

ORIGINAL ARTICLE

The response of $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and cell anatomy of *Larix gmelinii* tree rings to differing soil active layer depths



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ARTICLE INFO

Article history:

Received 3 December 2014

Accepted 10 May 2015

Available online 19 May 2015

Keywords:

Central Siberia

Permafrost

Thermo-hydrological regime of soils

Tree-ring width

Quantitative wood anatomy

Stable C and O isotopes

ABSTRACT

Global warming is most pronounced in high-latitude regions by altering habitat conditions and affecting permafrost degradation, which may significantly influence tree productivity and vegetation changes. In this study, by applying a “space-for-time” approach, we selected three plots of *Larix gmelinii* forest from a continuous permafrost zone in Siberia with different thermo-hydrological soil regimes and ground cover vegetation with the objective of assessing how tree growth and productivity will change under different stages of permafrost degradation. A tree-ring multi-proxy characterization of mature trees was used to identify shift in ecophysiological responses related to the modified plant-soil system. Variability of tree-ring width (1975–2009), stable isotope ratios (oxygen and carbon, 2000–2009) and xylem structural characteristics (2000–2009) under climatic conditions of particular years indicated that an increased depth of the soil active layer will initially lead to increase of tree productivity. However, due to an expected water use increase through transpiration, the system might progressively shift from a temperature to a moisture-limited environment.

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Introduction

Over the last century, the consequences of global climatic change have been recorded throughout the world (IPCC, 2013). It is expected that in the 21st century climate change will further modify ecosystems in their functions and structures (White et al., 1999) and alter the vegetation on zonal, ecosystem, species and population levels (Iverson and Prasad, 2001; Tchebakova et al., 2003, 2010). These changes are driven by changing temperature and precipitation patterns and by lengthening of the growing season (Linderholm, 2006), which influence the rate of photosynthetic carbon assimilation and thus biomass production.

Projected climate changes suggest that forest ecosystems at high-latitude regions of Siberia, which are generally low in precipitation due to high continentality, will likely be subjected to the most significant impacts arising from the rapid increase in

temperature (Osterkamp and Romanovsky, 1999; Serreze et al., 2000; Sugimoto et al., 2002; Delisle, 2007). These forest ecosystems of the boreal zone will be particularly exposed to permafrost degradation resulting from warming and changes in precipitation regimes (Romanovsky et al., 2008; Schuur et al., 2008). To quantify the future impact of global warming on permafrost forest ecosystems, a better understanding is needed on how warming will affect both soils and vegetation.

Tree-ring growth parameters provide a valuable tool to trace past and predict future changes in the interactions between trees and environment (e.g. Fritts, 1976; Schweingruber, 1996). A significant stimulating influence of high air temperature on tree growth has been observed in boreal forest at local, regional and hemispheric scales (e.g. Vaganov et al., 1999; Holtmeier and Broll, 2005; Esper et al., 2010; Sidorova et al., 2011, 2012). However, tree growth on permafrost is habitat-specific and can be affected by other environmental factors such as drought, water logging or lack of nutrients (e.g., Barber et al., 2000; Lloyd and Bunn, 2007; Vaganov and Kirdyanov, 2010; Ohse et al., 2012). In recent studies radial tree growth in permafrost-affected forested terrains of Eastern Siberia

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is shown to depend on active soil layer thickness (seasonally thawing layer of soil) and its hydrothermal regime (Nikolaev et al., 2009; Kirdyanov et al., 2013).

The responses of boreal permafrost ecosystems to climate change are rather complex since transient responses of the depth of the active soil layer may be controlled by a combination of local habitat conditions and vegetation composition (Turetsky et al., 2012). Indeed, accumulation of ground vegetation (i.e. feather-moss) and organic layer on the surface of mineral soil play an important role in permafrost stability by insulating underlying soil and thus buffering an increase of air temperatures. In the frost-free season, soil surface temperatures are negatively affecting the thickness of the insulating organic layer (Harden et al., 2006; Romanovsky et al., 2008). Both, observations and manipulative studies have quantified the importance of moss covers to ground heat flux (Van Der Wal and Brooker, 2004; Gornall et al., 2007; Blok et al., 2011).

Disentangling the interconnections among plant, permafrost, and thickness of the organic soil layer and predicting how future warming and related potential changes in moisture availability will affect these relationships requires a concerted effort and a trans-disciplinary approach (Berner et al., 2013). A better mechanistic understanding of the tree-growth responses to climatic changes can be achieved by combining comparative year-to-year variability of tree-ring growth parameters together with physiological processes. Stable carbon and oxygen isotope compositions along with tree-ring width and anatomical parameters measured in the same tree rings provide information on the impact of the climate variability on tree physiological responses like photosynthetic rate and stomatal conductance. The combination of the stable C and O isotopes (dual isotope approach) facilitates the distinction between stomatal and photosynthetic responses (Scheidegger et al., 2000). Based on this approach it is possible to derive the impact of temperature and water availability as the driving climatic parameter (Sidorova et al., 2009; Knorre et al., 2010; Roden and Farquhar, 2012). Tree-ring anatomy measured in series of tree rings provides additional information about xylem functional adjustment to varying environmental conditions (e.g. Bryukhanova and Fonti, 2013; Fonti et al., 2013, 2015).

