






Original Article


Larch growth across thermal and moisture gradients in the Siberian Mountains


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Abstract: Climate-driven changes in the thermal and moisture regimes may variously influence different tree species growth and ranges. We hypothesize that drought resistant Siberian larch (*Larix sibirica* Ledeb.) and precipitation-sensitive Siberian pine (*Pinus sibirica* Du Tour) responded differently to climate change along the elevational thermal and precipitation gradients. We studied the influence of air temperature, precipitation, soil moisture, and atmospheric drought (indicated by the drought index SPEI) on larch and pine growth along the southward megaslope of the West Sayan Ridge. We found that since 2000 climate change resulted in increasing larch and pine radial growth index (GI) (c. 1.5–3 times) within treeline (2000–2300 m) and timberline (1900–2000 m) ecotones, i.e. within high

precipitation zones. Within the forest-steppe ecotone (1100–1200 m) in which *L. sibirica* is the only species, larch GI stagnated or even decreased. The total forested area increased since 2000 up to +50% in the high elevations, whereas in the low elevations (<1400 m) area changes were negligible. Within treeline and timberline, trees' GI was stimulated by summer temperature. Meanwhile, temperature increase in early spring reduces GI due to living tissue activation followed by tissue damage by desiccation. Within forest-steppe, larch radial growth was mostly dependent on soil moisture. Warming shifted dependence on moisture to the early dates of the growing period. Acute droughts decreased GI within forest-steppe as well as within treeline, whereas the drought influence on both species within highlands was insignificant. Within forest-steppe seedlings establishment was poor, whereas it was successful within treeline and timberline. Current climate change leads to stagnation or even decrease in *Larix*

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sibirica growth in the southern lowland habitat. In combination with poor seedlings establishment, reduced growth threatens the transformation of open lowland forests into forest-steppe and steppe communities. Meanwhile, in the highlands warming facilitated the growth of Siberian larch and pine and the increase of forested area.

Keywords: Larch; Siberian pine; Climate influence on tree radial growth; Mountain forests; Treeline; Timberline; Foreststeppe; Drought stress; Moisture stress

1 Introduction

Larch-dominant communities are the largest forest formation in east Eurasian boreal forests. In Siberia, larch species (*Larix sibirica* Ledeb., *L. gmelinii* Rupr. and *L. cajanderi* Mayr.) cover c. 70% of the permafrost zone. *Larix sibirica* is also dominant species within the southern Siberian Mountains (Koropachinskiy and Vstovskaya 2002). This species is also well adapted to wildfires and possesses competitive advantages in seedlings within post-fire burns (Kharuk et al. 2021a). Due to its resistance to the harsh environment, larch forms treelines in the Arctic and alpine forest-tundra ecotones. In Siberian Mountains, *Larix sibirica* formed the upper treeline within the relatively dry habitats, whereas Siberian pine (*Pinus sibirica* Du Tour) formed a treeline within the wet habitats. In the southern range of the Siberian boreal forests, larch populated forest-steppe ecotone.

Changing thermal and moisture regimes in Siberia influenced larch and the other tree species growth and health. Elevated air temperature led to moisture supply limitation in the southern part of the boreal forests range due to increased climate aridity, and frequency and severity of droughts. In combination with activated pest attacks, that resulted in the shrinkage of evergreen conifer distribution in North America (Allen et al. 2009; Millar and Stephenson 2015; Restaino et al. 2016), Europe and Russia (Fettig et al. 2013; Kharuk et al. 2017a, b; Kolb et al. 2016). In European Russia and Belarus, vast decline and mortality of spruce (*Picea abies* L.) have been observed (Chuprov 2008; Zamolodchikov 2011; Kharuk et al. 2015b; Sarnatskii 2012). In Siberia, fir (*Abies sibirica* Ledeb.) and Siberian pine forests experienced decline and mortality over vast areas

caused by water stress in synergy with bark-beetles and defoliators attacks (Kharuk et al. 2017a,b, 2021b). Even drought-resistant Scotch pine (*Pinus sylvestris* L.) growth decrease and mortality increase were reported for the Ukrainian forest-steppe and Belarus southwestern forests (Luferov and Kovalishin 2017). Larch, the main conifer species in Siberia, is the most drought-resistant tree due to its high efficiency of water use and deciduous habit, which allows this species to grow at semi-desert precipitation (up to 250 mm/year) (Kloppel et al. 1998). In the warmer and drier climate larch was considered a potential substitute for precipitation-sensitive “dark needles conifers” (*A. sibirica*, *P. sibirica*, and *P. obovata* Ledeb.) within southern Siberian lowlands (Kharuk et al. 2017a,b, 2018b, 2021b). Meanwhile, in the habitats with sufficient precipitation tree growth and forested area were increased (Millar and Stephenson 2015; Liu et al. 2013). For instance, area of forests composed by Siberian pine and fir increased and both species were migrated uphill within the zone of sufficient precipitation (Kharuk et al. 2017c, 2021a, 2022).

As for larch, climate changes were mostly favorable for this species. Indeed, since warming in the 1970s, larch growth has increased, and larch forest densification was reported in the Ural Mountains (Shiyatov et al. 2007; Esper et al. 2010) and in northern and southern Siberian Mountains (Kharuk et al. 2006, 2015a; Kirilyanov et al. 2013). Elevated air temperatures were considered as a primary driver of larch growth. Meanwhile, there are evidences that in a warming climate even drought-resistant larch may experience limitation by moisture followed by growth decrease which was observed not only within larch southern lowland habitats, but also even in mountains and in high latitudes (Zhang et al. 2016; Kharuk et al. 2015a, 2018, 2019).

