

Sunshine as culprit: It induces early spring physiological drought in dark coniferous (*Pinus sibirica* and *Abies sibirica*) alpine forest

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ARTICLE INFO

Keywords:

Dark conifers
Radial growth
Mountain forest
Climate change
Physiological drought

ABSTRACT

Trees comprising high mountain forests have different requirements for site conditions (such as the water supply), thus current climate warming leads to varying reactions of upper forest boundaries depending on the site conditions and ecophysiological features of species. Positive reactions to an increasing heat supply during vegetative season may be hindered for drought-sensitive species by a water deficit in a cold environment, particularly during late winter or early spring.

We investigated the radial growth of dark coniferous forest species Siberian stone pine (*Pinus sibirica* Du Tour) and Siberian fir (*Abies sibirica* Ledeb.) growing on slopes of different orientation (south-west, east, and north) near the upper forest boundary in an area undergoing fast climate warming: the Western Sayan Mountains (South Siberia, Russia), near a massive water reservoir. Correlations of tree-ring width chronologies with moving 21-day temperature series were used to more precisely determine the timing of temperature influence; an analysis of extreme and optimal years and multifactor regression modeling were applied to assess the most favorable/unfavorable thermal conditions in the study area and to estimate the tree growth reaction to the current climatic trends, respectively.

Despite relatively low variation in growth (standard deviation < 0.2), a significant common climatic signal in tree-ring width was found at all sampling sites. On the shaded northern slopes, *P. sibirica* is only mildly limited by summer temperatures and has a low similarity (correlations and synchronicity of extreme/optimal years) with other sites. Conversely, the growth of *A. sibirica* and *P. sibirica* on two sunlit slopes is similar ($r = 0.44\text{--}0.81$) and has a common pattern of regulation by temperatures before ($r = -0.17\text{--}-80.40$; April 3 – May 4 on average) and more significantly during vegetative season ($r = 0.31\text{--}0.44$; May 17 – August 27 on average). We hypothesize that both species, being drought-sensitive, undergo water stress in the early spring, and exposition of previous years' needles to severe temperature variation may lead to partial defoliation and xylem embolism, thus suppressing growth. The patterns of climatic response and species distribution on slopes indicate that *A. sibirica* is more sensitive to this physiological drought and needs gentler slopes than *P. sibirica*.

Temperature increase in the study area during the last decades have occurred about five times faster in the early spring (being enhanced by the reservoir) than in summer. This combination of spring and summer warming leads to an increase in *P. sibirica* radial growth on the northern slope and the stable growth of both species on sunlit slopes, i.e. providing a tentatively optimistic assessment of the dark coniferous forests' near future in the region.

1. Introduction

The common belief about the growth of trees near upper forest boundaries being limited mostly by the heat supply during the vegetative season is very simplistic and, thus, is not always consistent with

reality (Naurzbaev and Vaganov, 2000; Körner, 2003; Briffa et al., 2004; Wang et al., 2005; Helama and Sutinen, 2016; Jiao et al., 2016; Jochner et al., 2018 and others). In the cold conditions of highlands physiological drought is an important factor at low temperatures, when transpiration begins to rise in late winter or early spring in response to

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<https://doi.org/10.1016/j.foreco.2019.117458>

Received 11 June 2019; Received in revised form 3 July 2019; Accepted 4 July 2019

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rise of air temperature, but the roots are not capable of providing water from the frozen or cold soil (Grace and James, 1993; Körner, 1998; Sudachkova et al., 2002; Mayr, 2007) despite the increasing elevational gradient of precipitation. We suggest that this phenomenon may weaken the positive response to the temperature increase of the more drought-sensitive species. Therefore, climate warming can give competitive advantages to moisture-loving dark coniferous species in areas with sufficient moisture and to more drought-resistant species in regions with a moisture deficit (Bigler et al., 2007; Chytrý et al., 2008; Kharuk et al., 2009; Berner et al., 2013; Walker et al., 2015; Jiao et al., 2019).

Dark coniferous Siberian stone pine (*Pinus sibirica* Du Tour) and Siberian fir (*Abies sibirica* Ledeb.) occupy some of the leading places among tree species forming upper forest limits in the continental part of Siberia (Sapozhnikov, 1901, 1913; Krylov, 1931; Kuminova, 1960; Kuminova et al., 1976; Sedelnikov, 1988; Chytrý et al., 2008). Observations of the contemporary dynamics of the forest upper boundary and the state of the high-mountain dark conifer forests are contradictory, grading from the expansion of *P. sibirica* in both elevational directions (Grace and James, 1993; Bocharov, 2009; Kharuk et al., 2009) to dark conifers' dieback from droughts (Zamolodchikov, 2012; Kharuk et al., 2013, 2017; Allen et al., 2015). Unlike, for example, larch, the growth of which in the high mountains is largely controlled by spring-summer temperatures (Panyushkina et al., 2005; Peters et al., 2017; Kukarskih et al., 2018; Bai et al., 2019), *P. sibirica* and *A. sibirica* tend to have less pronounced and homogeneous climatic signals even at the upper forest boundary (D'Arrigo et al., 2001; Gerasimova et al., 2010; Nazarov and Mygland, 2012). However, these species have several important ecophysiological features that can contribute to their climatic responses: they are evergreen (retaining needles of the past several years, which ensures photosynthesis activity before bud break), have dark needles (more effectively absorbing and using light; Kozłowski and Pallardy, 1997) and have greater moisture demands compared to larch (Chytrý et al., 2008; Kharuk et al., 2009; Tchebakova et al., 2009).

Therefore, the question of the current state and forecasting the dynamics of the upper treeline and high mountain forests as a whole is still not clearly resolved and requires further detailed consideration on the scale of individual regions and even plots (due to the relief and microclimate mosaic in mountains), especially for species with a complicated climate response. In the Republic of Khakassia, especially in mountainous areas, climate warming proceeds more intensively and significantly exceeds not only the average regional trends but also global trends (Babushkina et al., 2018). Therefore, a convenient testing ground for addressing this issue is the northern-central area of the Western Sayan Mountains, where the rapid rate of regional temperature increase is enhanced by local warming by the massive water reservoir. According to Liu et al. (2013), there is no significant drop in the moisture level (PDSI) in this region; therefore the reaction of tree stands to a temperature increase with a stable level of moisture can be observed here. In this study, we analyzed two dark coniferous species' growth in high mountain area of the Western Sayan and their responses to the temperature using moving short-term climatic series to achieve a high temporal resolution, and we attempted to identify the possible reasons for the complexity of this response, including local conditions such as the slope orientation.

2. Materials and methods

The study was conducted on the northern macroslope of the Alan Ridge of the Western Sayan Mountains (Fig. 1). Most of the mountain range is covered by conifer forests, represented by *Pinus sylvestris* L., *Pinus sibirica* Du Tour, *Larix sibirica* Ledeb., *Picea obovata* Ledeb., and *Abies sibirica* Ledeb. At the upper forest boundary, *P. sibirica* and *A. sibirica* prevail. Soils are loamy, thin and stony, with numerous outcrops of solid rocks. The climate of the study area is continental, with high

daily and seasonal temperature variation. Precipitation throughout the year is unevenly distributed; approximately 80% of its annual amount falls in April–October with a maximum in July and a minimum in the second half of winter. In the foothills, the average annual temperature is 0–6 °C and the annual sum of precipitation is 400–800 mm. Substantial elevational climatic gradients are observed: the air temperature drops by 0.6–0.65 °C per 100 m and the annual precipitation amount increases by 100–200 mm per 100 m of elevation (Polikarpov and Nazimova, 1963; Stepanov, 2006). In the 1970s, the massive Sayano-Shushenskoe Reservoir was created on the Yenisei River near the study area, and the hydroelectric station was launched in the end of 1979. This led to a mitigation of climate continentality, particularly the winter temperature increase, on the background of regional warming, which is also more pronounced in winter (Babushkina et al., 2018).

