, Marlon JR, Martinez P, Masson-Delmotte V, Nehrbass-Ahles C, Otto-Bliesner BL, Raible CC, Risebrobakken B, Sánchez Goñi MF, Saleem Arrigo J, Sarinthein M, Sjolte J, Stocker TF, Velasquez Álvarez PA, Tinner W, Vogel H, Wanner H, Yan Q, Yu Z, Ziegler M, Zhou L (2018). Palaeoclimate constraints on the impact of 2 °C anthropogenic warming and beyond. *Nature Geoscience* 11: 474-485. - doi: [10.1038/s41561-018-0146-0](https://doi.org/10.1038/s41561-018-0146-0)
- Francey RJ, Allison CE, Etheridge DM, Trudinger CM, Enting IG, Leuenberger M, Langenfelds RL, Michel E, Steele LP (1999). A 1000-year high precision record of  $\delta^{13}\text{C}$  in atmospheric  $\text{CO}_2$ . *Tellus B* 51: 170-193. - doi: [10.3402/tellusb.v51i2.16269](https://doi.org/10.3402/tellusb.v51i2.16269)
- Fyodorov-Davydov DG, Kholodov VE, Ostroumov VE, Kraev GN, Sorokovikov VA, Davydov SP, Merekalova AA (2008). Seasonal thaw of soils in the North Yakutian ecosystems. In: Proceedings of the 9<sup>th</sup> International Conference on "Permafrost on a Warming Planet: Impacts on Ecosystems, Infrastructure and Climate". University of Alaska, Fairbanks (AK, USA) 29 Jun - 3 Jul 2008, pp. 481-486. [online] URL: <http://www.researchgate.net/publication/265249057>
- Gerten D, Schaphoff S, Haberlandt U, Lucht W, Sitch S (2004). Terrestrial vegetation and water balance - Hydrological evaluation of a dynamic global vegetation model. *Journal of Hydrology* 286 (1-4): 249-270. - doi: [10.1016/j.jhydrol.2003.09.029](https://doi.org/10.1016/j.jhydrol.2003.09.029)
- Haese B, Werner M, Lohmann G (2013). Stable water isotopes in the coupled atmosphere-land surface model ECHAM5-JSBACH. *Geoscientific Model Development* 6 (5): 1463-1480. - doi: [10.5194/gmd-6-1463-2013](https://doi.org/10.5194/gmd-6-1463-2013)
- Harris I, Jones PD, Osborn TJ, Lister DH (2014). Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 dataset. *International Journal of Climatology* 34 (3): 623-642. - doi: [10.1002/joc.3711](https://doi.org/10.1002/joc.3711)
- Ikeda T (1983). Maximum principle in finite ele-

- ment models for convection-diffusion phenomena. North Holland, Amsterdam, Netherlands, pp. 170.
- Keel SG, Joos F, Spahni R, Saurer M, Weigt RB, Klesse S (2016). Simulating oxygen isotope ratios in tree-ring cellulose using a dynamic global vegetation model. *Biogeosciences* 13: 3869-3886. - doi: [10.5194/bg-13-3869-2016](https://doi.org/10.5194/bg-13-3869-2016)
- Keller KM, Lienert S, Bozbiyik A, Stocker TF, Churakova-Sidorova OV, Frank DC, Klesse S, Koven CD, Leuenberger M, Riley WJ, Saurer M, Siegwolf RTW, Weigt RB, Joos F (2017). 20<sup>th</sup>-century changes in carbon isotopes and water-use efficiency: tree-ring based evaluation of the CLM4.5 and LPX-Bern models. *Biogeosciences* 14 (10): 2641-2673. - doi: [10.5194/bg-14-2641-2017](https://doi.org/10.5194/bg-14-2641-2017)
- Körner C (2012). *Alpine tree lines*. Springer, Basel, Switzerland, pp. 122.
