

Water-use strategies of conifer trees from the Swiss National Park to recent climatic changes

O.V. Churakova (Sidorova)^{1,2,3}, M. Saurer^{4,5}, M. Bryukhanova^{2,6}, R. Siegwolf⁵, C. Bigler³

¹University of Geneva, Institute for Environmental Sciences, Switzerland

²Siberian Federal University, Russia

³Institute of Terrestrial Ecosystems, ETH Zürich, Switzerland

⁴Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Switzerland

⁵Paul Scherrer Institute, Switzerland

⁶V.N. Sukachev Institute of Forest, Russia

Abstract

We aim to reveal the long-term physiological response of larch (*Larix decidua*) and mountain pine (*Pinus mugo* var. *uncinata*) trees that grow on north- and south-facing aspects in the Swiss National Park to recent and past climate changes. We measured and analyzed $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in wood chronologies from 1900 to 2013. We found that July temperature influenced larch $\delta^{18}\text{O}$ from both aspects and pine from the south-facing aspect. A decrease in water availability was reflected in increasing $\delta^{13}\text{C}$ and decreasing tree-ring width for larch trees in July and for pine trees in May. Intrinsic water use efficiency (WUEi) calculated for larch trees since 1990s reached a saturation, which may indicate the trees' plasticity to elevated CO_2 . Opposite, divergent trends between pine WUEi and $\delta^{18}\text{O}$ are most likely indicating a decline of mountain pine trees and decoupling mechanisms between needles and tree-ring width.

Keywords

tree-ring width; $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in wood; intrinsic water use efficiency, climate

Introduction

Over the last decades forest ecosystems have been affected by water deficits during summer droughts due to increasing temperatures and shortage in precipitation (ALLEN et al. 2010; CHURAKOVA (SIDOROVA) et al. 2016). Climate models predict that drought frequency will continue to increase during the 21st century and beyond (CH 2011, IPCC 2014). In the future, increasing temperatures will enhance the evaporative demand and water loss from plants and may reduce productivity and carbon sequestration in many forest ecosystems (SIDOROVA et al. 2009, ANDEREGG et al. 2012).

Temperature, water availability, air humidity and ambient CO_2 (c_a) influence photosynthetic CO_2 assimilation and water balance, which is reflected in the isotopic carbon and oxygen isotope ratios of the plant organic matter, yielding a specific isotope pattern in the wood of tree rings. Under warm and dry conditions trees respond to limited water resources by reducing stomatal conductance (g_s), resulting in a diminished CO_2 uptake and biomass production, in reduced intercellular CO_2 concentration (c_i). The latter leads to reduced ^{13}C discrimination (FARQUHAR et al. 1989) and increased $\delta^{18}\text{O}$ values (FARQUHAR & LLOYD 1993). The $\delta^{18}\text{O}$ values in tree rings are reflecting the condensation temperature during rain formation, which represents the source water for trees and leaf water enrichment (CRAIG 1961, MCCARROLL et al. 2004).

Enrichment in ^{18}O occurs in the needles during transpiration, which may be enhanced under drought conditions (YAKIR 1998). A mixed seasonal signal of water source and water enrichment in leaves is finally stored in the wood and cellulose of tree rings (SAURER et al. 1997, RODEN & EHLENGER 2000).

In this study, we addressed the following research questions:

1. Which of the climatic factors are predominantly reflected in $\delta^{18}\text{O}$ of wood in larch and mountain pine trees in the long-term?
2. Do mountain pine and larch trees show different water use efficiency strategies under recent climatic changes?

Material and Methods

The study site is situated at 1959-1964 m a.s.l. at Champlönch in the Swiss National Park, Switzerland (46°N, 10°E). Around 28% of the SNP are forested, 21% are alpine grasslands and 51% unproductive terrain. Mountain pine (*Pinus mugo* subsp. *uncinata*) and dwarf mountain pine (*Pinus mugo* subsp. *mugo*) predominantly grow on limestone in the SNP, and cover ca. 73% of the forests in the SNP.