Cores of adult living trees of *Pinus sibirica* (PiSi) and *Abies sibirica* (AbSi) without signs of growth suppression and damage were collected at Gladenkaya Mt., 6–8 km north-west of the Cheryomushki weather (1951–2015 daily temperature and precipitation series; 52.87°N 91.42°E, 330 m a.s.l.) located on the Yenisei River shore near the Sayano-Shushenskoe dam (Fig. 1b). Sampling sites were selected on slopes of different orientations (Fig. 1cd): on the closed forest boundary on the southwestern slope (Gla-SW, 10–15° slope, 1600–1640 m a.s.l.), in sparse stand on the eastern slope (Gla-E, ~30° slope, 1530–1570 m a.s.l.), and in the closed forest on the northern slope (Gla-N, ~30° slope, 1330–1350 m a.s.l.). *P. sibirica* grows at all sites, while *A. sibirica* grows only on the southwestern slope.

The collection of cores, the measurement and cross-dating of tree-ring width (TRW), and developing site TRW chronologies were carried out using standard dendrochronology techniques (Cook and Kairiukstis, 1990). During standardization, age trends were fitted as cubic smoothing splines with a frequency response of 0.50 at 67% of the individual series lengths and then removed. Both standard (*std*) and residual (*res*; after removing of autocorrelation) chronologies were used in the study. Additionally, the first differences ($\Delta TRW_t = TRW_t - TRW_{t-1}$) of site *std* TRW chronologies were used to analyze the year-to-year variation of tree growth.

We considered the following statistical characteristics of the TRW chronologies: arithmetic mean value (*mean*); standard deviation (*stdev*); mean sensitivity coefficient (*sens*, the ratio of the modulus of two successive values' difference to their arithmetic mean, averaged over the entire length of the chronology); mean interserial correlation coefficient (r_{bar} , a correlation coefficient calculated between every pair of individual series at the site with a 50-year window and a 1-year step and then averaged); and a first-order autocorrelation coefficient (ar_{-1}). To assess the representativeness of the sample (the number of series to obtain a chronology containing a sufficient total signal), we used the signal-to-noise ratio ($SNR = N \cdot r_{bar} / (1 - r_{bar})$, where N is number of cores) and the expressed population signal (*EPS*) calculated with a 50-year window and a 1-year step (Wigley et al., 1984; Cook, 1985; Shiyatov, 1986; Cook and Kairiukstis, 1990).

To identify the main time intervals of the climatic impact on TRW, the 21-day average temperature moving series with daily steps were calculated on the basis of the weather station daily data and correlated with TRW chronologies. The relationships of the TRW chronologies among themselves and with the temperature were estimated by Pearson correlation coefficients. Multifactor regression models were also constructed to describe the dependence of the conifers' radial growth on crucial climatic factors and the growth during the previous year (autocorrelation component); the quality of the models was evaluated with standard statistical characteristics (R^2_{adj} , F , p , SE ; Cook et al., 1994). In addition, years of optimal/extreme conditions for the growth of conifers were identified by residual TRW chronologies: optimal, $TRW > (mean + stdev)$; semi-optimal, $mean \leq TRW \leq (mean + stdev)$; semi-extreme, $(mean - stdev) \leq TRW < mean$; and extreme, $TRW < (mean - stdev)$ (see Jetschke et al., 2018).



Fig. 1. Study area: (a) location of the study area in the Asian territory of Russia; (b) relative position of Gladenkaya Mt. and the Cheryomushki weather station; (c) location of the sampling sites on Gladenkaya Mt.; (d) photo of the eastern slope.

3. Results

The obtained site TRW chronologies are shown in Fig. S2, and their statistical characteristics are represented in Table 1. On the south-western slope, most of the *A. sibirica* trees have an age of 50–80 years, and the total length of site chronology is 129 years; *P. sibirica* at this site, conversely, has an average age of ca. 200 years and a chronology length of 385 years. At sites selected on the eastern and northern slopes, *P. sibirica* stands have a similar age structure: the average age is ca. 150 years and the length of chronologies exceeds 200 years. All chronologies are representative ($EPS > 0.85$) during the period of instrumental climate observations. Since 1951, the average radial growth of *P. sibirica* is 0.63–0.68 mm, and the average growth of *A. sibirica* is 0.90 mm. Growth depression (negative trends in TRW) was not observed during the recent decades, regardless of the species and site local

conditions. The variability of growth is low for both species, both in general ($stdev < 0.2$) and year-to-year component ($sens < 0.16$) (cf. *Pinus cembra* in Carrer et al., 2018; Cerrato et al., 2019). The common external signal is not very high either ($r_{bar} < 0.4$); the first-order autocorrelation of std chronologies is essential ($ar_{-1} = 0.415–0.608$) but is lower than typical values that are observed for dark conifers in the mountains of continental Asia (e.g., Fan et al., 2009; Lei et al., 2016; Babushkina et al., 2018 and others). A visual inspection of cores during measurement did not reveal any frost rings in the xylem.

The dynamics of *A. sibirica* radial increment on the southwestern slope has a significant similarity with the chronologies of *P. sibirica* (Table 2), both at the same site and on the eastern slope ($r = 0.44–0.60$). *P. sibirica* growth is highly correlated at the Gla-SW and Gla-E sites ($r = 0.72–0.81$), but on the northern slope its dynamics have weaker correlations with *P. sibirica* ($r = 0.04–0.35$) and *A. sibirica*

Table 1
Statistical characteristics of site TRW chronologies of *A. sibirica* and *P. sibirica*.

Statistics	AbSi_Gla-SW	PiSi_Gla-SW	PiSi_Gla-E	PiSi_Gla-N
<i>Sample</i>				
<i>N</i>	81	29	27	11
length, years	129	385	232	246
time span	1889–2017	1633–2017	1786–2017	1772–2017
mean TRW(mm) whole/1951–2017	0.75/0.90	0.63/0.64	0.90/0.68	1.08/0.63
<i>std/res chronologies</i>				
<i>stdev</i>	0.190/0.148	0.197/0.146	0.174/0.140	0.174/0.135
<i>sens</i>	0.143/0.159	0.137/0.155	0.130/0.152	0.133/0.154
<i>ar₋₁</i>	0.415/−0.021	0.608/0.063	0.568/0.024	0.511/−0.011
<i>r_{bar}</i>	0.296/0.305	0.263/0.346	0.224/0.279	0.294/0.382
<i>SNR</i>	34.06/35.55	10.35/15.34	7.79/10.45	4.58/6.80
<i>EPS > 0.85 from</i>	1919/1923	1679/1787	1830/1827	1816/1808

Table 2
Correlation coefficients between site TRW chronologies (std/res) of *A. sibirica* and *P. sibirica* during 1951–2017.

Chronology	AbSi_Gla-SW	PiSi_Gla-SW	PiSi_Gla-E
PiSi_Gla-SW	0.475/0.444		
PiSi_Gla-E	0.599/0.493	0.716/0.807	
PiSi_Gla-N	0.177/0.159	0.036/0.095	0.343/0.254

Bold coefficients are significant at $p < 0.05$.

($r = 0.16–0.18$) at other sites.

For all considered chronologies, the response to precipitation is unstable and practically does not go beyond the threshold of significant correlations (at $p < 0.05$) and is, therefore, not shown. The temperature response of *P. sibirica* has common patterns on the southwestern and eastern slopes (Fig. 2), as a negative reaction to the April temperature is combined with a stable positive temperature response from May to August. For *A. sibirica*, the response patterns are the same, but the temperature influence during the vegetative season is less stable and insignificant in August. Notably, a more pronounced response to the April temperature is observed in standard chronologies, while summer temperatures correlate more strongly with residual chronologies, but in both cases the most significant response is observed in the year-to-year variation of the radial growth, i.e., its first differences. In *P. sibirica* on the northern slope, there is no negative reaction to the April temperature, and the influence of summer temperatures is the least pronounced; however, *P. sibirica* growth here significantly responds to the August temperature.