In our study we selected three plots within a forest site as model ecosystems representing three stages of progressive permafrost degradation to study the effects of expected environmental changes on high-latitude permafrost larch stands. Changes in responses of tree-ring parameters (tree-ring width, carbon and oxygen isotopes, lumen area and cell wall area of tracheids) are analyzed in detail to identify tree responses to climatic changes. In addition, differing tree physiological and structural responses to specific climatic years among the permafrost degradation stages are used to propose the mechanisms leading to a potential change observed along the permafrost degradation gradient selected in this study.

Materials and methods

Study area and description of the plots

The studied area is located in the northern part of central Siberia, close to the settlement of Tura (Evenkia, 64°18' N, 100°11' E, 150 m a.s.l.). The area is part of the permafrost zone of the northern taiga and is mainly dominated by larch forests (*Larix gmelinii* (Rupr.) Rupr.). The ground vegetation mainly consists of shrubs (*Vaccinium vitis-idaea* L. and *Ledum palustre* L.), mosses (*Pleurozium schreberi* (Brid.) Mit., *Aulacomnium palustre* (Hedw.) Schwaegr.), and lichens (*Cladonia* spp., *Cetraria* spp.). The climate is continental, characterized by long and very cold winters and short and cool to mild summers. The annual air temperature is −9°C and the annual

precipitation is 370 mm. Mean monthly temperatures vary between +16.6°C in July and −36.2°C in January. About 60% of the annual precipitation falls as rain (data from the Tura meteorological station of the Russian Research Institute of Hydrometeorological Information for the period 1936–2009). The growing season usually starts at the end of May and ends in late August (Bryukhanova et al., 2013).

The three study plots were selected within the even-age 60-year old larch forest developed after stand-replacing ground fire. The plots were established along a 100 m transect perpendicular to the Kochechum River and characterized by clear thermo-hydrological soil and ground cover vegetation differences (Fig. 1a) with increasing degree of soil thawing depths. The shallowest active soil (plot RZ) is located in a slightly depressed floodplain of an ephemeral creek and is characterized by a poorly-drained thick organic layer. The deepest active soil is located on the river bank (plot RB) and is characterized by a well-drained soil. The third plot (RZ) lies in between the two previous plots and is located on a slightly uplifted terrace. In this study we consider TER and RB as progressive stages of permafrost degradation in comparison to RZ, where RB is likely at the stage where the rooting zone is only affected by the permafrost meltwater at the beginning of the growing season.

The active soil layer depth (i.e., including the layer of mosses and the thawed mineral soil by temperatures > 0°C) was measured at 1 m interval along a transect of 100 m during June, July and in mid-September 2007. Additionally soil temperature and soil moisture content (expressed in % after drying in the oven at 105°C) were measured at max root abundance at 5 cm depth and deeper every 10 cm until reaching the permafrost layer.

Wood sampling

Wood cores 5-mm in diameter were collected from stems at breast height to determine tree growth, tracheid anatomical structure and stable carbon and oxygen isotope ratios in cellulose. Wood sampling was performed on about 20 dominant and non-tilted trees per plot during the summer 2010. Two cores per tree free of reaction wood were collected along the same radius, one for the dendrochronological and cell structure analyses and one for the isotopic measurements. The cores were collected perpendicular to the stem axis within 2–5 cm axial distance from each other in order to reduce the intra-tree variability between the cores. Dendrochronological measurements and climate–growth relationship between tree-ring width and monthly climatic data have been presented by Kirdyanov et al. (2013).

Measurement of tracheid anatomical structure

Tracheid anatomical measurements were carried out for the five trees per plot, which tree-ring width series showed the highest correlation to the site chronology ($r > 0.60$, $P < 0.01$). The measurements were performed for the last 10 annual rings, i.e. the rings formed from 2000 to 2009. Micro-sections (20 µm thick) were prepared using a sliding microtome (Reichert, Germany) and stained with methylene blue. Images of each ring cross-section were captured using a digital camera connected to a microscope (Axio Imager A1m, Carl Zeiss, Germany) with a 400× magnification. The image analysis software AxioVision Rel. 4.8.2 (Carl Zeiss) was used to measure cell anatomical structure. Tracheids in each ring were measured along five radial files of cells, which were selected among those with the larger tangential cell diameter. For each selected radial file we counted the number of cells (NC) and measured the tangential cell diameter (T). For each tracheid we assessed the radial lumen size (LD), the double cell wall thickness (dCWT), and the radial cell diameter (D). Finally, the cell wall area (CWA = dCWT × (T + D – dCWT)) and the cell lumen area

