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Tracheid anatomical responses to climate in a forest-steppe in Southern Siberia☆

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ABSTRACT

Tree-rings are precious natural archives to assess ecosystem variability over time. Xylem anatomy in woody tissue is a promising source of information in tree-rings since it is closely linked to tree hydraulics and carbon fixation. However, despite the rising interest for cell anatomy in dendrochronology, still little is known about the interpretation of the variability of cell anatomical responses observed across different environments and species.

Here we analyze cell anatomical responses to increasing summer drought on 18 trees from 3 conifer species (*Picea obovata*, *Pinus sylvestris*, and *Larix sibirica*) growing in the transition zone between forest and steppe in the Republic of Khakassia (Russia). Analyses include the comparison of tracheid size distributions along climatic gradients and contrasting micro-topography from 1986 to 2008.

Results indicate an overall decrease of earlywood tracheid lumen and cell wall thickness to high temperature and drought regardless of species and site conditions. In particular an increase of one degree Celsius during the summer caused up to 5% reduction of earlywood cell lumen and wall thickness. These anatomical shifts suggest that a downscaling of hydraulic efficiency is not paralleled by increased hydraulic safety, presumably due to carbon limitation.

Based on the results of this case study, we suggest that increasing drought stress might hamper the formation of a functional xylem structure, thus being a possible trigger for a miss-acclimation causing long-term decline and higher exposure to hydraulic failures. Despite the promising study approach, more studies including more data (trees, years) and broader climatic gradients would be needed to further improve our mechanistic understanding.

1. Introduction

Annually dated tree-rings are a precious natural archive for assessing past and current ecosystem adaptability. Tree growth is frequently documented to be sensitive to environmental changes (St. George, 2014) and thus the widths and properties of the annual layers are recording precious information of changes in growing conditions between and within years (Fritts, 1976). The newly formed tree-ring represents both a relative measure of the annual growth performance, as well as the means through which the xylem has been adjusted to contribute to the future tree functioning. Thus, not only the total number of cells, but also the structure and the material from which they are made contribute to define the functional xylem properties (Lachenbruch and McCulloh, 2014).

In this perspective, the anatomy of xylem cells (as tracheids and vessels) is a promising tree-ring proxy to reconstruct past tree responses to environment because of its high intra-annual resolution and its direct link to important functional and physiological processes as sap transport and carbon fixation (Fonti et al., 2010; Fonti and Jansen, 2012). Thanks to these characteristics, the study of cell anatomical changes over time can help understanding the causes and the impact of xylem in relation to changing environmental conditions, especially in drought-prone areas, where drought-induced tree mortality is increasing (van Mantgem et al., 2009; Allen et al., 2010; Phillips et al., 2010; Peng et al., 2011). There is in fact an increasing body of evidence suggesting that warming and increasing drought are important triggers for forest decline and dieback in several ecosystems across the globe (e.g.; Allen et al., 2010; Rigling et al., 2013; Sangüesa-Barreda et al., 2015). The mechanism for mortality in this environment, although still under debate, seems to be mainly related to unbalances in the availability of carbon assimilates and/or the hydraulic functionalities

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(McDowell et al., 2008; McDowell and Sevanto, 2010; Sala et al., 2010; McDowell et al., 2011; Sevanto et al., 2014). In particular, it is proposed that these more stressful environmental conditions reduce net carbon assimilation and storage and/or alters the newly forming wood structure through which water moves from the soil up to the leaves, as observed for several species and environments (e.g.; Eilmann et al., 2009; DeSoto et al., 2011; Gea-Izquierdo et al., 2012; Martin-Benito et al., 2013; Hetzer et al., 2014; Olano et al., 2014; Venegas-Gonzalez et al., 2015). Yet, both characteristics are related to the process of wood formation and their results is permanently stored in the anatomical structure of the tree rings. The first determine the amount of resources available to build up the structure of an efficient water-transporting xylem, while the second determine the safety level against hydraulic failures when drought occurs. Thus, changed average environmental conditions or increased frequency and magnitude of extremes, will not only limit the trees' growth capacity, but, also deteriorate the hydraulic and mechanical properties of the xylem tissue over multiple sapwood layers, which can have an detrimental legacy on trees' future performance and survival (Anderegg et al., 2013; Heres et al., 2014).