A more detailed analysis of the intra-seasonal temperature dynamics and the reaction of *A. sibirica* and *P. sibirica* on the sunlit southwestern and eastern slopes showed that the negative impact of prevegetative season temperatures (T_{pv}) is maximum from early April to early May (Table 3), when average daily temperatures at the sampling sites are negative, but for some days they can rise up to +5–7 °C (Fig. 3). The positive effects of vegetative season temperatures (T_v) begin from the second or third decade of May, when the average daily temperatures are 2–3 °C above zero, and their minimum rises to 5–6 °C below zero. Notably, the seasonality of the temperature influence on the *P. sibirica* growth has differences between sites of 1–4 days in accordance with the elevational temperature gradient: at higher elevations, the periods of the prevegetative season and the beginning of the vegetative season shift to later dates, and the end of the growing season occurs earlier.

The analysis of daily precipitation series at the Cheryomushki station showed averages of 61% of days without precipitation and 17% of days with low precipitation (< 1 mm) in April. At this station, there are no available data on maximum and minimum air temperatures during the day, but according to other stations in the region, the daily

temperature variation ($T_{max}–T_{min}$) most often observed in April is in the range of 8–10 °C both on plains and in the highlands (Supplementary material).

The results of multifactor regression modeling of the conifers' radial growth on sunlit slopes based on the previous year's increment and the average temperatures of the prevegetative and vegetative seasons, whose average time intervals are determined according to the maximum correlations of chronologies with the moving temperature series (Fig. 2, Table 3), are given in Table 4. Models describe 30–38% of the growth variability. The numerical coefficients at the temperature components of these models suggest that an increase in T_{pv} leads to a decrease in growth by 1.4–2.3%/1 °C, and an increase in T_v leads to an increase in growth by 4.6–6.5%/1 °C. During the period of instrumental climatic observations, the warming rate is ca. 0.5 °C/10 years for T_{pv} and ca. 0.1 °C/10 years for T_v (estimated by linear trends for 1951–2017); therefore, the influence of both trends on conifer growth on the sunlit slopes currently is relatively balanced (imbalance is < 1% of growth, which is much less than the variability not described with models).

Years when conifers consistently formed narrow or wide rings (extreme and optimal years) occurred relatively synchronously for *A. sibirica* and *P. sibirica* on sunlit slopes (Table S1 in Supplementary material), while for *P. sibirica* on the northern slope the synchronicity of high and low radial growth with the other chronologies was minimal. During the period of instrumental climatic observations, we identified years with consistent patterns of radial growth for all three chronologies on sunlit slopes (Table 5), averaged and analyzed the deviations (anomalies) of temperature from the mean intra-seasonal dynamics (Fig. 4). In extreme and semi-extreme years, April temperatures are generally above average, often returning to cold in late April or May. Additionally, extreme years are characterized by low temperatures during the growing season as a whole, and possible days with frost. The opposite pattern is observed for semi-optimal and optimal years: low April temperatures with fast warming afterwards are typical for both categories, and the warm growing season (especially May) is observed during optimal years. Interestingly, since the launch of the Sayano-Shushenskoe power station, the number of extreme years common to *P. sibirica* and *A. sibirica* decreased, the number of optimal years increased, and the number of extreme years decreased in site TRW chronologies.

4. Discussion

With rapid warming in continental Asia, as well as the species-specific and topographic variability of the climatic reactions of trees on the upper forest boundary and in its vicinity observed in this macro-region (e.g., Liang et al., 2006; Babushkina et al., 2018; Bai et al., 2019; Jiao et al., 2019), the analysis of these reactions and the monitoring of forest stands on regional and local scales are important for predicting the dynamics of vegetation under various scenarios of future climate change. Dark conifer species, such as *P. sibirica* and *A. sibirica*, are widely distributed in the region and provide a valuable source of industrial wood, but at the same time are vulnerable to climate variations (Kharuk et al., 2013, 2017); therefore, investigation of their climatic responses is of particular interest for the management of Southern Siberian mountain forests.

4.1. Main patterns of radial growth and its climatic response

The radial growth dynamics of both conifer species in this study indicates the stability of their state in the current climatic conditions despite climate change. A relatively weak but significant common signal, especially in the *std* chronologies, the low variability and the sensitivity of chronologies, combined with relatively low level of autocorrelation, are indirect evidence of a substantial contribution of growing conditions at the level of individual trees (*Picea obovata*, Babushkina et al., 2018; cf. Barber et al., 2000; Kulagin et al., 2006;

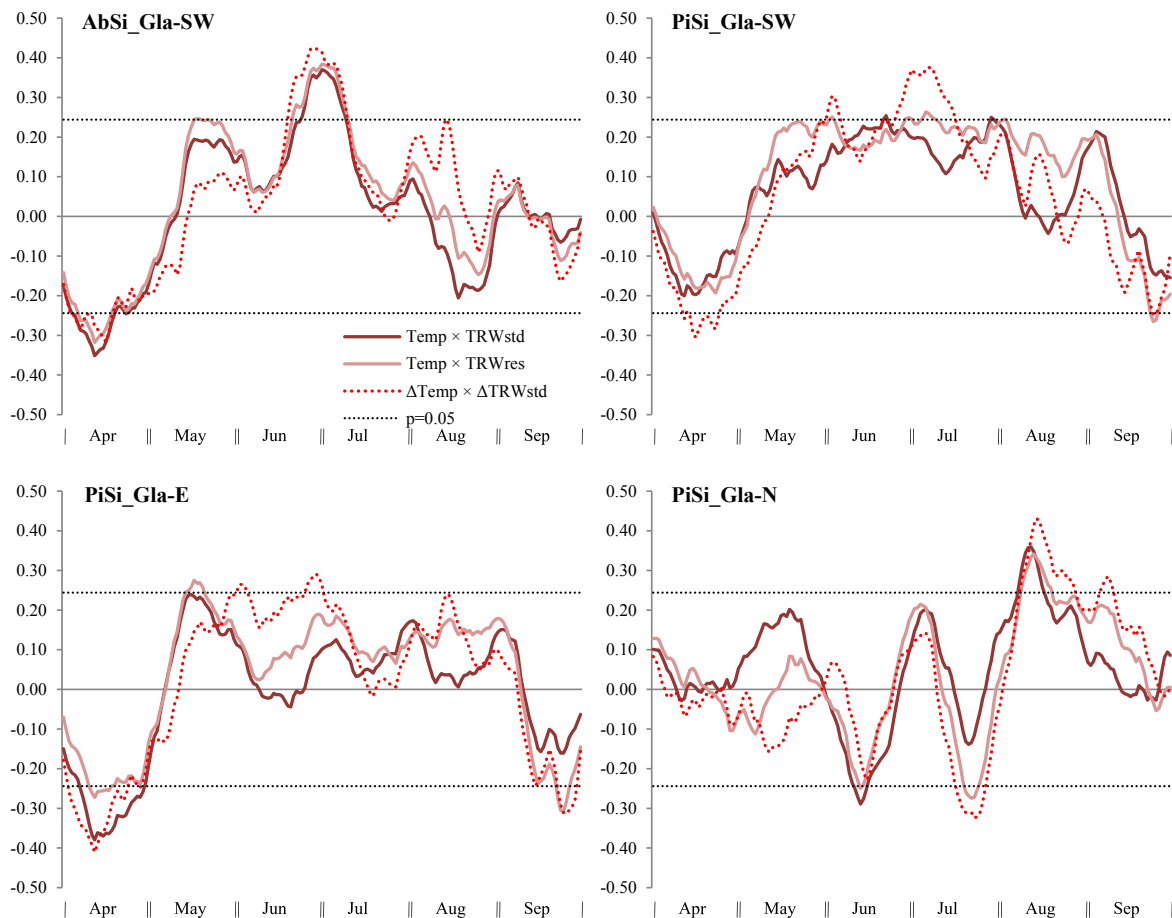


Fig. 2. Correlation coefficients of *A. sibirica* and *P. sibirica* radial growth with 21-day moving series of mean air temperature (based on daily data of the Cheryomushki weather station) from March to September. Site *std* and *res* TRW chronologies were correlated with temperature series *per se* (dark and light solid lines), while the first differences of *std* chronologies were correlated with the first differences of temperature series (dotted lines). Horizontal thin dotted lines mark thresholds of correlation significance at $p < 0.05$.