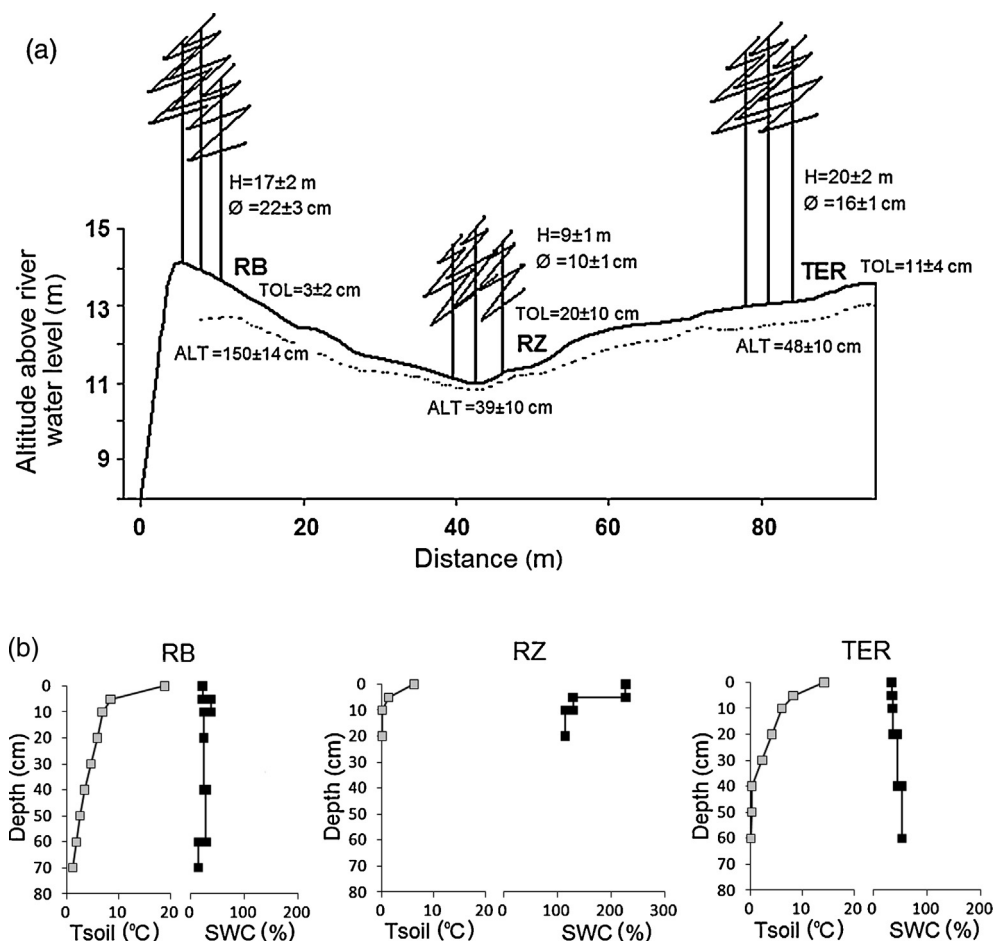


Fig. 1. (a) Topographic profile with plots' location along the studied transect (modified Fig. 1 from Kirdyanov et al., 2013) and (b) profiles of soil temperature (Tsoil – gray square) and gravimetric soil water content (SWC – black square) obtained for the middle of the growing season. RB – River bank, RZ – Riparian zone, TER – Terrace. In (a), the dotted line below the soil surface indicates the maximum active layer thickness (ALT, data from mid September 2007) of seasonally thawing soil. TOL – mean thickness of organic layer $\pm$ standard deviation.

($LUM = D \times T - CWA$) were calculated. LUM and CWA were averaged for each tree ring and considered as indicators of stem hydraulic conductivity and carbon assimilation, respectively.

Measurement of carbon and oxygen isotopes

Isotopic measurements were performed for the same 5 trees per plot, which were used for cell structure measurements. Isotope ratios were determined on wood cellulose of each annual ring separately for all trees over the period 2000–2009 for $\delta^{13}C$ and $\delta^{18}O$. To extract cellulose, the cores were split ring by ring using a razor blade. Cellulose extraction was carried out according to the methods described by Loader et al. (1997). Then, 0.2–0.3 mg of cellulose for $\delta^{13}C$ and 0.5–0.6 mg for $\delta^{18}O$ from each ring were weighed into tin and silver capsules respectively. The $\delta^{13}C$ values were determined by sample combustion under excess oxygen at a reactor temperature of 1020 °C in an elemental analyzer (EA-1110 Carlo Erba, Italy). The elemental analyzer was linked to an isotope ratio mass spectrometer (IRMS) Delta-S via a variable open split interface (CONFLO-II, both Finnigan MAT, Bremen, Germany). For the $\delta^{18}O$ determination samples were subject to a thermal decay at 1080 °C under oxygen exclusion (Saurer et al., 1998) in an elemental analyzer (EA-1108, Carlo Erba, Italy) linked to an IRMS (Delta Plus XP) via a CONFLO III (both Thermo Finnigan, Bremen, Germany). The isotopic values were expressed in the delta notation (δ) relative to the international standards, Vienna Pee Dee Belemnite (VPDB) for

carbon and Vienna Standard Mean Ocean Water (VSMOW) for oxygen. Since $\delta^{13}C$ data were covering a short period and were used only for comparisons among the plots, no correction for changes in $\delta^{13}C$ of atmospheric CO_2 has been applied.

Analysis of responses to climate

To explore structural and physiological responses of trees to climate variability, the relationship between cell anatomical and isotopic tree-ring parameters with the climate were analyzed in two ways. First, climate–growth relationships (Pearson's correlation) were calculated for the period from June to August (from 2000 to 2009) to evaluate the presence of different responses. Due to the short anatomical and isotopic time-series (10 years) and due to the absence of clear trend in this period, no age-detrending was applied. Second, physiological and structural responses among the plots, resulting from the qualitative analysis of selected pointer years, was used to derive the mechanistic coherency of climatic sensitivity with the expected physiological and structural cause-effect responses under different stages of permafrost degradation. A comparison among the growing seasons (from June to August) over the last 74 years (1936–2009) indicated that the last 10 years (2000–2009) were among the warmest of the period covered by the available climatic data (Fig. 2). Thus, for our qualitative comparison of the responses to climatically differing growing seasons among the last decade, we selected the warmest and wettest (2001), the