The study site is characterized by a continental climate. According to the climate station Buffalora (ca. 5 km from study site; 1968 m a.s.l., 46° 38' N and 10° 16' E) the average winter temperature is -9.2°C and summer temperature is +9.5°C (monthly averages from 1917 to 2013). Since the 1990s mean annual and spring temperatures increased by 0.5°C and 1.0°C, respectively, while the average summer temperature increased by 0.6°C. The annual sum of precipitation is 910 mm (period 1917 to 2013). Since the 1990s annual precipitation decreased by 88.9 mm compared to the mean value of 931.2 mm from 1917 to 1989.

We selected two contrasting aspects at Champlönch, a south-facing (-S) sunny slope at 1964 m a.s.l and a north-facing (-N) shady slope at 1959 m a.s.l. Tree cores were collected from twelve trees per species and aspect for the construction of tree-ring width index chronologies. Each tree core from larch and mountain pine was glued on core mounts and cut for visualization of tree cells (COOK & KAIRIUKSTIS 1990). Then tree rings were counted and measured using a LINTAB 5 measurement bench (Rinntech, Germany) under a stereomicroscope (Leica MZ6). The cross-dating procedure to determine the exact formation year of each tree ring and for building individual tree-ring width chronologies was carried out using TSAPWin (Rinntech, Germany) and the software COFECHA (HOLMES 1983). To remove the age trend for each tree-ring width series we standardized each series by applying a negative exponential or linear function (HOLMES et al. 1983). For the further analysis residual tree-ring index chronologies were used.

Two increment cores from each tree were sampled for the stable isotope analysis from the same trees used for tree-ring analysis. Resins from the samples were extracted with a Soxhlet apparatus with a 1:1 ethanol-methanol mixture during 48 h. Tree cores were then washed with distilled water for 24 h and air dried at room temperature. For a better visualization of the tree rings the surface of the tree cores were slightly cut by hand without polishing or application of powder, to avoid cross contamination between the tree-rings, which must be considered for the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ stable isotope analysis in wood. The tree rings were measured and cross-dated against the dated tree-ring series, which were used for tree-ring analyses. For each tree, each annual ring (including early and late wood) was split separately using a scalpel. Wood samples were then milled to fine powder and packed into silver capsules. Simultaneous measurements for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of wood samples were performed with a vario PYRO cube (Elementar, Hanau, Germany) via thermic decomposition at 1450°C and conversion to CO under O₂ exclusion in helium (WOODLEY et al. 2012).

Results and discussion

To reveal the driving factors of tree growth in the long-term we calculated Pearson's correlations between tree-ring index, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in wood chronologies and temperature, precipitation, and drought index (DRI) for the period from 1917 to 2013. Carbon isotopes and larch tree-ring index chronologies suggest that a decrease in water availability occurs in July, while for pine from both aspects mainly in May and July. Mountain pine trees from both aspects were sensitive to changes of relative humidity during warm June and July. The positive significant correlations between $\delta^{18}\text{O}$ for larch with May and July precipitation could be explained by a high vapor pressure deficit (VPD). A similar finding was reported by SCHOLLAEN et al. (2013), who revealed a positive relationship between $\delta^{18}\text{O}$ in tree cellulose and precipitation during dry seasons. Mountain pine trees indicate a developing water shortage during earlier spring only, and show a positive significant relationship with VPD, resulting in a reduction of stomatal conductance reflecting in further increase in ^{18}O enrichment of needle water, which is not the case for larch trees. In contrast, STREIT et al. (2014) reported a positive linear relationship between $\Delta^{18}\text{O}$ and VPD for both larch and mountain pine at Stillberg (Davos, Switzerland). The contrasting patterns at our study site, e.g. high positive correlations between pine trees and VPD and negative correlations with larch trees suggest different hydrological conditions, which could be explained by differences in the root development resulting in different water sources for these tree species (ALVAREZ-URIA & KÖRNER 2007). We found that the physiological response of mountain pine trees is different from larch trees. RH and July temperature highly influenced larch trees, while the impact of precipitation becomes more important for pine trees. This indicates that pine trees rather use the soil surface water, whereas larch trees seems to be able to utilize water from the deeper soil layers and most likely can penetrate with their rooting system into rock cracks and access water from deeper ground levels.