- Kropp H, Loranty MM, Natali SM, Kholodov AL, Alexander HD, Zimov NS, Mack MC, Spawn SA (2019). Tree density influences ecohydrological drivers of plant-water relations in a larch boreal forest in Siberia. *Ecohydrology* 12 (7): e2132. - doi: [10.1002/eco.v12.7](https://doi.org/10.1002/eco.v12.7)
- Kurita N, Sugimoto A, Fujii Y, Fukazawa T, Makarov VN, Watanabe O, Ichiyanaği K, Numaguti A, Yoshida N (2005). Isotopic composition and origin of snow over Siberia. *Journal of Geophysical Research* 10: D13102. - doi: [10.1029/2004JD005053](https://doi.org/10.1029/2004JD005053)
- Lamarque J-F, Dentener F, McConnell J, Ro C-U, Shaw M, Vet R, Bergmann D, Cameron-Smith P, Dalsoren S, Doherty R, Faluvegi G, Ghan SJ, Josse B, Lee YH, MacKenzie IA, Plummer D, Shindell DT, Skeie RB, Stevenson DS, Strode S, Zeng G, Curran M, Dahl-Jensen D, Das S, Fritzsche D, Nolan M (2013). Multi-model mean nitrogen and sulfur deposition from the Atmospheric Chemistry and Climate Model Intercomparison Project (ACCMIP): evaluation of historical and projected future changes. *Atmospheric Chemistry Physics* 13: 7997-8018. - doi: [10.5194/acp-13-7997-2013](https://doi.org/10.5194/acp-13-7997-2013)
- Luo YH, Sternberg L (1992). Hydrogen and oxygen isotope fractionation during heterotrophic cellulose synthesis. *Journal of Experimental Botany* 43: 47-50. - doi: [10.1093/jxb/43.1.47](https://doi.org/10.1093/jxb/43.1.47)
- MacFarling Meure C, Etheridge D, Trudinger C, Steele P, Langenfelds R, Van Ommen T, Smith A, Elkins J (2006). Law Dome CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O ice core records extended to 2000 years BP. *Geophysical Research Letters* 33 (14): L14810. - doi: [10.1029/2006GL026152](https://doi.org/10.1029/2006GL026152)
- Majoube M (1971). Fractionation in O-18 between ice and water vapor. *Journal de Chimie Physique et de Physico-Chimie Biologique* 68: 1424-1436.
- Melnikov ES, Leibman MO, Moskalenko NG, Vasiliev AA (2004). Active-layer monitoring in the cryolithozone of West Siberia. *Polar Geography* 28 (4): 267-285. - doi: [10.1080/789610206](https://doi.org/10.1080/789610206)
- Merlivat L (1978). Molecular diffusivities of H<sub>2</sub><sup>16</sup>O, HD<sup>18</sup>O, and H<sub>2</sub><sup>18</sup>O in gases. *Journal of Chemical Physics* 69 (6): 2864. - doi: [10.1063/1.436884](https://doi.org/10.1063/1.436884)
- Nikolaev AN (2003). The influence of soil temperature on radial increments of larch and pine stems in Central Yakutia. In: Proceedings of the "8<sup>th</sup> International Conference on Permafrost" (Phillips M, Springman SM, Arenson LU eds). Zurich (Switzerland) 21-25 Jul 2003. Swets and Zeitlinger, Lisse, Netherlands, pp. 811-814. [online] URL: [http://www.arlis.org/docs/voh/ICOP/55700698/Pdf/Chapter\\_142.pdf](http://www.arlis.org/docs/voh/ICOP/55700698/Pdf/Chapter_142.pdf)
- Overland JE, Hanna E, Hanssen-Bauer I, Kim S-J, Walsh JE, Wang M, Bhatt US, Thoman RL (2015). Surface Air Temperature. Arctic Report Card: Update for 2015. Arctic Essays, NOAA Arctic Program, web site. [online] URL: <http://www.arctic.noaa.gov/Report-Card/Report-Card-2015/ArtMID/5037/ArticleID/210/Surface-Air-Temperature>
- Pavlov AV, Skachkov Yu B, Kakunov NB (2004). An interaction between the active layer depth changing and meteorological factors. *Earth Cryosphere* 8 (4): 3-11. [in Russian]
- Pearcy RW, Schulze E-D, Zimmermann R (1989). Measurement of transpiration and leaf conductance. In: "Plant Physiological Ecology" (Pearcy RW, Ehleringer JR, Mooney HA, Rundel PW eds). Chapman and Hall, London, UK, pp. 137-160.