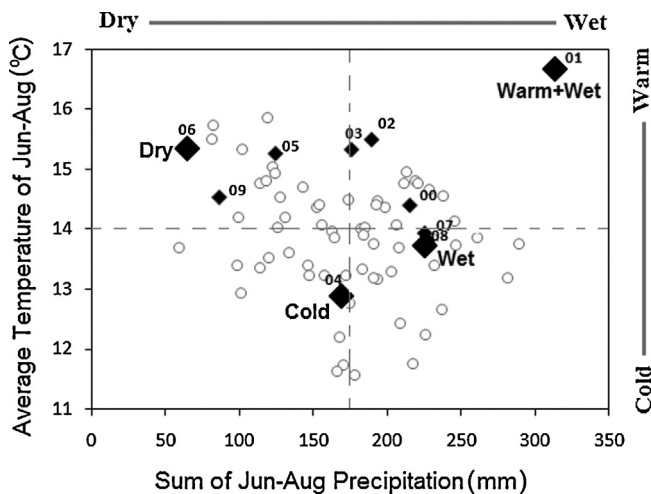


Fig. 2. Mean air temperature plotted against sum of precipitation for the period from June to August. Graph includes all recorded instrumental data (from 1936 to 2009 shown as open circle) and the studied years from 2000 to 2009 are shown in black rhombs. Dotted lines indicates threshold (14°C) between cold and warm years, and between dry and wet years (175 mm per June–August period).

coldest (2004), and the driest (2006) growing season, as well as a year characterized by wet growing conditions (2008). Since all the selected years were not preceded by extreme conditions, we assume that there is not unusual carry-over effect biasing our observations.

Results

Soil hydrothermal parameters and stands data

RZ displayed the thinnest active soil layer (it thawed to a maximum of 20 cm depth), and was water saturated over the growing season (gravimetric soil water content varying from 227% to 114%). TER showed an active soil layer depth between 19 cm in early June and 60 cm in late August with water content between 52% and 33%. The third plot (RB) had the thickest active soil layer (ranging from 54 cm in early June to 150 cm at the end of August) and lowest soil water content up to 21% (Fig. 1b).

Despite the similar age of the trees, the forest structure and the soil vegetation clearly differed among the plots (Fig. 1a). At RZ, the average tree height is 9 m and diameter at breast height is 10 cm. Because of the extremely wet and cold soil, trees at RZ have a very shallow root system (mainly extended in the peat layer and also to a depth of 5 cm into mineral soil) growing only on uplifted patches. The thickness of the moss and peat layer (organic layer) is 20–30 cm. At TER the stand is characterized by taller tree (20 m) with 16 cm thick stem diameter. The thickness of the organic layer is 10–15 cm. The stand structure at RB is characterized by 17 m tall trees with average stem diameter of 22 cm. The thickness of the moss and peat layer is only 3–5 cm.

Tree growth and climatic responses

Trees at the three plots show quite different growth patterns, despite their close vicinity (Fig. 3). The trees of RZ not only diverge from the other two plots in the average radial increment (0.79 ± 0.36 mm at RZ versus 1.84 ± 0.82 mm and 1.94 ± 0.68 mm for RB and TER respectively), but also differ in the year-to-year variability (data from Kirdyanov et al., 2013). Although a fairly strong common signal between individual trees within each plot is evident (mean inter-series correlation of 0.64, 0.45, and 0.55 for RB, RZ, and TER, respectively), the relatively low correlations with the RZ detrended chronology ($R_{\text{RB-RZ}} = -0.04$ and $R_{\text{TER-RZ}} = 0.35$,

$P > 0.01$) indicate plot specific growth responses. Between RB and TER chronologies the correlation was $R_{\text{RB-TER}} = 0.60$, $P < 0.01$).

Temperature of the current summer appears to correlate significantly only at RZ (correlation with July temperature $R = 0.35$, $P < 0.05$). Tree radial growth at all the plots correlates positively with late summer temperature (August) of the previous years with $R > 0.43$. Only RZ was also significantly correlated with previous year's July temperature ($R = 0.36$). In contrast, RB and TER tree growth clearly respond to summer precipitations for both the current and previous year ($R > 0.30$, $P < 0.05$), while RZ responds only negatively to previous year June precipitation ($R = -0.47$, $P < 0.05$). No significant correlation with the winter climate has been found.

Variability of tracheid anatomical parameters

Over the last ten annual rings (ranging from 2000 to 2009), relatively smaller cells with thinner walls are formed in RB and TER in the years characterized by unfavorable growing condition (when trees formed narrow tree rings as, e.g., for the dry growing season 2006; Fig. 4a). This seems to be more evident especially for the earlywood cells since values over the whole ring are strongly influenced by the proportion of latewood, which tend to be narrower in years with dry and/or cold conditions for plots with deep active soil layer. For RB and TER, it results in very low values both for earlywood CWA ($452 \mu\text{m}^2$ and $600 \mu\text{m}^2$) and LUM ($895 \mu\text{m}^2$ and $975 \mu\text{m}^2$) (Fig. 4a). In contrast, during wet and warm growing seasons (i.e., 2001, 2002 and 2008) larger cells were produced. RZ, unlike the other plots, is characterized by quite stable cell parameter values over time, but earlywood cells indicate an increase in LD from 36 to $43 \mu\text{m}$ during the last 10 years. Over this period, the limiting effects of the cold year 2004 and partially of the dry year 2006 on CWA can also be observed in cell structure of trees at RZ.