Intrinsic water use efficiency (WUEi) for larch from south- (LS) and north-facing (LN) aspects (Fig. 1 a) showed increasing trends over time with saturating characteristic since the last 20 years. This is in agreement with increasing tree-ring values (Fig. 2a) and increasing trends of c_i/c_a for both aspects (Fig. 2c), that could be explained by the plasticity of larch trees to improving growth conditions, i.e. rapidly increasing CO₂, and non limiting water supply for larch (deep rooting tree).

In contrast, we found a divergent trend between WUEi for PS and PN (Fig. 1b) and $\delta^{18}\text{O}$ during the last 20 years (Fig. 1d). WUEi increases for both aspects (Fig. 1 b) along with a slight decrease c_i/c_a (Fig. 2 d), while tree-ring width did not change significantly (Fig. 2b) suggesting a constant assimilation rate. Surprisingly, $\delta^{18}\text{O}$ decreases (Fig. 1d).

According to Scheidegger et al. (2000) decreasing $\delta^{18}\text{O}$ in organic matter reflects an increase in stomatal conductance (g_s). Considering the results above this is not plausible from eco-physiological point of view. However, it could be the consequence of an impaired stomatal regulation, which is often observed in either senescing or dying plants.

Eventually, this will lead to a decoupling of the isotopic signals between needles and tree-rings. PFLUG et al. (2015) observed a progressive decrease in tree ring growth and photosynthesis with increasing drought. They found that the amount of carbohydrates became insufficient for tree ring growth. Thus, the isotopic signal formed in the needles during periods with growth limiting conditions is no longer stored in the tree rings. What remains are the sections of the tree rings, which were formed under less limiting, usually more humid conditions during spring and fall, when $\delta^{18}\text{O}$ in precipitation is more depleted than in summer.