Savva et al., 2006; Sidor et al., 2015; Lei et al., 2016). Nevertheless, the climate also has an important effect on the tree growth, causing the similarity in *A. sibirica* and *P. sibirica* chronologies on the sunlit southwestern and eastern slopes and the common pattern of their correlations with temperature. More pronounced correlations of the April temperature with *std* than with *res* chronologies and opposite patterns for the vegetative season temperature are most likely due to the auto-correlation component of growth in evergreen conifers being associated with the presence of needles from previous years, which are subject to extreme temperature effects during the prevegetative season. This effect is later reflected in the development of the current year xylem. Observations of previous years' needles input in current growth are given in earlier studies (Larson, 1964; Zweifel et al., 2006; Kurkela et al., 2009; Velisevich and Khutornoy, 2009). After the formation of new shoots and needles, regulated by current climatic fluctuations, they begin to play a greater role in providing assimilates for secondary

growth processes, thereby enhancing the predominance of the reaction to these conditions in *res* chronologies. On the northern slope, the reaction of *P. sibirica* to the temperature of the vegetative season is less pronounced, primarily because samples were taken substantially below the upper boundary of the forest (on the northern slope of the Gladenkaya Mt., closed stands are present to the very top; Fig. 1c). High correlations between first differences of TRW chronologies and temperature series ensure that not only long-term trends, but also year-to-year climatic fluctuations make input in the tree growth.

4.2. Impact of prevegetative season temperature

The negative reaction of both conifers to the prevegetative season temperatures in the study area was observed only on sunlit eastern and southwestern slopes. In the spring, the sun does not rise above the horizon as high as in summer, which leads to a differing exposures of

Table 3

Maximal correlation coefficients of *A. sibirica* and *P. sibirica* site TRW chronologies with temperature (1951–2017) of the prevegetative season (T_{pv}) and vegetative season (T_v) *per se* and in the first differences.

Sample	$T_{pv} \times TRW_{std}$		$\Delta T_{pv} \times \Delta TRW_{std}$		$T_v \times TRW_{res}$		$\Delta T_v \times \Delta TRW_{std}$	
	Period	<i>r</i>	Period	<i>r</i>	Period	<i>r</i>	Period	<i>r</i>
AbSi_Gla-SW	Apr4–May4	-0.351	Mar28–May11	-0.315	May12–Aug11	0.324	May23–Aug24	0.343
PiSi_Gla-SW	Apr7–May3	-0.173	Apr6–May3	-0.306	May12–Sep1	0.425	May24–Aug29	0.435
PiSi_Gla-E	Apr4–May3	-0.389	Apr2–May2	-0.398	May10–Sep2	0.307	May19–Sep1	0.421

Bold correlation coefficients are significant at $p < 0.05$.

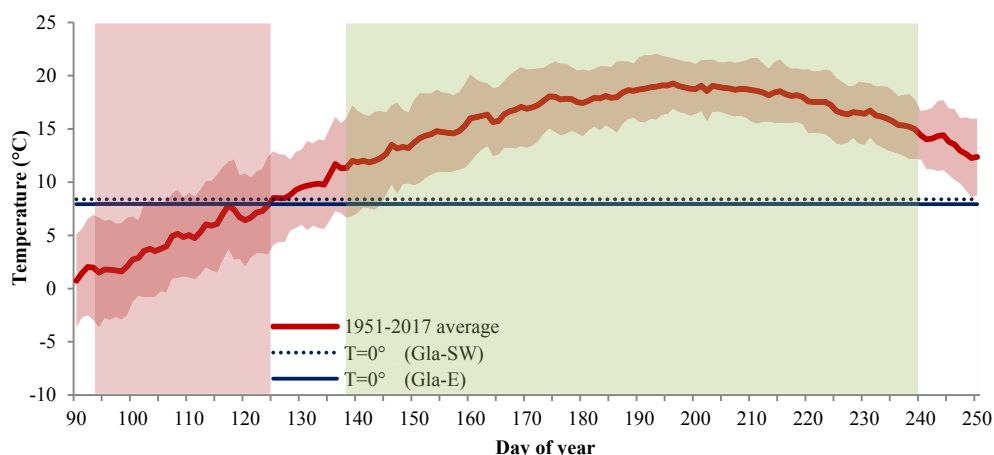


Fig. 3. Daily mean air temperature from April to the beginning of September at the Cheryomushki weather station (1951–2017). Horizontal lines show estimations of the temperature at the station when $T = 0^{\circ}\text{C}$ at Gla-SW and Gla-E sites (assuming that the elevational temperature lapse rate is $-0.65^{\circ}\text{C}/100\text{ m}$), i.e. estimated lines of zero temperature for sampling sites. Shaded rectangles represent average intervals of the highest temperature impact on growth before (April 3 – May 4/94–125 day of year) and during (May 17 – August 27/138–240 day of year) the vegetative season.

Table 4

Multifactor regression models of conifer growth on the sunlit slopes based on site *std* TRW chronologies, temperature anomalies of mean prevegetative (April 3 – May 4, TA_{pv}) and vegetative season (May 17 – August 27, TA_v).

Chronology	Equation	R^2_{adj}	F	p	SE
AbSi_Gla-SW	$TRW_t = 0.567 + 0.428 \cdot TRW_{t-1} - 0.0204 \cdot TA_{pv} + 0.0471 \cdot TA_v$	0.34	12.1	< 0.0001	0.096
PiSi_Gla-SW	$TRW_t = 0.524 + 0.477 \cdot TRW_{t-1} - 0.0142 \cdot TA_{pv} + 0.0650 \cdot TA_v$	0.30	10.4	< 0.0001	0.114
PiSi_Gla-E	$TRW_t = 0.534 + 0.461 \cdot TRW_{t-1} - 0.0225 \cdot TA_{pv} + 0.0458 \cdot TA_v$	0.38	14.5	< 0.0001	0.099

All numerical coefficients in equations are significant at $p < 0.05$.

direct sunlight on the slopes up to several times if the weather is clear (Huang et al., 2008), and the high proportion of days without precipitation observed at the weather station in April is an indicator of the high probability of clear weather. Lower direct radiation on the eastern slope compared with the southwestern slope is compensated by the thinner stand, i.e., a larger proportion of a sunlit crown for any individual tree. In the mountains, the air has high transparency, and during the cold season the snow cover increases the albedo, which also leads to an increase in light.

As shown in Ermida et al. (2014), sunlit surfaces heat up substantially more than air. For needles, the temperature can rise by 4°C on average and up to 10°C maximum above the air temperature, and at night it can drop down to $8\text{--}10^{\circ}\text{C}$ below the air temperature (Wieser, 2007). This means that with daily fluctuations in the air temperature of $8\text{--}10^{\circ}\text{C}$, the magnitude of the daily temperature variation of the needles in the study area can be twice as large as the magnitude of the air temperature variation. Transpiration and respiration, having a cooling effect, can lessen or even reverse this temperature difference during the daytime and aggravate it at night; however, under water stress, i.e.,

when transpiration is suppressed due to the lack of moisture, the overheating of the sunlit needles increases (Jackson et al., 1981; Ermida et al., 2014). Partial shading of the lower branches should also be taken into account, especially with dense crowns and in a closed tree stand (Hadley and Smith, 1987; Wieser, 2002).