Variability of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$

The stable carbon and oxygen isotope ratios in cellulose were determined for the period 2000–2009 (Fig. 4b). All plots showed a similar year-to-year pattern. The least negative $\delta^{13}\text{C}$ values of cellulose in tree rings were observed at RB ($-23.89 \pm 1.21\text{‰}$, mean $\pm$ SE), whereas trees from RZ had the most negative $\delta^{13}\text{C}$ values of all the plots ($-25.84 \pm 0.84\text{‰}$). The mean $\delta^{13}\text{C}$ value for TER was $-25.04 \pm 1.09\text{‰}$. Correlations among the plots in mean $\delta^{13}\text{C}$ of tree-ring cellulose ranged from 0.63 (between RB and RZ, $P < 0.05$) and 0.82 (between RB and TER, $P < 0.05$). All plots showed higher values in $\delta^{13}\text{C}$ in the dry year 2006 and more negative values in wetter years (2001, 2007, 2008, and except for RB in the cold 2004) than the average over all ten years.

The mean $\delta^{18}\text{O}$ value of tree-ring cellulose was largest for trees from RZ ($23.19 \pm 1.12\text{‰}$, $P < 0.05$) and very similar for RB and TER ($21.71 \pm 0.97\text{‰}$ and $21.76 \pm 0.70\text{‰}$, respectively). The variability of $\delta^{18}\text{O}$ at RZ was characterized by a year-to-year variation of up to 4‰. A significant positive correlation was found between RZ and TER ($R = 0.92$, $P < 0.05$), which were also positive but not statistically significant between the other plots.

Inter-annual variability of $\delta^{13}\text{C}$ with $\delta^{18}\text{O}$ showed synchronic character for RZ with $R = 0.64$ ($P < 0.05$) (Table 1). In contrast, no synchronic pattern was found between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in tree rings of RB and TER ($P < 0.05$).

The comparisons between tree-ring width and isotope ratios for all studied plots show mainly negative, but not significant correlations ($P > 0.05$). A positive correlation was found between $\delta^{13}\text{C}$ and LUM for trees from RB ($R = 0.74$, $P < 0.05$) and a negative with cell wall parameters (with CWT $R = -0.89$ and with CWA $R = -0.81$, $P < 0.05$). Similarly, trees from TER show high correlation between $\delta^{13}\text{C}$ and CWA ($R = -0.63$, $P < 0.05$) (Table 1).