- Roden JS, Lin G, Ehleringer JR (2000). A mechanistic model for interpretation of hydrogen and oxygen isotopic ratios in tree-ring cellulose. *Geochimica et Cosmochimica Acta* 64: 21-35. - doi: [10.1016/S0016-7037\(99\)00195-7](https://doi.org/10.1016/S0016-7037(99)00195-7)
- Saurer M, Kirdeyanov AV, Prokushkin AS, Rinne KT, Siegwolf RTW (2016). The impact of an inverse climate-isotope relationship in soil water on the oxygen-isotope composition of *Larix gmelinii* in Siberia. *New Phytologist* 209 (3): 955-964. - doi: [10.1111/nph.13759](https://doi.org/10.1111/nph.13759)
- Saurer M, Robertson I, Siegwolf R, Leuenberger M (1998). Oxygen isotope analysis of cellulose: an inter laboratory comparison. *Analytical Chemistry* 70: 2074-2080. - doi: [10.1021/ac971022f](https://doi.org/10.1021/ac971022f)
- Sidorova OV, Siegwolf R, Saurer M, Naurzbaev M, Shashkin AV, Vaganov EA (2010). Spatial patterns of climatic changes in the Eurasian north reflected in Siberian larch tree-ring parameters and stable isotopes. *Global Change Biology* 16: 1003-1018. - doi: [10.1111/j.1365-2486.2009.02008.x](https://doi.org/10.1111/j.1365-2486.2009.02008.x)
- Sidorova OV, Siegwolf RTW, Saurer M, Naurzbaev MM, Vaganov EA (2008). Isotopic composition ( $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$ ) in wood and cellulose of Siberian larch trees for early Medieval and recent periods. *Journal of Geophysical Research Biogeosciences* 113 (G2): 1-13. - doi: [10.1029/2007JG000473](https://doi.org/10.1029/2007JG000473)
- Sternberg LS, DeNiro MJ (1983). Biogeochemical implications of the isotopic equilibrium fractionation factor between the oxygen atoms of acetone and water. *Geochimica Cosmochimica Acta* 47: 2271-2274. - doi: [10.1016/0016-7037\(83\)90049-2](https://doi.org/10.1016/0016-7037(83)90049-2)
- Streit K, Siegwolf RTW, Hagerdon FH, Schaub M, Buchmann N (2014). Lack of photosynthetic or stomatal regulation after 9 years of elevated [CO<sub>2</sub>] and 4 years of soil warming in two conifer species at the alpine tree line. *Plant, Cell and Environment* 37: 315-326. - doi: [10.1111/pce.12197](https://doi.org/10.1111/pce.12197)
- Sugimoto A, Yanagisawa N, Fujita N, Maximov TC (2002). Importance of permafrost as a source of water for plants in east Siberian taiga. *Ecological Research* 17 (4): 493-503. - doi: [10.1046/j.1440-1703.2002.00506.x](https://doi.org/10.1046/j.1440-1703.2002.00506.x)
- Timofeeva G (2017). Elucidating the drought response of Scots pine (*Pinus sylvestris* L.) using stable isotopes. Doctoral Thesis, ETH, Zurich, Switzerland, pp. 208. - doi: [10.3929/ethz-b-000274056](https://doi.org/10.3929/ethz-b-000274056)
- Yakir D, Berry JA, Giles L, Osmond CB (1993). The <sup>18</sup>O of water in the metabolic compartment of transpiring leaves. In: "Stable Isotopes and Plant Carbon/Water Relation" (Ehleringer JR, Hall AE, Farquhar GD eds), Academic Press, S. Diego, CA, USA, pp. 529-540. - doi: [10.1016/B978-0-08-091801-3.50043-X](https://doi.org/10.1016/B978-0-08-091801-3.50043-X)
- Yakir D, DeNiro MJ (1990). Oxygen and hydrogen isotope fractionation during cellulose metabolism in *Lemna gibba* L. *Plant Physiology* 93 (1): 325-332. - doi: [10.1104/pp.93.1.325](https://doi.org/10.1104/pp.93.1.325)
- Young-Robertson JM, Ogle K, Welker JM (2017). Thawing seasonal ground ice: an important water source for boreal forest plants in Interior Alaska. *Ecohydrology* 10: 1-16. - doi: [10.1002/eco.1796](https://doi.org/10.1002/eco.1796)
- Yuan W, Zheng Y, Piao S, Ciais P, Lombardozzi D, Wang Y, Ryu Y, Chen G, Dong W, Hu Z, Jain AK (2019). Increased atmospheric vapor pressure deficit reduces global vegetation growth. *Science Advances* 5 (8): eaax1396. - doi: [10.1126/sciadv.aax1396](https://doi.org/10.1126/sciadv.aax1396)
- Weigt RB, Bräunlich S, Zimmermann L, Saurer M, Grams TEE, Dietrich HP, Siegwolf RTW, Nikolaeva PS (2015). Comparison of  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values between tree-ring whole wood and cellulose in five species growing under two different site conditions. *Rapid Communications in Mass Spectrometry* 29 (23): 2233-2244. - doi: [10.1002/rcm.7388](https://doi.org/10.1002/rcm.7388)