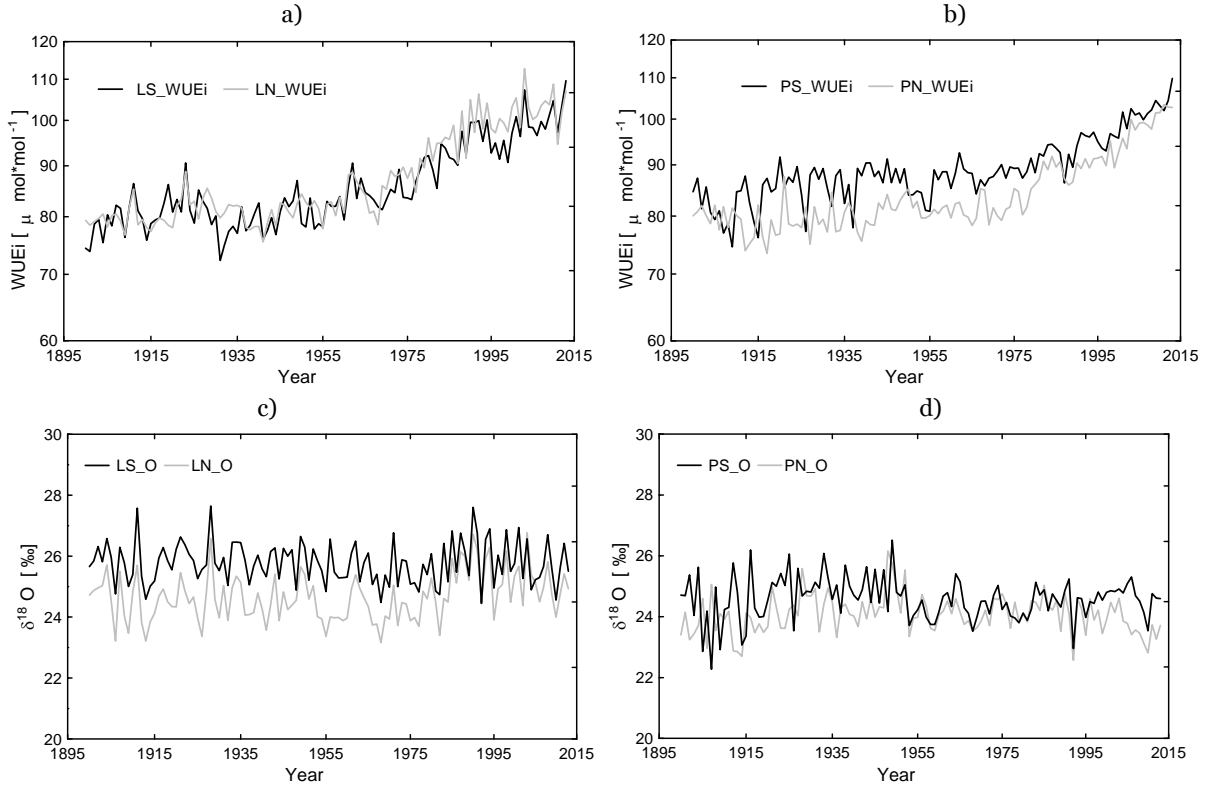


Figure 1: Intrinsic water use efficiency (WUEi) calculated for larch from south- (LS) and north-facing (LN) aspects (a) and mountain pine trees from south- (PS) and north – (PN) facing aspect (b) and $\delta^{18}\text{O}$ isotope chronologies in comparison for larch (c) and pine (d), respectively.