During this season, the average daily air temperature rises above zero on some days (Fig. 4), but the soil is still covered with snow, i.e., it is cold or even frozen. High illumination on sunny slopes leads to the heating of the upper tiers of the crown in the daytime to temperatures substantially higher than the photosynthesis threshold (ca. $+2^{\circ}\text{C}$ according to Suvorova et al., 2005, 2011), especially considering the dark color of the needles of both species (high light absorption and fast heating). However, potentially high activity of photosynthesis and transpiration (typical for dark conifers) is hampered by soil dryness at low temperatures. In high elevation conditions, the mechanism of water stress compensation by the closure of stomata in conifers does not work fully since during the short and cool vegetative season, trees do not have enough time nor a sufficient heat supply to fully mature the needles' cuticle, and a significant proportion of respiration is carried

Table 5

Years with consistent growth patterns in site *res* TRW chronologies on the sunlit slopes (AbSi_Gla-SW, PiSi_Gla-SW, PiSi_Gla-E) for two equal periods before and after power plant launching.

Pattern	Years	
	Before power plant launching	After power plant launching
Optimal years: $TRW > mean$ for all three chronologies; $TRW > (mean + stdev)$ for 2–3 chronologies	1946; 1950; 1959; 1963; 1968	1992; 2002
Semi-optimal years: $TRW > mean$ for all three chronologies; $TRW > (mean + stdev)$ for 0–1 chronologies	1942; 1944; 1952; 1955; 1957; 1960; 1964; 1974	1984; 1989; 2004; 2005; 2008; 2010
Background years without consistent pattern (different signs of TRW deviation from mean)	1943; 1945; 1948; 1949; 1951; 1953; 1954; 1958; 1962; 1965; 1966; 1969; 1971; 1976; 1979	1982; 1983; 1986; 1987; 1990; 1991; 1993; 1994; 1995; 1996; 1998; 1999; 2000; 2001; 2003; 2006; 2007; 2009; 2012; 2015; 2016; 2017
Semi-extreme years: $TRW < mean$ for all three chronologies; $TRW < (mean - stdev)$ for 0–1 chronologies	1956; 1973; 1975; 1978	1980; 1981; 1985; 1997; 2011; 2013; 2014
Extreme years: $TRW < mean$ for all three chronologies; $TRW < (mean - stdev)$ for 2–3 chronologies	1947; 1961; 1967; 1970; 1972; 1977	1988

Years written in italic are beyond the period of instrumental observations and are not included in the calculations for Fig. 4.

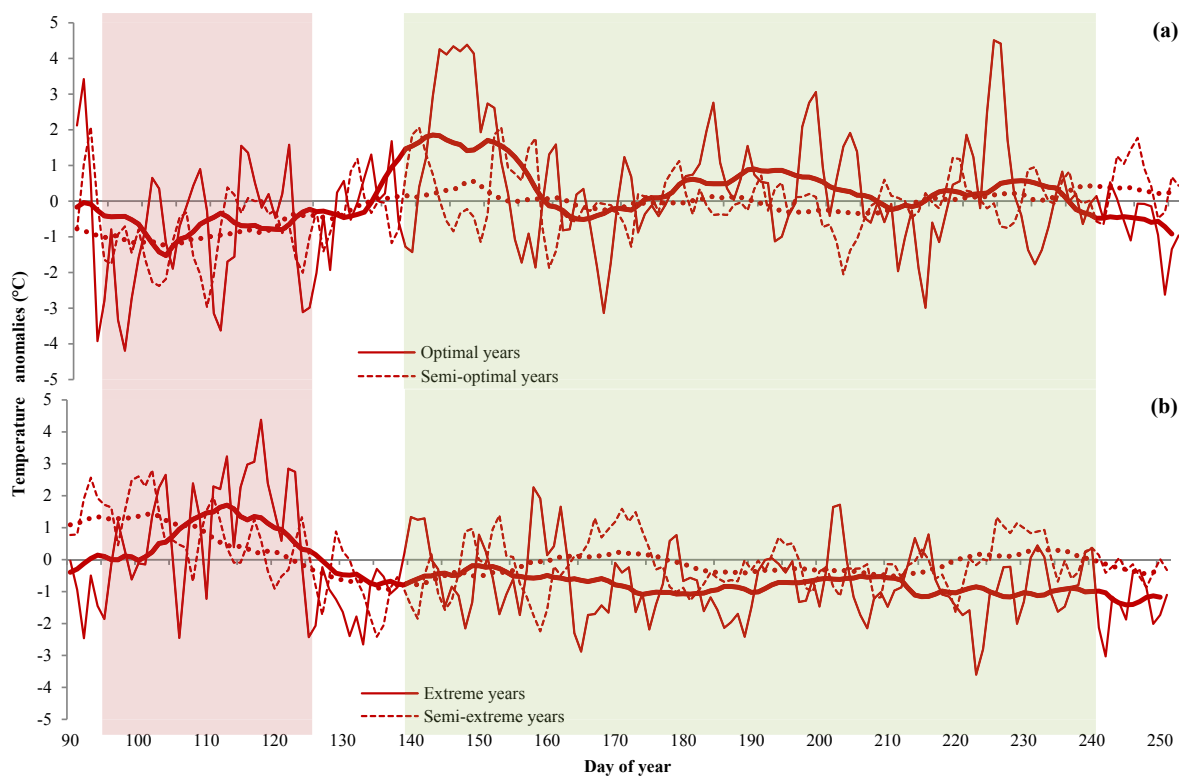


Fig. 4. Intra-seasonal temperature anomalies (deviations from averaged curve of daily mean temperatures over 1951–2017) during years with consistent growth patterns in residual site TRW chronologies on the sunlit slopes (Table 5): (a) average for optimal (solid lines) and semi-optimal (dotted lines) years; (b) average for extreme (solid lines) and semi-extreme (dotted lines) years. Thin lines represent daily temperature anomalies averaged over all years with the same growth pattern during 1951–2017; thick lines represent their 21-day smoothed curves; shaded rectangles mark average intervals of the highest temperature impact on growth before and during the vegetative season (sf. Fig. 3).

out through the cuticle (Tranquillini, 1979; Mayr, 2007). In addition, physiologically active needles are more vulnerable to negative temperatures at night when their temperature is lower than the air temperature. As a result of all these factors, a large magnitude of daily temperature fluctuations in the needles increases the risk of their damage (decrease in photosynthetic activity; Nagel et al., 1987; Yamazaki et al., 2003) and the partial defoliation of the upper branches, as well as xylem embolism (Sperry and Robson, 2001); both leading to the suppression of the tree growth. Therefore, an increase in April temperature may lead to an increase in the duration of the risk of needle loss due to physiological drought.

Another possible temperature factor of the prevegetative season is the return of cold weather. Together with high magnitudes of daily temperature variation observed in both the needles and in the apical meristem, i.e., buds (Wieser, 2007), this phenomenon can lead to premature bud swelling or even bud burst and subsequent cold damage of emerging shoots, thus negatively affecting the primary growth and, consequently, growth hormones' concentrations during the vegetative season. However, the absence of frost rings in the tree rings indicates that in the study area, the tissues of trees are sensitive to the returning cold mainly before the onset of secondary growth, with other possible reason being better protection from frost damage of the trunk cambium.

4.3. Probable forest stands' dynamics in the past and in the future

The negative reaction in *A. sibirica* on the gentle southwestern slope to the April temperature is more pronounced than in *P. sibirica* at the same site, which can be associated with the lower drought tolerance of *A. sibirica* (cf., their distribution ranges in the mountains of Southern Siberia, Chytrý et al., 2008). The age structure of *A. sibirica* stand (dynamics of the number of cores, Fig. S2a in Supplementary material) shows a small number of trees older than 80–100 years and a maximum

age of ca. 130 years. Such stand dynamics and the slow growth of young *A. sibirica* trees in the first decades of the 20th century may have been caused by the dieback during the long-term regional drought period (low precipitation, including winter; cf., Rogozin et al., 2010; Babushkina et al., 2017); some saplings and young trees at this site may have survived under snow cover. On steeper slopes, the snow cover is lower and less stable, which leads to the absence of *A. sibirica* (probably associated with an inability of establishment) and a more pronounced *P. sibirica* response to the April temperature on the eastern slope compared to the southwest slope, despite lower direct solar radiation.