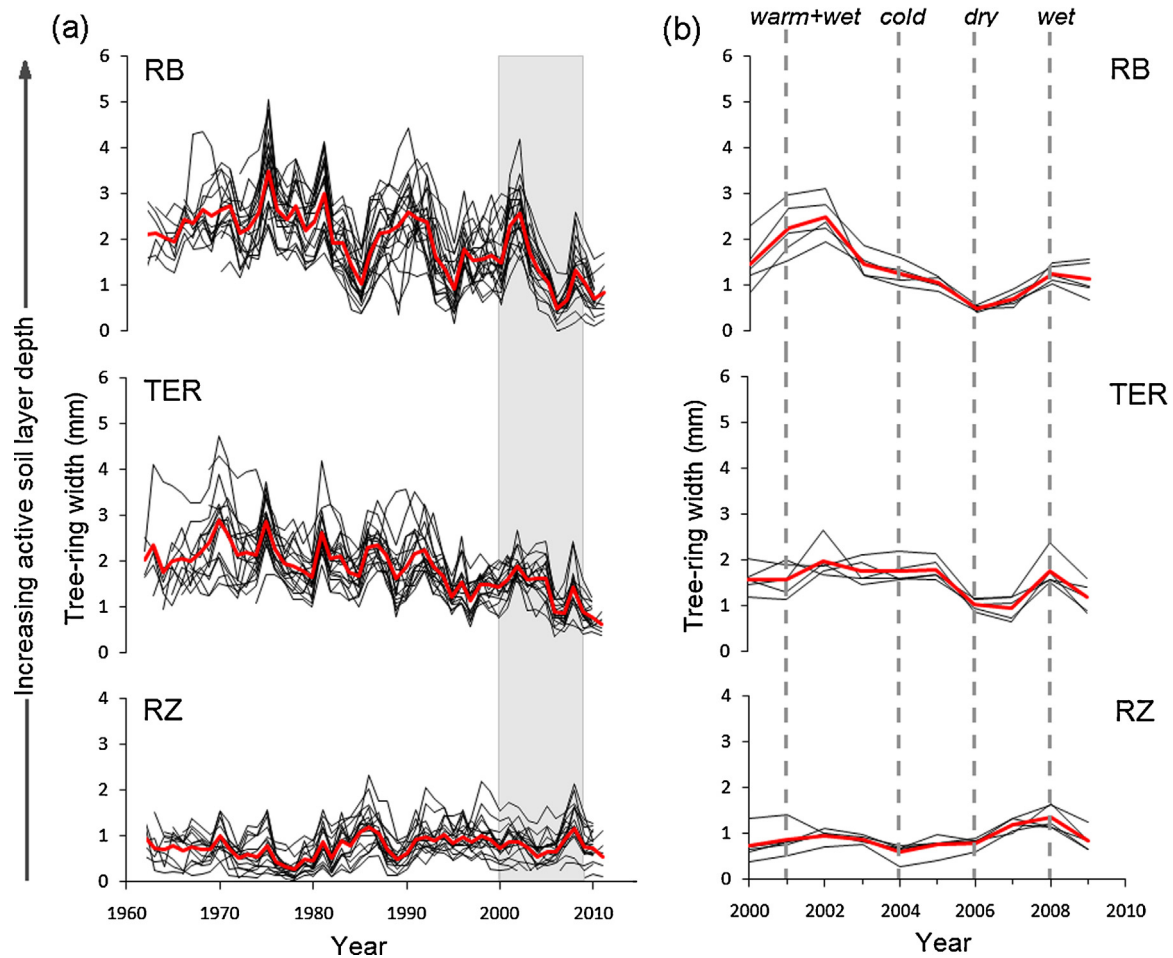


Fig. 3. Individual time-series (black thin lines) of tree-ring width for the three studied plots (a) for the period from 1962 to 2011 ($n=18$). Gray surface indicates the period used for isotopes and anatomical analyses and (b) for the period from 2000 to 2009 ($n=5$). Red bold lines are the mean plot chronologies. The dotted lines indicate a warm and wet (2001), a cold (2004), a dry (2006) and a wet (2008) year within the last decade. RB – River bank, RZ – Riparian zone, TER – Terrace.

Discussion

This case study, based on a detailed comparison of multi-proxy tree-ring measurements of physiological and structural tree responses, proposes a mechanistic framework explaining the development of our high-latitude larch stand under projected climate change and permafrost degradation. The topographic constellation of the three selected plots is characterized by clearly different soil thermo-hydrological regimes, and proved to be an ideal model of the progressive stages of permafrost degradation, to test our hypothesis and to propose a possible mechanism explaining warming-induced change in our forest ecosystem.

The effect of warming on permafrost degradation depends not only on the direct input of heat, but also on the thickness of the

insulating organic layer with living moss and lichens as well as the amount of precipitation (Pozdnyakov, 1986; Knorre et al., 2009; Matsuura and Hirobe, 2010; Kharuk et al., 2011). The thick moss and peat layers of the riparian zone (RZ) clearly created a barrier for thermal exchange between air and soil. Although the plots were experiencing similar air temperatures, the temperature at the mineral soil surface differed significantly due to the insulation, reaching 8.4 °C at RB and only 1.2 °C at RZ at mineral soil surface in the middle of June (the period of maximum rate of tree-ring growth). Thick moss and peat layers at RZ affects the rate at which the soil thawing occurs within the season (Fig. 1b) since irradiative heat and “warm” precipitation are intercepted by the ground vegetation. Moreover, water has a high heat capacity therefore more heat is needed to melt the water-saturated soil at RZ. The thin organic layer on TER

Table 1

Correlation between tree-ring parameters for each plot for the period 2000–2009 (significant correlation at $P < 0.05$ are in bold).

	RZ					TER					RB				
	TRW	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	CWA	LUM	TRW	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	CWA	LUM	TRW	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	CWA	LUM
TRW	1					1					1				
$\delta^{13}\text{C}$	–0.31	1				–0.47	1				–0.40	1			
$\delta^{18}\text{O}$	–0.60	0.64	1			–0.01	0.43	1			–0.23	0.12	1		
CWA	0.77	–0.16	–0.38	1		0.91	–0.63	–0.21	1		0.62	–0.81	–0.01	1	
LUM	–0.01	0.04	0.25	–0.28	1	–0.02	0.17	0.02	–0.34	1	0.11	0.74	–0.05	–0.66	1

RB – River bank, TER – Terrace, RZ – Riparian zone. TRW – tree-ring width, CWA – cell wall area, LUM – lumen area. Plots in the table are ordered by increasing active soil layer depth (from RZ to RB).