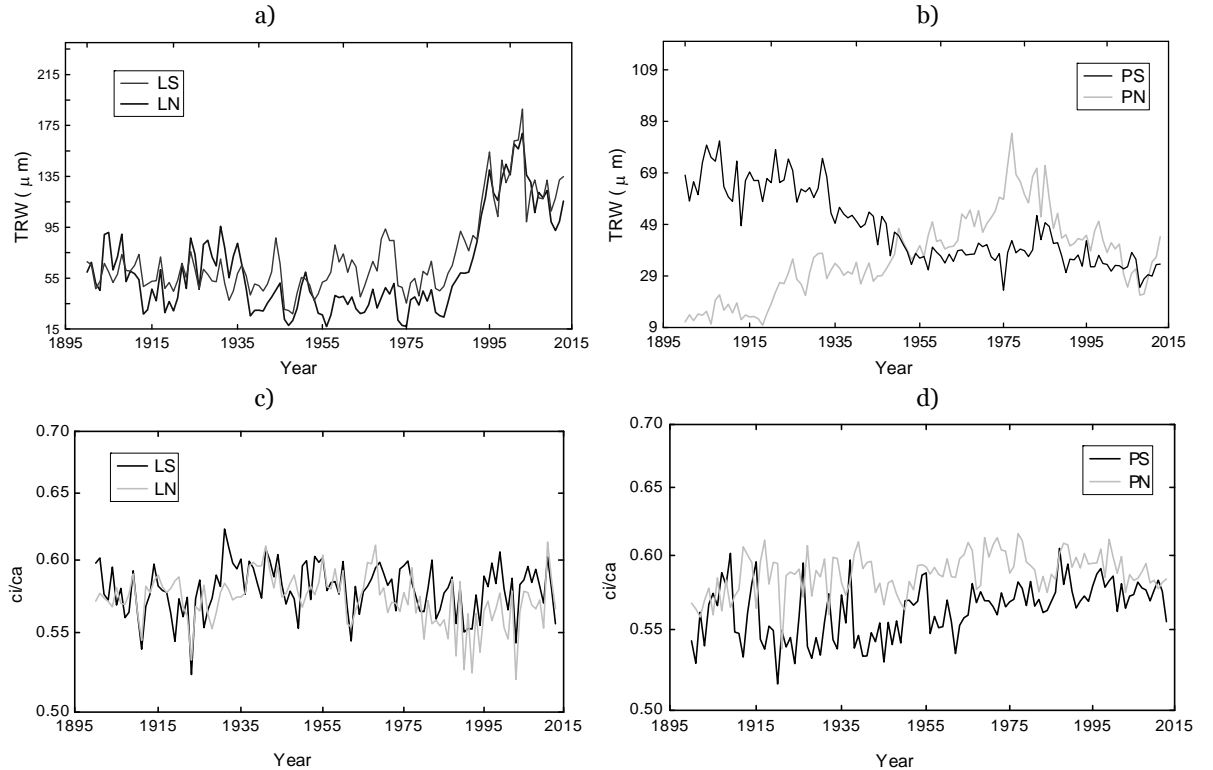


Figure 2: Tree-ring chronologies and calculated ratios of intercellular CO_2 vs. ambient CO_2 (c_i/c_a) for larch (a, c) and mountain pine (b, d), respectively.

Conclusion

Our study showed:

1. The $\delta^{18}\text{O}$ of wood in larch at both aspects and mountain pine from the south-facing aspect captured the July temperature signal. The $\delta^{13}\text{C}$ and tree-ring index chronologies suggest a decrease in water availability for larch during July and for mountain pine most likely during May and July.
2. Water use efficiency (WUEi) strategies differ between mountain pine and larch trees under recent climatic changes. Since the 1990s WUEi calculated for larch reached saturation, possibly showing an adaptation to elevated CO_2 . However, WUEi calculated for mountain pine trees from the same period continuously increased. Divergent trends between pine WUEi and $\delta^{18}\text{O}$ values and narrow tree-ring widths could be the result of senescence or declining mountain pine trees in the Swiss National Park resulting in a decoupling isotopic signal between needles and tree-ring with chronology.

Acknowledgements

This work was supported by the Marie Heim-Voegtlin Programm PMPD2-145507 granted to Olga Churakova (Sidorova). We are grateful to Ruedi Haller, Thomas Scheurer and Samuel Wiesmann for their help and we would like to acknowledge the research committee of the Swiss National Park for the sampling permission in the protected area. We thank our colleagues from ETH Zurich and Paul Scherrer Institute, who helped with the field sampling and supported us in the laboratory.

