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Application of eco-physiological models to the climatic interpretation of $\delta^{13}C$ and $\delta^{18}O$ measured in Siberian larch tree-rings☆

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ABSTRACT

Tree-ring width and stable isotopic composition are widely used for the reconstruction of environmental conditions. Eco-physiological models simulating $\delta^{13}C$ and $\delta^{18}O$ provide tools to constrain the interpretation of measured tree-ring variations and their relationships to environmental variables. Here, we apply biochemical models of photosynthesis and a model of stomatal conductance to simulate the intra-annual dynamics of $\delta^{13}C$ values in photo assimilates and tree-rings. We use these models to investigate the physiological responses of larch trees growing on permafrost to variability in precipitation and permafrost depth associated with regional temperature and precipitation changes. Tree-ring width, $\delta^{13}C$ and $\delta^{18}O$ in wood and cellulose were measured in larch (*Larix cajanderi* Mayr.) samples from northeastern Yakutia (69°N, 148°E) for the period from 1945 to 2004 and used for comparisons with modeled $\delta^{13}C$ and $\delta^{18}O$ data.

Mechanistic models that quantify physical and biochemical fractionation processes leading to oxygen isotope variation in organic matter are used to identify source water for trees growing on permafrost in Siberia. These models allowed us to investigate the influence of a variety of climatic factors on Siberian forest ecosystem water relations that impact isotope fractionation.

Based on $\delta^{13}C$ and $\delta^{18}O$ in tree wood and cellulose measurements as well as outputs from different eco-physiological models, we assume that larch trees from northeastern Yakutia can have limited access to the additional thawed permafrost water during dry summer periods.

1. Introduction

Boreal forests are the largest ecosystems on the earth (Apps et al., 2006). Trees growing on permafrost in these ecosystems are sensitive to climate change, e.g., temperature increase, reduction in precipitations, thawing permafrost (Sugimoto et al., 2002; ACIA, 2004). Because of temperature increases, vapour pressure deficit (VPD) will likely increase as well resulting in increased evapotranspiration, which is especially impactful on tree's water relations. Measurements have shown no change in precipitation inputs, which may enhance drought stress in situations where enhanced water loss is not compensated by greater moisture inputs (Pachauri et al., 2014). Trees from the Boreal zone respond to both the timing and magnitude of changes in soil moisture and soil temperature, as well as permafrost thickness and its distribution, which itself is directly affected by snow and vegetation cover, soil

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texture and geothermal heat flux (Cable et al., 2013; Boike et al., 2013). The fate of trees growing on permafrost undergoing climatic and environmental changes is of great interest, because of the important role permafrost plays in these ecosystems and the large amounts of carbon stored in these soils (Cable et al., 2013). Boreal forests are particularly at risk with rising temperatures due to consistently low precipitation inputs (200–250 mm per year) (Sidorova et al., 2010; Boike et al., 2013). A number of studies have reported a pronounced deepening of seasonal permafrost thaw in Western Siberia (Moskalenko, 2001; Melnikov, 2004; Pavlov, 2004; Fyodorov-Davydov et al., 2009). Fyodorov-Davydov et al. (2009) investigated the spatial and temporal trends in the active soil layer (ASL) in North Yakutia, which is the top layer of soil with high activity of microbial processes and which thaws during the summer and freezes again during the autumn. No long-term measurements of active soil layer depth are known for northeastern Yakutia. Previous studies (Vaganov et al., 1998; Naurzbaev et al., 2002; Hughes et al., 1999) have shown the importance of June–July temperatures for larch tree growth in the Siberian north. Precipitation and permafrost melt water are particularly crucial for trees growing in regions with severe temperature limitations (Sidorova et al., 2007, 2010). Due to low temperatures in Siberian north, water loss is not yet as large as observed in European forest ecosystems (Saurer et al., 2014). However, with a continued increase in temperature (Sidorova et al., 2010), drought stress may increase accordingly.

Subarctic forests are remote from population centers, which, on one hand, allow the study of natural processes controlling these systems without direct anthropogenic impacts (i.e., management, introduction of exotic species). The disadvantage is that there are very few weather stations. There is only one weather station near Chokurdach, which is located 200 km away from our study site and unfortunately contains gaps in weather observations making it difficult to obtain appropriate meteorological data. Gridded large scale climate data (5° × 5° latitude/longitude) can help to fill in the gaps in the missing climate data from the local weather stations. Using the gridded temperature and precipitation data is an important source of information that can be used to quantify climate reconstructions during the last decade and further back in time (first half of 20th century). For example, based on tree-ring width chronologies we extracted temperature signals using both, local weather, and gridded data (http://climexp.knmi.nl) back in time (>100 years) (Sidorova et al., 2010). However, changes in precipitation for theses tree-line sites, where temperature is such an important factor, are difficult to reconstruct.

Stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotopes capture not only temperature signals but also record important information about moisture and precipitation changes. Climatic parameters like temperature, water availability, air humidity and the impact of changes in ambient CO_2 on photosynthetic CO_2 assimilation and water balance are reflected in the isotopic carbon and oxygen ratios of plant organic matter, potentially providing an isotopic fingerprint in the wood of tree rings. The analysis of tree physiological properties using carbon isotope ratios is particularly useful when combined with a photosynthesis model that considers the influence of meteorological conditions on plant functions, such as stomatal conductance and the substomatal vs. the ambient CO_2 concentrations (c_i/c_a ratio) (Farquhar et al., 1989; Arneth et al., 2002; Vaganov et al., 2006).

Oxygen isotopes in organic matter are modified by variation in the isotopic composition of source water, which is closely related to that of precipitation and soil water (though modified by evaporation at the soil surface). The $\delta^{18}O$ of meteoric water is directly related to cloud/atmosphere air temperatures (Dansgaard, 1964) as well as evaporation and condensation processes in the global water cycle. Input waters are modified (enrichment in ^{18}O) in the leaf during transpiration, which is imprinted on photosynthates and cellulose through biochemical fractionation and exchange processes.

In Siberia, the inter-annual variability of winter precipitation $\delta^{18}O$ is closely related to temperature variability and the North Atlantic Oscillation, while the variability of summer $\delta^{18}O$ appears to be dominated by regional—scale processes involving evaporation and convection (Butzin et al., 2014). Therefore, $\delta^{18}O$ values of tree rings reflect, as a first approximation, average ambient temperatures and humidity. Progress has been made in understanding the fractionation processes, which an $H_2{}^{18}O$-molecule undergoes from soil water to cellulose in tree rings (Craig and Gordon, 1965; Dongmann et al., 1974; Farquhar and Lloyd 1993; Roden et al., 2000). These models have been validated with experimental data from deciduous and coniferous tree species. Roden et al. (2000) developed a model, which takes environmental inputs as well as the isotopic exchange between cellulose and xylem water into account. The isotopic composition of leaf water can be theoretically estimated using the Craig–Gordon model (Craig and Gordon, 1965). The maximal enrichment according to the Craig–Gordon model is only reached at the evaporating surfaces. Bulk leaf water is less enriched than Craig–Gordon estimates because xylem water moves into the leaf via transpirational flux, which is modified by the back diffusion of enriched water from the evaporating surfaces as described by the Péclet effect (Farquhar and Lloyd, 1993).

In our study, we hypothesize that Siberian larch trees (*Larix cajanderi* Mayr.) from northeastern Yakutia growing on continuous permafrost will profit from using thawed permafrost water as an additional water source to survive periods of drought stress. An alternative hypothesis is that trees may go into decline because thawed permafrost water will still be too cold to be taken up by roots.

To test our hypotheses we applied mechanistic $\delta^{13}C$, $\delta^{18}O$ eco-physiological models and measured $\delta^{13}C$, $\delta^{18}O$ in wood and cellulose of larch trees (i) to reveal the interaction between trees and precipitation changes as well as changes of active soil layers due to thawing of permafrost under temperature and CO_2 changes in the atmosphere; (ii) to reveal the most important climatic variables that influence intra-annual dynamics of $\delta^{13}C$ and $\delta^{18}O$ in tree-ring wood and cellulose formation; and (iii) to describe the water-use of trees in permafrost ecosystems and the impact of permafrost thaw depth.

2. Material and methods

2.1. Study site and tree-ring width chronologies

Sampling of larch (*L. cajanderi* Mayr) was performed in northeastern Yakutia (69°N, 148°E), near the At-Khaya Mountains at the upper timberline in the forest tundra of the central Indigirka lowland at 250–350 m a.s.l. Crown density of larch forest tundra is low 0.5. The peat–gley and shallow gley soils prevail in the tundra zone as well as gley frozen soils that dominate under sparse taiga forests in southern part of the province. The lower part of the soil profile is covered by continuous low-temperature permafrost that is 500–650 m. thick and has a temperature range of −10 °C −12 °C (Fyodorov-Davydov et al., 2009). Surface soil moisture has decreased during June–August in Central Yakutia (Sugimoto et al., 2002). The vegetative period is short and can vary between 50 and 90 days. The average January temperature is −34.5 °C, and mean July air temperature is +9.6 °C obtained from the Chokurdach weather station (70°30′N and 148°08′ E) for the period from 1945 to 2004. The highest monthly mean soil temperature for the tundra zone that is covered by continuous permafrost is recorded in August (+4.1 °C) from a sensor depth of 0.06 m, while year to year variability in the mean soil temperatures from June to October