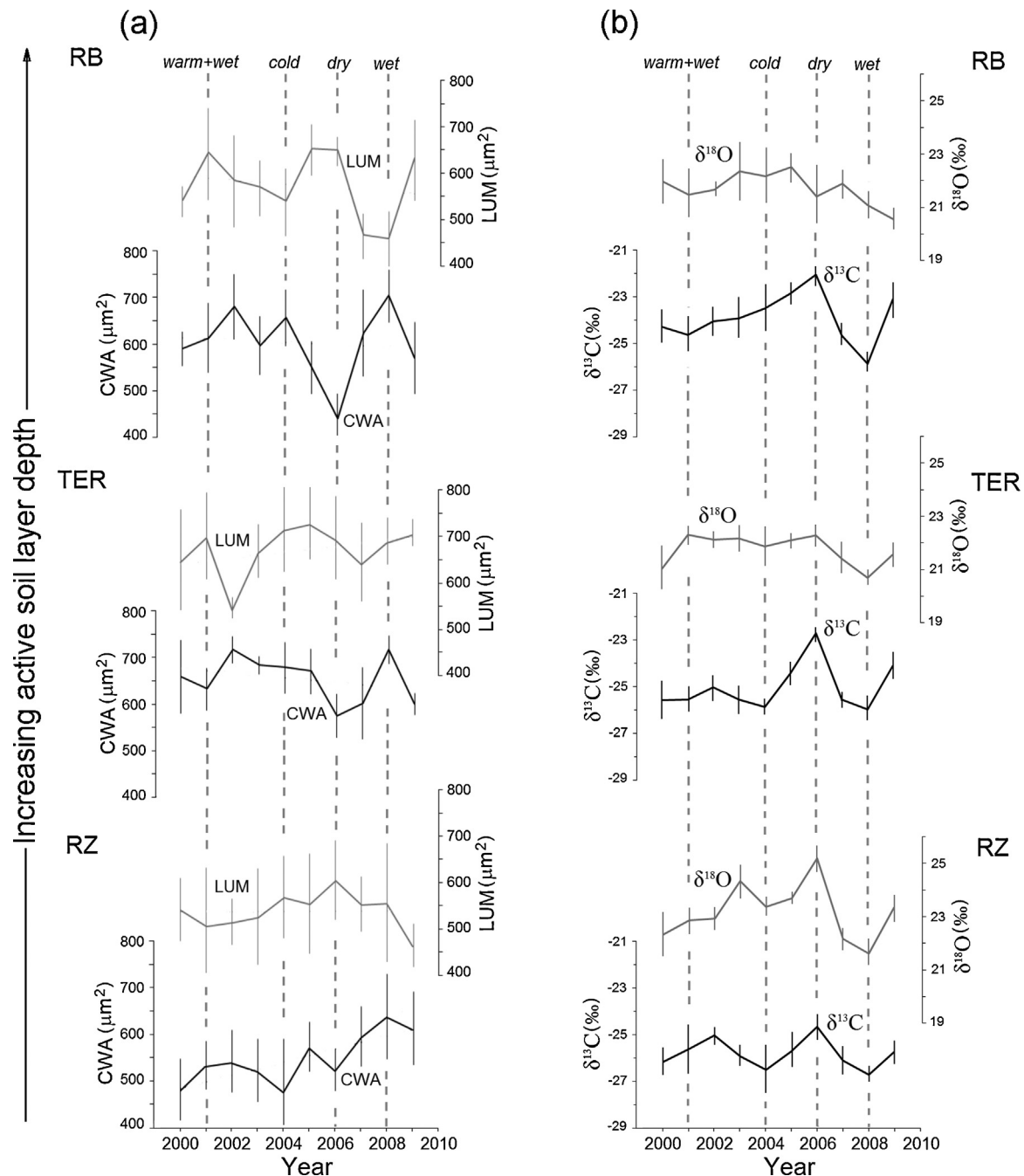


Fig. 4. (a) Mean values of cell wall area (CWA – thick black lines) and lumen area (LUM – thick gray lines) in the cellulose for the three studied plots. RB – River bank, RZ – Riparian zone, TER – Terrace. Vertical thin lines are the standard deviation. The dotted lines indicate a warm and wet (2001), a cold (2004), a dry (2006) and a wet (2008) year within the last decade.

and RB were not sufficient to impede the ingress of heat flux into the soil promoting a faster soil thawing (Fig. 1b). These modifications of the soil thermal and hydrological properties at TER and RB compared to RZ (i.e.; the maximal depth and seasonal dynamic of the thawing soil layer) might have stimulated growth changes in the root environment. Thus, trees could profit from an increased temporal and spatial access of their roots to a much larger nutrient and water pool in deeper active layers under warm condition enhancing metabolic and growth processes.

Recent tree-ring studies on permafrost soils are confirming this dependence of radial tree growth on the active soil layer depth and its hydrothermal regime (Nikolaev et al., 2009; Kirdyanov et al., 2013). The changes in the permafrost regimes are also clearly

reflected in the growth responses to climatic changes observed in our plots. As a consequence of the seasonal active soil layer thawing, the onset of the growing season has started earlier at RB. Xylogenesis observations from the same plots during 2007–2008 showed differences in the onset of wood formation among the plots. It was observed that RB trees initiated the onset of cell radial enlargement by one week earlier and the onset of cell wall lignification and maturation by up to two weeks earlier compared to the trees on the RZ plot (Bryukhanova et al., 2013). The increase in the timing of assimilation favored an increase of productivity for TER and RB compared to RZ.

As a consequence, however, increased growth productivity also accelerates the exhaustion of soil moisture reservoirs due to

Table 2

Observed response of tree-ring parameters under the progressive transition from RZ to TER and from TER to RB stages of permafrost degradation.

			Habitat				
			RZ	–	TER	–	RB
Driving variables		Temperature	Soil	↑			↑
		Moisture		↓			↘
		Active layer depth		↑			↑
		Nutrient availability		↑			↗
Responding variables	Physiology	Stomatal conductance	Plant	↑			↗
		Photosynthetic rate		↑			↗
	Xylem hydraulic	LUM		↑			↓
		CWA		↑			↓
	Xylem structure	δ ¹³ C		↑			↗
		δ ¹⁸ O		↓			↘
	Productivity	TRW		↑			↗

RZ – Riparian zone, TER – Terrace, RB – River bank. TRW – tree-ring width, CWA – cell wall area, LUM – lumen area. ↑ = increase, ↗ = slight increase, → = constant, ↘ = slight decrease, ↓ = decrease.

increased water losses by evapotranspiration. Direct evidence of the absolute differences in water use is observed in the characteristics of the water conducting cells, i.e. in the size of the earlywood tracheids. The higher CWA values observed for TER and RB indicate that trees benefited from the improved soil conditions by investing more assimilates in the cell wall construction. This phenomenon is apparent also when considering the year-to-year variability. The wet year 2008 promoted higher CWA since all plots could benefit from an increased heat transfer via precipitation infiltrating into the soil resulting in an increased C-assimilation due to a longer growing season. In contrast, the drought conditions (e.g. dry year 2006) displayed small CWA, especially strongly expressed in RB, resulting from a reduced assimilation and stomatal closure induced by drought (Lebourgeois et al., 1998; Lawson et al., 2003). In general, an unfavorable year for the formation of cells with high CWA is followed by a year with relatively low LUM. These findings suggest a reduction of tree's carbohydrate reserves in unfavorable (drought) years that does not allow the production of large conductive cells in the successive years. It is noteworthy to report that the trees at RZ showed the smallest CWA in the cold year summer 2004, while the other two plots displayed the smallest CWA during the driest summer 2006.