References

- ALLEN, C.D., MACALADY A.K., CHENCHOUNI H., et al 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259: 660-684.
- ALVAREZ-URIA, P., KÖRNER, C. 2007. Low temperature limits of root growth in deciduous and evergreen temperate tree species. *Funct Eco* 21: 211-218.
- ANDEREGG, W.R.L., BERRY, J.A., SMITH, D.D., et al. 2012. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proceedings of the National Academy of Sciences of the United States of America* 109: 233-237.
- CH 2011 Swiss Climate Change Scenarios CH2011. In: C2SM, MeteoSwiss, ETH, NCCR Climate, and OcCC, 88.
- CHURAKOVA (SIDOROVA), O.V., SAURER, M., BRYUKHANOVA, M., SIEGWOLF, R., BIGLER, C. 2016. 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.
- COOK, E.R., KAIRIUKSTIS, L.A. 1990. Methods of dendrochronology. Applications in the environmental sciences. Eds. Cook ER, Kairiukstis LA, 1990. 393 p.
- CRAIG, H. 1961. Isotopic variations in meteoric waters. *Science* 133: 1702– 1703.
- FARQUHAR, G.D., EHLERINGER, J.R., HUBICK, K.T. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* 40: 503-537.
- FARQUHAR, G.D., LLOYD, J. 1993 Carbon and oxygen isotope effects in the exchange of carbon dioxide between terrestrial plants and the atmosphere. In: Ehleringer, J.R., Hall, A.E., Farquhar, G.D. (eds) *Stable Isotopes and Plant Carbon-Water Relations*. Academic Press, San Diego, pp 47–70.
- HOLMES, R. L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 43: 69-78.
- MCCARROLL, D, LOADER, N.J. 2004. Stable isotopes in tree rings. *Quaternary Science Review* 23:771-801.
- IPCC 2014. CLIMATE CHANGE 2014: Synthesis Report Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Pachauri, R.K., Meyer, L.A. eds. IPCC, Geneva, Switzerland, 151 pp.
- PFLUG, E.E., SIEGWOLF, R.T.W., BUCHMANN, N., DOBBERTIN, M., KUSTER, T.M., GÜNTHARDT-GOERG, M.S., AREND, M. 2015. Growth cessation uncouples isotopic signals in leaf and tree rings of drought-exposed oak trees. *Tree Physiology*.
- RODEN, J.S., LIN, G., EHLERINGER, J.R. 2000. A mechanistic model for interpretation of hydrogen and oxygen isotopic ratios in tree-ring cellulose. *Geochimica et Cosmochimica Acta* 64: 21-35.
- SAURER, M., AELLEN, K., SIEGWOLF, R. 1997. Correlating $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in cellulose of trees. *Plant, Cell and Environment* 20: 1543-1550.
- SCHEIDEgger, Y., SAURER, M., SIEGWOLF, R.T.W. 2000. Linking stable oxygen and carbon isotopes with stomatal conductance and photosynthetic capacity: a conceptual model. *Oecologia* 125: 350-357.
- SCHOLLAEN, K., HEINRICH, I., NEUWIRTH, B., KRUSIC, P.J., D'ARRIGO, R.D., KARYANTO, O., HELLE, G. 2013. Multiple tree-ring chronologies (ring width, $\delta^{13}\text{C}$, $\delta^{18}\text{O}$) reveal dry and rainy season signals of rainfall in Indonesia. *Quaternary Science Review* 73: 170-181.
- SIDOROVA, O.V., SIEGWOLF, R., SAURER, M., SHASHKIN, A.V., KNORRE A.A., PROKUSHKIN, A.S., VAGANOV, E.A., KIRDYANOV, A.V. 2009 Do centennial tree-ring and stable isotope trends of *Larix gmelinii* (Rupr.) indicate increasing water shortage in the Siberian north? *Oecologia* 161 (4): 825-835, 10.1007/s00442-009-1411-0.
- STREIT, K., SIEGWOLF, R.T.W., HAGERDON, F., SCHAUB, M., BUCHMANN, N. 2014. Lack of photosynthetic or stomatal regulation after 9 years of elevated CO_2 and 4 years warming in two conifer species at the alpine treeline. *Plant, Cell and Environment* 37(2): 315-326.
- WOODLEY, E.J., LOADER, N.J., MCCARROLL, D., YOUNG, G.H., ROBERTSON, I., HEATON, T.H., GAGEN, M.H., WARHAM, J.O. 2012. High-temperature pyrolysis/gas chromatography/ isotope ratio mass spectrometry: simultaneous measurement of the stable isotopes of oxygen and carbon in cellulose. *Rapid Commun. Mass Spectrom* 26 (2): 109-114.
- YAKIR, D. 1998. Oxygen-18 of leaf water: a crossroad for plants-associated isotopic signals: In: Griffiths H (ed) *Stable isotopes and the integration of biological, ecological and geochemical processes*. Bios, Oxford, 147-168.

Contact

Olga Churakova (Sidorova)
olga.churakova@unige.ch