However, both the growth regression models' characteristics and the comparison of the climatic conditions during years with the consistent conifer growth patterns show that the temperature has a more pronounced effect on the growth during the vegetative season than during the prevegetative season. This determines the observed reaction of the considered tree stands to the current climate warming; an increase in the duration and heat supply of the growing season causes a decrease in the number of extreme years, but does not lead to positive trends in growth, as it is balanced by the negative impact of early spring temperatures. This is also supported by the positive dynamics of *P. sibirica* growth on the northern slope, where under low direct insolation, early spring warming does not cause needle damage and growth limitation.

Regional warming trend is similar in magnitude to the local trend in the study area in summer, but is much slower during winter, leading to the less pronounced spring warm-up shift coupled with increase of heat supply during vegetation currently and in close future (Babushkina et al., 2018; see also Liu et al., 2013 for broader spatial scale of warming trends). Thus, the prospects of the dark conifer forests' survival and prosperity seem to be more optimistic in the high mountain areas of the South Siberia located further from the massive reservoir, as long as warming is not accompanied by decrease of precipitation. These

expectations are supported by comparison of our findings with study of Gerasimova et al. (2010) carried out in ca. 100 km from reservoir, where more pronounced positive growth trends for both species and not significant negative response of tree growth to April temperature are observed at sites located on sunlit terrain. It means that monitoring of the most climatic-sensitive stands on sunlit slopes in vicinity of the reservoir is important as an early warning system for regional dark coniferous forests' vulnerability to the possible negative consequences of climate change. Other implication for the regional management of mountainous forests is recommendation to concentrate reforestation of *P. sibirica* and especially *A. sibirica* on the more shaded slopes. In regards to possible application of the observed patterns for other regions of these species' distribution ranges, further research of their climatic reactions seems to be of interest.

5. Conclusion

In the high mountain forests of the northern macroslope of the Western Sayan Mountains, dependencies of the growth of dark conifers *P. sibirica* and *A. sibirica* on the slope orientation and temperature were revealed. On a shaded northern slope, the closed stands of *P. sibirica* grow at higher elevations, and their growth is slightly dependent on summer temperatures. At the same time, on sunlit slopes, the impact of heat supply of the vegetative season is more stable; an additional factor limiting the growth of both species in these conditions is the temperature from the beginning of April to the beginning of May. Since warming in the study area during recent decades is much faster in winter and early spring than in late spring and summer temperatures, the resulting climatic trend leads to an increase in *P. sibirica* radial growth on the northern slope and the stability of both species on the sunlit slopes. An extrapolation of these findings to the mountain areas located further from the Sayano-Shushenskoe Reservoir gives us a tentatively optimistic assessment of the dark coniferous forests' near future, because in these areas the positive influence of summer warming is similar to the study area, whereas the negatively impacting prevegetative season temperature increases less rapidly. However, in the future, climate change can shift this balance and disrupt forest stands stability; therefore monitoring of the mountain forests of the region should be performed regularly, taking into account found patterns of the dark conifers' growth and climatic signal.

Acknowledgments

The study was supported by the Russian Science Foundation (project no. RSF-19-77-30015).

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.117458>.

References

- Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6 (8), 129. <https://doi.org/10.1890/ES15-00203.1>.
- Babushkina, E.A., Belokopytova, L.V., Grachev, A.M., Meko, D.M., Vaganov, E.A., 2017. Variation of the hydrological regime of Bele-Shira closed basin in Southern Siberia and its reflection in the radial growth of *Larix sibirica*. *Reg. Environ. Change* 17 (6), 1725–1737. <https://doi.org/10.1007/s10113-017-1137-1>.
- Babushkina, E., Belokopytova, L., Zhirnova, D., Barabantsova, A., Vaganov, E., 2018. Divergent growth trends and climatic response of *Picea obovata* along elevational gradient in Western Sayan mountains, Siberia. *J. Mt. Sci.* 15 (11), 2378–2397. <https://doi.org/10.1007/s11629-018-4974-6>.
- Bai, X., Zhang, X., Li, J., Duan, X., Jin, Y., Chen, Z., 2019. Altitudinal disparity in growth of Dahurian larch (*Larix gmelinii* Rupr.) in response to recent climate change in northeast China. *Sci. Total Environ.* 670, 466–477. <https://doi.org/10.1016/j.scitotenv.2019.03.232>.
- Barber, V.A., Juday, G.P., Finney, B.P., 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature* 405 (6787), 668. <https://doi.org/10.1038/35015049>.
- Berner, L.T., Beck, P.S., Bunn, A.G., Goetz, S.J., 2013. Plant response to climate change along the forest-tundra ecotone in northeastern Siberia. *Glob. Change Biol.* 19 (11), 3449–3462. <https://doi.org/10.1111/gcb.12304>.
- Bigler, C., Gavin, D.G., Gunning, C., Veblen, T.T., 2007. Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. *Oikos* 116 (12), 1983–1994. <https://doi.org/10.1111/j.2007.0030-1299.16034.x>.