Usually, droughts cause stomatal closure and lower C-isotope discrimination, leading to less negative $\delta^{13}\text{C}$ values of assimilated C, which is confirmed by higher average $\delta^{13}\text{C}$ values at the drier RB. The anticipated shift of our forest ecosystem toward a water-limited environment is clearly indicated by the $\delta^{13}\text{C}$ isotopic response of the plots with a deep and well-drained active soil layer (TER and RB). In a dry year, like 2006, a lower discrimination of the heavy carbon isotope and more positive $\delta^{13}\text{C}$ values has been observed (Fig. 4b). In contrast, the wet year 2008 shows a decrease in the $\delta^{13}\text{C}$ values, indicating increased ^{13}C discrimination, due to an improved water supply. Interestingly, the extremely wet and warm year 2001 did not cause any remarkable change in the C-isotopic signature in the annual rings. Obviously, the increased transpiration was compensated by sufficient water supply under the given environmental conditions. Consequently, photosynthesis increased, leading to a higher accumulation of carbohydrates, and the next year tree-ring width, which at drier plots TER and RB were the largest over the period 2000–2009. This effect clearly implies a significant carryover effect (Kagawa et al., 2006) of the photosynthates formed in 2001 to tree-ring growth in 2002. At RZ, the responses of $\delta^{13}\text{C}$ to changes in temperature and precipitation are coherent with the other two plots, but occurring at a lower magnitude (see level and annual variability of $\delta^{13}\text{C}$ in Fig. 4b), because the small affluent creek maintains the soil moisture content and

continuous water supply. Moreover, the effect of warm and wet 2001 is less pronounced in tree-ring width at RZ since the soil at this plot is water saturated and any additional water supply can diminish or even inhibit tree-ring growth (as a result of anaerobic conditions in the rhizosphere), which is only partly compensated by higher summer temperature.

The oxygen isotopic ratio in tree rings from RZ shows 1–2‰ higher values than at TER and RB. The explanations of the enrichment of ^{18}O at RZ could be due to physiological drought caused by low temperatures or by waterlogging (anaerobiosis) of rhizosphere impeding water uptake by root. The roots of trees at TER and RB were not water logged and therefore not under anaerobic conditions, the trees had probably a higher transpiration rate, due to higher stomatal conductance. This would reduce the H_2^{18}O leaf water enrichment as a result of the Péclet effect (Farquhar and Lloyd, 1993; Scheidegger et al., 2000), compared to trees at the RZ plot. At the intra-annual level, we would therefore expect an enrichment of $\delta^{18}\text{O}$ under these conditions (Yakir and Sternberg, 2000). Differences of tree-rings $\delta^{18}\text{O}$ among plots can also be influenced by different water sources. Particularly, wood at RZ is ^{18}O -enriched, which could be related to higher values of $\delta^{18}\text{O}$ in source water in both creek and permafrost (and both recharged by “heavy” creek waters) supplying trees with water during the growing season in addition to rains (which is also heavy). The low inter-tree variability in $\delta^{18}\text{O}$ is due to the continuous input of creek water, buffering the $\delta^{18}\text{O}$ variability in the source water; whereas at TER and RB, trees are supplied by rain and permafrost water.

In Table 2 we summarized observed cause-response relationships between environment, tree physiology, and tree-ring structure. We consider the transitions from RZ to TER and from TER to RB along progressive stages of permafrost degradation exerting strong transformations in growing season length, thermo-hydrological regime of soils and nutrient availability for larch trees developed within continuous permafrost. In turn, soil water content will affect stomatal conductance and photosynthetic rate, leaving their fingerprints in tree-ring parameters such as lumen area and cell wall area of tracheids, and isotope composition $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of the cellulose. The observed changes in tree-growth responses along our transect suggest future climate driven changes. Initially permafrost will provide additional water resources for trees during the growing season. Yet we can assume that the limited precipitation will lead to chronic drought stress, eventually growing in its intensity (Sugimoto et al., 2002), while the permafrost water reserve is gradually exhausted. Based on studies of century-long stable isotope chronologies in tree rings first indications for a slowly developing water shortage of larch trees in Northern

(Sidorova et al., 2009) and Southern (Knorre et al., 2010) Siberia have been observed in the last fifty years.

In conclusion, our study case suggests that permafrost degradation can lead to an initial increase of forest productivity due to an increase of the active soil layer depth providing an increased water and nutrient availability. However, under the current precipitation regime in the studied region the soil water reserves will be gradually exhausted, with the possible consequences of a progressively increasing drought stress. The rate of change however might vary depending on the thickness of the ground covering vegetation, which regulates the heat exchange between soil and atmosphere.

Acknowledgements

This work was supported by the Swiss National Science Foundation (Valorization Grant IZ76Z0.141967/1), the Joint Research Project SCOPES (IZ73Z0.128035/1) and Ministry of Education and Science of the Russian Federation (Grants from the President of RF for Young Scientists MK-5498.2012.4 and MK-1589.2014.4). The research is linked to activities conducted within the COST FP1106 network.

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