Quantitative wood anatomy is a viable method commonly used to detect cell anatomical changes along variation in climatic conditions such as increasing warmth and drought. Moreover, thanks to recent developments in wood preparation (e.g.; Gartner et al., 2014) and computational image analysis (e.g.; Silkin, 2010; Wegner et al., 2013; von Arx and Carrer, 2014), it is now possible to quantify changes of different tissues and parameters at intra-annual scale with an acceptable effort. In particular, it has already been evidenced that environmental variability affects the size and structure of the water conducting xylem (see Fonti et al., 2010 for a review). Recent studies are also demonstrating that the xylem anatomical properties can have a possible impact on the hydraulic properties of the wood (e.g.; Schuldt et al., 2013; Chenlemuge et al., 2014; Hajek et al., 2014), and only few studies have demonstrated that on the long-term this affects tree vitality and performance (Heres et al., 2014). In addition to the measurement of the conduit size (e.g.; Abrantes et al., 2013; González-González et al., 2015), these developments have made possible for example to also analyze the conduit grouping (e.g.; von Arx et al., 2013), and the amount of ray parenchyma (e.g.; Olano et al., 2013; Fonti et al., 2015), making the link between anatomical changes and their functional meaning more quantifiable. However, despite the rising interest of cell anatomy in dendrochronology and its potential contribution in supplying a long-term perspective beyond the processes of mortality, the use of tree-ring anatomy in environmental science is still hampered by a limited mechanistic understanding. This is mainly due to complex interactions between short- and long-term environmental change on xylem formation and structure; and by difficulties in assessing how these changes in structure can long-term impact the functioning of trees, forests and ecosystems (Lachenbruch and McCulloh, 2014). To improve our mechanistic understanding of the environmental impact on xylem properties, we thus need to collect information of responses in a broader range of climatic gradient and contrasting environmental conditions.

In this study we analyzed intra-annual tracheid anatomical characteristics along series of tree-rings in order to assess how xylem structure of tree from the forest-steppe in the Republic of Khakassia (Siberia, Russia) are responding to increasing summer temperature and drought. In particular, based on a study case including mature trees from three conifer species (*Picea obovata*, *Pinus sylvestris*, and *Larix sibirica*) growing at two sites with differing soil water availability, we aim at assessing at what rate increasing temperature and/or water-limiting conditions affect the anatomical characteristics of the water conducting cells of the xylem.

Table 1
Sampling size and main tree characteristics (mean ± standard deviation).

Group	Number of trees[a]	DBH [cm]	Age [years]	Ring width[b] [mm]
Larix Dry	14 (5)	13.9 ± 3.6	138 ± 46.0	1.01 ± 0.78
Larix Wet	10 (5)	14.3 ± 3.0	156 ± 7.7	0.92 ± 0.61
Picea Wet	10 (5)	10.5 ± 2.5	110 ± 21.8	0.96 ± 0.67
Pinus Dry	14 (3)	15.7 ± 3.0	186 ± 46.9	0.85 ± 0.59

Dry = trees located on a south facing slope; Wet = trees located at the bottom of the slope (see Fig. 1).
[a] Numbers in brackets refer to the numbers of trees used for the anatomical measurements.
[b] Ring width data refers to the period 1986–2008.

2. Materials and methods

2.1. Study site, site characteristics, and sampled wood cores

The study site is situated in the Chulym–Yenisei Hollow (54°24′ N, 89°57′ E) in the Altai–Sayan region of the Republic of Khakassia in Russia (Fig. 1a). The region belongs to the forest-steppe belt in the Southern Siberia and is characterized by a moderately cold and dry continental climate. According to records from the Shira meteorological station (54°30′ N, 89°56′ E, 450 m asl, from 1966 to 2012, located 32 km northeast from the study site; Fig. 1b), the average annual temperature is 0.8 °C and the annual precipitation sum is 294 mm. The period with temperatures above 10 °C lasts 110–120 days, and the growing season usually onsets in April when daily temperatures rise above 5 °C. The majority of precipitation (90%) falls during the warm season (April–October), but summer droughts may occur in particularly warm and dry years. These events (defined as when total summer precipitation is at least one standard deviation less than the mean) occurred six times over the period 1969–2008.

The trees considered for this study have been selected in contrasting soil water conditions, i.e., on a steep south-facing slope and at its valley bottom, in the vicinity of the floodplain of an intermittent stream with a relatively high groundwater level (Fig. 1c). The distance between the sites is less than 500 m and the difference in elevation is 150 m. The slope site (Dry site) is characterized by higher amount of solar radiation, thin and well-drained soil and is covered by a mixture of *P. sylvestris* and *L. sibirica* with few *Betula pendula*. The floodplain site (Wet site) has podzolic chernozemic soil and is covered by an open woodland area dominated by *P. obovata* with sporadic *L. sibirica*.

A total of 48 wood cores have been collected at stem breast height from 4 group of dominant, healthy, damage-free, and mature trees, i.e.; from 14 *L. sibirica* (*Larix* Dry) and 14 *P. sylvestris* (*Pinus* Dry) at the dry site, and from 10 *L. sibirica* (*Larix* Wet) and 10 *P. obovata* (*Picea* Wet) at the wet site (Table 1 and Fig. 1e).

2.2. Tree-ring width and anatomical measurements and analyses

All 48 collected cores were sanded for tree-ring width (TRW) measurement (using a LINTAB measuring table connected to a TSAP Win software; RINNTECH, Heidelberg, Germany) and visually cross-dated. Cross-dating accuracy was assessed using COFECHA (Holmes, 1983). To perform climate-growth relationships, individual time-series were standardized to remove age-related and other trends using a flexible 32-yrs spline and averaged using a biweight mean into group chronologies (Cook and Kairiukstis, 1990). The strength of the common signal was quantified as the mean correlation between the detrended individual time-series (rbt).

Cell anatomical measurements were performed for the annual rings from 1986 to 2008 on a sub-selection of trees where the TRW was most highly correlated to its corresponding group average and