- Bocharov, A.Y., 2009. Climatogenetic radial growth of conifers in the upper forest belt of the Seminsky Range (the Central Altai Mountains). *J. Sib. Fed. Univ. Biol.* 2 (1), 30–37 (In Russian).
- Briffa, K.R., Osborn, T.J., Schweingruber, F.H., 2004. Large-scale temperature inferences from tree rings: a review. *Glob. Planet. Change* 40 (1–2), 11–26. [https://doi.org/10.1016/S0921-8181\(03\)00095-X](https://doi.org/10.1016/S0921-8181(03)00095-X).
- Carrer, M., Unterholzner, L., Castagneri, D., 2018. Wood anatomical traits highlight complex temperature influence on *Pinus cembra* at high elevation in the Eastern Alps. *Int. J. Biometeorol.* 62 (9), 1745–1753. <https://doi.org/10.1007/s00484-018-1577-4>.
- Cerrato, R., Salvatore, M.C., Gunnarson, B.E., Linderholm, H.W., Carturan, L., Brunetti, M., De Blasi, F., Baroni, C., 2019. A *Pinus cembra* L. tree-ring record for late spring to late summer temperature in the Rhaetian Alps, Italy. *Dendrochronologia* 53, 22–31. <https://doi.org/10.1016/j.dendro.2018.10.010>.
- Chytrý, M., Danihelka, J., Kubešová, S., Lustyk, P., Ermakov, N., Hájek, M., Hájková, P., Kočí, M., Otýpková, Z., Roleček, J., Řezníčková, M., Šmarda, P., Valachovič, M., Popov, D., Pišút, I., 2008. Diversity of forest vegetation across a strong gradient of climatic continentality: Western Sayan Mountains, southern Siberia. *Plant Ecol.* 196 (1), 61–83. <https://doi.org/10.1007/s11258-007-9335-4>.
- Cook, E.R., 1985. A Time Series Analysis Approach to Tree-Ring Standardization. PhD thesis. Univ. of Arizona, Tucson.
- Cook, E.R., Kairiukstis, L.A. (Eds.), 1990. *Methods of Dendrochronology*. Springer Netherlands, Dordrecht.
- Cook, E.R., Briffa, K.R., Jones, P.D., 1994. Spatial regression methods in dendroclimatology: a review and comparison of two techniques. *Int. J. Climatol.* 14, 379–402. <https://doi.org/10.1002/joc.3370140404>.
- D'Arrigo, R., Frank, D., Pederson, N., Cook, E., Buckley, B., Nachin, B., Mijidjorj, R., Dugarjav, C., 2001. 1738 years of Mongolian temperature variability inferred from a tree-ring width chronology of Siberian pine. *Geophys. Res. Lett.* 28 (3), 543–546.
- Ermida, S.L., Trigo, I.F., DaCamara, C.C., Götsche, F.M., Olesen, F.S., Hulley, G., 2014. Validation of remotely sensed surface temperature over an oak woodland landscape – the problem of viewing and illumination geometries. *Remote Sens. Environ.* 148, 16–27. <https://doi.org/10.1016/j.rse.2014.03.016>.
- Fan, Z.X., Bräuning, A., Cao, K.F., Zhu, S.D., 2009. Growth–climate responses of high-elevation conifers in the central Hengduan Mountains, southwestern China. *For. Ecol. Manag.* 258 (3), 306–313. <https://doi.org/10.1016/j.foreco.2009.04.017>.
- Gerasimova, O.V., Zharikov, Z.Y., Knorre, A.A., Myglen, V.S., 2010. Climatically induced dynamic of radial growth of Siberian stone pine and Siberian fir in the mountain-taiga belt in "Ergaki" National Park. *J. Sib. Fed. Univ. Biol.* 3 (1), 18–29 (In Russian).
- Grace, J., James, J., 1993. Physiology of trees at treeline. In: Alden, J.N., Mastrantonio, J.L., Ødum, S. (Eds.), *Forest Development in Cold Climates*. NATO ASI Series (Series A: Life Sciences). Springer, Boston, MA, pp. 105–114.
- Hadley, J.L., Smith, W.K., 1987. Influence of krummholz mat microclimate on needle physiology and survival. *Oecologia* 73 (1), 82–90. <https://doi.org/10.1007/BF00376981>.
- Helama, S., Sutinen, R., 2016. Inter- and intra-seasonal effects of temperature variation on radial growth of alpine treeline Norway spruce. *J. Mt. Sci.* 13 (1), 1–12. <https://doi.org/10.1007/s11629-015-3665-9>.
- Huang, S., Rich, P.M., Crabtree, R.L., Potter, C.S., Fu, P., 2008. Modeling monthly near-surface air temperature from solar radiation and lapse rate: application over complex terrain in Yellowstone National Park. *Phys. Geogr.* 29 (2), 158–178. <https://doi.org/10.2747/0272-3646.29.2.158>.
- Jackson, R.D., Idso, S.B., Reginato, R.J., Pinter, P.J., 1981. Canopy temperature as a crop water stress indicator. *Water Resour. Res.* 17 (4), 1133–1138. <https://doi.org/10.1029/WR017i004p01133>.
- Jetschke, G., van der Maaten, E., van der Maaten-Theunissen, M., 2018. Towards the extremes: a critical analysis of pointer year detection methods. *Dendrochronologia* 53, 55–62. <https://doi.org/10.1016/j.dendro.2018.11.004>.
- Jiao, L., Jiang, Y., Wang, M., Kang, X., Zhang, W., Zhang, L., Zhao, S., 2016. Responses to climate change in radial growth of *Picea schrenkiana* along elevations of the eastern Tianshan Mountains, northwest China. *Dendrochronologia* 40, 117–127. <https://doi.org/10.1016/j.dendro.2016.09.002>.
- Jiao, L., Jiang, Y., Zhang, W., Wang, M., Wang, S., Liu, X., 2019. Assessing the stability of radial growth responses to climate change by two dominant conifer trees species in the Tianshan Mountains, northwest China. *For. Ecol. Manag.* 433, 667–677. <https://doi.org/10.1016/j.foreco.2018.11.046>.
- Jochner, M., Bugmann, H., Nötzli, M., Bigler, C., 2018. Tree growth responses to changing temperatures across space and time: a fine-scale analysis at the treeline in the Swiss Alps. *Trees* 32, 645–660. <https://doi.org/10.1007/s00468-017-1648-x>.
- Kharuk, V.I., Ranson, K.J., Im, S.T., Dvinskaya, M.L., 2009. Response of *Pinus sibirica* and *Larix sibirica* to climate change in southern Siberian alpine forest–tundra ecotone. *Scand. J. For. Res.* 24 (2), 130–139. <https://doi.org/10.1080/02827580902845823>.
- Kharuk, V.I., Im, S.T., Oskorbin, P.A., Petrov, I.A., Ranson, K.J., 2013. Siberian pine decline and mortality in southern Siberian mountains. *For. Ecol. Manag.* 310, 312–320. <https://doi.org/10.1016/j.foreco.2013.08.042>.
- Kharuk, V.I., Im, S.T., Petrov, I.A., Dvinskaya, M.L., Fedotova, E.V., Ranson, K.J., 2017. Fir decline and mortality in the southern Siberian Mountains. *Reg. Environ. Change* 17 (3), 803–812. <https://doi.org/10.1007/s10113-016-1073-5>.

- Körner, C., 1998. A re-assessment of high elevation treeline positions and their explanation. *Oecologia* 115 (4), 445–459. <https://doi.org/10.1007/s004420050540>.
- Körner, C., 2003. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Springer-Verlag, Berlin, Heidelberg, Springer Science & Business Media.
- Kozlowski, T.T., Pallardy, S.G., 1997. *Physiology of Woody Plants*. Academic Press, San Diego, CA.
- Krylov, P.N., 1931. Flora of Western Siberia. Iss. 5. Tomsk Branch of Russian Botanical Society, Tomsk (In Russian).
- Kukarskih, V.V., Devi, N.M., Moiseev, P.A., Grigoriev, A.A., Bubnov, M.O., 2018. Latitudinal and temporal shifts in the radial growth-climate response of Siberian larch in the Polar Urals. *J. Mt. Sci.* 15 (4), 722–729. <https://doi.org/10.1007/s11629-017-4755-7>.
- Kulagin, A.Y., Davydychev, A.N., Zaitsev, G.A., 2006. Specific features of the growth of Siberian spruce (*Picea obovata* Ledeb.) at early stages of ontogeny in broadleaf-conifer forests of the Ufa plateau. *Russ. J. Ecol.* 37 (1), 66–69. <https://doi.org/10.1134/S1067413606010115>.
- Kuminova, A.V., 1960. Vegetation Cover of the Altai. Siberian Branch of Academy of Sciences of USSR, Novosibirsk (In Russian).
- Kuminova, A.V., Zvereva, G.A., Maskae, Yu.M., Lamanova, T.G., 1976. Vegetation Cover of the Khakassia. Nauka, Novosibirsk (In Russian).
- Kurkela, T., Drenkhan, R., Vuorinen, M., Hanso, M., 2009. Growth response of young Scots pines to needle loss assessed from productive foliage. *For. Stud.* 50 (1), 5–22. <https://doi.org/10.2478/v10132-011-0066-x>.
- Larson, P.R., 1964. Contribution of different-aged needles to growth and wood formation of young red pines. *For. Sci.* 10 (2), 224–238. <https://doi.org/10.1093/forestscience/10.2.224>.
- Lei, J.P., Feng, X.H., Shi, Z., Bai, D.Z., Xiao, W.F., 2016. Climate-growth relationship stability of *Picea crassifolia* on an elevation gradient, Qilian Mountain, Northwest China. *J. Mt. Sci.* 13 (4), 734–743. <https://doi.org/10.1007/s11629-015-3784-3>.
- Liang, E., Shao, X., Eckstein, D., Huang, L., Liu, X., 2006. Topography-and species-dependent growth responses of *Sabina przewalskii* and *Picea crassifolia* to climate on the northeast Tibetan Plateau. *For. Ecol. Manag.* 236 (2–3), 268–277. <https://doi.org/10.1016/j.foreco.2006.09.016>.
- Liu, H., Park Williams, A., Allen, C.D., Guo, D., Wu, X., Anenkhonov, O.A., Liang, E., Sandanov, D.V., Yin, Y., Qi, Z., Badmaeva, N.K., 2013. Rapid warming accelerates tree growth decline in semi-arid forests of Inner Asia. *Glob. Change Biol.* 19 (8), 2500–2510. <https://doi.org/10.1111/gcb.12217>.
- Mayr, S., 2007. Limits in Water relations. In: Wieser, G., Tausz, M. (Eds.), *Trees at their Upper Limit: Treeline Limitation at the Alpine Timberline*. Springer, Dordrecht, pp. 145–162.
- Nagel, E.M., Buschmann, C., Lichtenthaler, H.K., 1987. Photoacoustic spectra of needles as an indicator of the activity of the photosynthetic apparatus of healthy and damaged conifers. *Physiol. Plant.* 70 (3), 427–437. <https://doi.org/10.1111/j.1399-3054.1987.tb02839.x>.
- Naurzbaev, M.M., Vaganov, E.A., 2000. Variation of early summer and annual temperature in east Taymir and Putoran (Siberia) over the last two millennia inferred from tree rings. *J. Geophys. Res.: Atmos.* 105 (D6), 7317–7326. <https://doi.org/10.1029/1999JD901059>.
- Nazarov, A.N., Mygland, V.S., 2012. The possibility of construction of the 6000-year chronology for Siberian pine in the Central Altai. *J. Sib. Fed. Univ. Biol.* 5 (1), 70–88 (In Russian).
- Panyushkina, I.P., Ovtchinnikov, D.V., Adamenko, M.F., 2005. Mixed response of decadal variability in larch tree-ring chronologies from upper tree-lines of the Russian Altai. *Tree-Ring Res.* 61 (1), 33–43. <https://doi.org/10.3959/1536-1098-61.1.33>.
- Peters, R.L., Klesse, S., Fonti, P., Frank, D.C., 2017. Contribution of climate vs. larch budmoth outbreaks in regulating biomass accumulation in high-elevation forests. *For. Ecol. Manag.* 401, 147–158. <https://doi.org/10.1016/j.foreco.2017.06.032>.
- Polikarpov, N.P., Nazimova, D.I., 1963. The dark coniferous forests of the northern part of the west Siberian mountains. In: *Forestry research in the forests of Siberia*. Institute for Forests and Wood, Krasnoyarsk, pp. 103–147 (In Russian).
- Rogozin, D.Y., Genova, S.N., Gulati, R.D., Degermendzhy, A.G., 2010. Some generalizations based on stratification and vertical mixing in meromictic Lake Shira, Russia, in the period 2002–2009. *Aquat. Ecol.* 44 (3), 485–496. <https://doi.org/10.1007/s10452-010-9328-6>.
- Savva, Y., Oleksyn, J., Reich, P.B., Tjoelker, M.G., Vaganov, E.A., Modrzyński, J., 2006. Interannual growth response of Norway spruce to climate along an altitudinal gradient in the Tatra Mountains, Poland. *Trees* 20 (6), 735–746. <https://doi.org/10.1007/s00468-006-0088-9>.
- Sapozhnikov, V.V., 1901. Katun and its origins. The journey of 1897–1899. *Proc. Imp. Tomsk Univ.* 18 (In Russian).
- Sapozhnikov, V.V., 1913. Expedition to Dzhungar and Przhewalsky counties. In: *A Preliminary Report on Botanical Research in Siberia and Turkestan in 1912*. Resettlement Department, Moscow (In Russian), pp. 23–25.
- Sedelnikov, V.P., 1988. High-Mountain Vegetation of the Altai-Sayan Mountains. Nauka, Novosibirsk (In Russian).
- Shiyatov, S.G., 1986. Dendrochronology of the Higher Timberline on the Urals. Nauka, Moscow (In Russian).
- Sidor, C.G., Popa, I., Vlad, R., Cherubini, P., 2015. Different tree-ring responses of Norway spruce to air temperature across an altitudinal gradient in the Eastern Carpathians (Romania). *Trees* 29 (4), 985–997. <https://doi.org/10.1007/s00468-015-1178-3>.
- Sperry, J.S., Robson, D.J., 2001. Xylem cavitation and freezing in conifers. In: Bigras, F.J., Colombo, S.J. (Eds.), *Conifer Cold Hardiness*. Kluwer Academic Publishers, Dordrecht, pp. 121–136.
- Stepanov, N.V., 2006. *Flora of the Northeast of the Western Sayan and the Otdyh Island on the Yenisei (Krasnoyarsk city)*. Krasnoyarsk State University, Krasnoyarsk (In Russian).
- Sudachkova, N.E., Milyutina, I.L., Semenova, G.P., 2002. Influence of water deficit on contents of carbohydrates and nitrogenous compounds in *Pinus sylvestris* L. and *Larix sibirica* Ledeb. *Tissues. Eurasian J. For. Res.* 4, 1–11.
- Tchebakova, N., Parfenova, E., Soja, A.J., 2009. The effects of climate, permafrost and fire on vegetation change in Siberia in a changing climate. *Environ. Res. Lett.* 4 (4), 045013. <https://doi.org/10.1088/1748-9326/4/4/045013>.
- Tranquillini, W., 1979. *Physiological ecology of the alpine timberline. Tree existence in high altitudes with special reference to the European Alps*. Ecol. Stu. Springer-Verlag, Berlin.
- Suvorova, G.G., Yankova, L.S., Kopytova, L.D., Filipova, A.K., 2005. Maximal photosynthesis intensity in Scots pine and Siberian spruce in Baikal region. *Sib. Ecol. J.* 12, 97–108 (In Russian).
- Suvorova, G.G., Oskorbina, M.V., Kopytova, L.D., et al., 2011. Seasonal changes in photosynthetic activity and chlorophylls in the Scots pine and Siberian spruce with optimal or insufficient moistening. *Contemp. Probl. Ecol.* 4 (6), 626–633. <https://doi.org/10.1134/S1995425511060105>.
- Velisevich, S.N., Khutorov, O.V., 2009. Effects of climatic factors on radial growth of Siberian stone pine and Siberian larch in sites with different soil humidity in the South of Western Siberia. *J. Sib. Fed. Univ. Biol.* 2 (1), 117–132 (In Russian).
- Walker, X.J., Mack, M.C., Johnstone, J.F., 2015. Stable carbon isotope analysis reveals widespread drought stress in boreal black spruce forests. *Glob. Change Biol.* 21 (8), 3102–3113. <https://doi.org/10.1111/gcb.12893>.
- Wang, T., Ren, H., Ma, K., 2005. Climatic signals in tree ring of *Picea schrenkiana* along an altitudinal gradient in the central Tianshan Mountains, northwestern China. *Trees* 19 (6), 736–742. <https://doi.org/10.1007/s00468-005-0003-9>.
- Wieser, G., 2002. The role of sapwood temperature variations within *Pinus cembra* on calculated stem respiration: implications for upscaling and predicted global warming. *Phyton* 42, 1–11.
- Wieser, G., 2007. Climate at the upper timberline. In: Wieser, G., Tausz, M. (Eds.), *Trees at their Upper Limit: Treeline Limitation at the Alpine Timberline*. Springer, Dordrecht, pp. 19–36.
- Wigley, T., Briffa, K., Jones, P., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *J. Appl. Meteorol. Climatol.* 23, 201–213. [https://doi.org/10.1175/1520-0450\(1984\)023<0201:OTAVOC>2.0.CO;2](https://doi.org/10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2).
- Yamazaki, J.Y., Ohashi, A., Hashimoto, Y., Negishi, E., Kumagai, S., Kubo, T., Oikawa, T., Maruta, E., Kamimura, Y., 2003. Effects of high light and low temperature during harsh winter on needle photodamage of *Abies mariesii* growing at the forest limit on Mt. Norikura in Central Japan. *Plant Sci.* 165 (1), 257–264. [https://doi.org/10.1016/S0168-9452\(03\)00169-9](https://doi.org/10.1016/S0168-9452(03)00169-9).
- Zamolodchikov, D.G., 2012. An estimate of climate-related changes in tree species diversity based on the results of forest fund inventory. *Biol. Bull. Rev.* 2 (2), 154–163. <https://doi.org/10.1134/S2079086412020119>.
- Zweifel, R., Zimmermann, L., Zeuglin, F., Newbery, D.M., 2006. Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. *J. Exp. Bot.* 57 (6), 1445–1459. <https://doi.org/10.1093/jxb/erj125>.