The goal of this study is an analysis of larch and Siberian pine growth along the moisture and temperature gradients in the southern Siberian Mountains. Elevation gradient is strongly linked with thermal and moisture regimes that are the main drivers of trees' growth. Thus, mountain forests are an ideal object for the studies of trees' response to a changing climate. We hypothesize that the influence of air temperature and moisture on the larch growth was significantly different along the elevational gradient, i.e., in direction from treeline ecotone to the forest-steppe ecotone. In addition, we consider larch vs Siberian pine growth within treeline ecotone in

which both species coexist.

We seek the answers to the following questions:

1. What are chronologies of the larch radial growth index (GI) within different elevational belts?
2. How does larch GI depend on the eco-climate variables (i.e., air temperature, precipitation, soil moisture content, and drought index) within different elevational belts?
3. How does climate change influence the forested area along the elevation gradient?
4. How does larch vs Siberian pine respond to warming within treeline ecotone?

2 Study Area and Tree Species

The study area was located in the West Sayan Ridge which is part of the Altai-Sayan Mountain Region (Fig. 1). This is the transition zone between Siberian taiga and Mongolian steppes and forest-steppes. The main tree species are larch and Siberian pine. *Larix sibirica* is anemochoric shade intolerant species with a life span up to 600–700 y. Larch possessed the highest cold-resistance and drought resistance among Siberian tree species. *Pinus sibirica* is zoochoric shade-tolerant species. That pine is precipitation-sensitive (an optimal precipitation c. 1000 mm/y) with a life span up to 400–500 y. The Sayan Ridge alpine ecotone is a breakpoint between Siberian pine dominant and larch dominant communities. Larch forests are located mostly on the dryer southern megaslope, whereas the rainward northern megaslope at elevations above c. 800 m are occupied mostly by precipitation-sensitive Siberian pine with a minor proportion of larch and broadleaves (*Betula* sp., *Populus tremula* L.). Within the treeline ecotone (elevations 2000–2300 m), tree vegetation presented by both larch and Siberian pine. Timberline ecotone, middle elevations, and forest-steppe of southward megaslope occupied by closed and sparse larch forests. At lower elevations (below ca. 1100 m), sparse larch forests switch to forest-steppes and steppes communities.

Air temperature and precipitation distributions along the elevational transect presented in Fig. 2d. The mean annual air temperature at the highlands was -4°C . Mean and maximal July temperatures are $+10^{\circ}\text{C}$ and $+20^{\circ}\text{C}$, respectively. The thermal degree-days (TDD, $T > +5^{\circ}\text{C}$) was about 140 days. During winter, the air temperature dropped up to -40°C . The

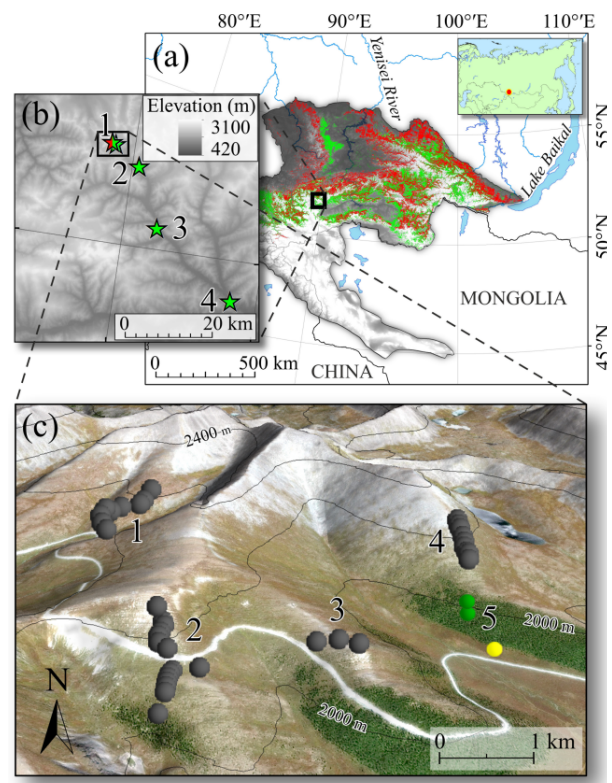


Fig. 1 (a) Study area location shown by the black box. This is the southern megaslope of the West Sayan Ridge, the part of the Altai-Sayan Mountain ecoregion. Evergreen (Siberian pine, fir, and spruce) and deciduous (larch) conifers are marked with red and green, respectively. (b) Study sites are located along the elevational gradient of the West Sayan Ridge. 1, 2 – sites within treeline and timberline ecotones, 3, 4 – sites within middle elevation belt and forest-steppe ecotone. Larch-dominant and mixed (larch + Siberian pine) sites were indicated by green and red stars, correspondingly. (c) Transects and test plots within the treeline and timberline ecotones. 1...4 – transects within treeline ecotone. Within timberline (5), test plots are indicated by green (closed forest) and yellow (forest edge) dots.

summer and annual precipitation are 390 and 760 mm, correspondingly. Within the forest-steppe ecotone (1000–1200 m), the average annual temperature is -1°C . The TDD number was about 180. Mean and maximal July temperatures are $+16^{\circ}\text{C}$ and $+26^{\circ}\text{C}$, correspondingly. In wintertime, the minimum temperature drops to -37°C . The summer and annual precipitation were 240 and 420 mm, correspondingly. Climate data averaged for the 1950–2020 period based on the ERA5-Land database (<https://cds.climate.copernicus.eu/cdsapp#!/dataset>).

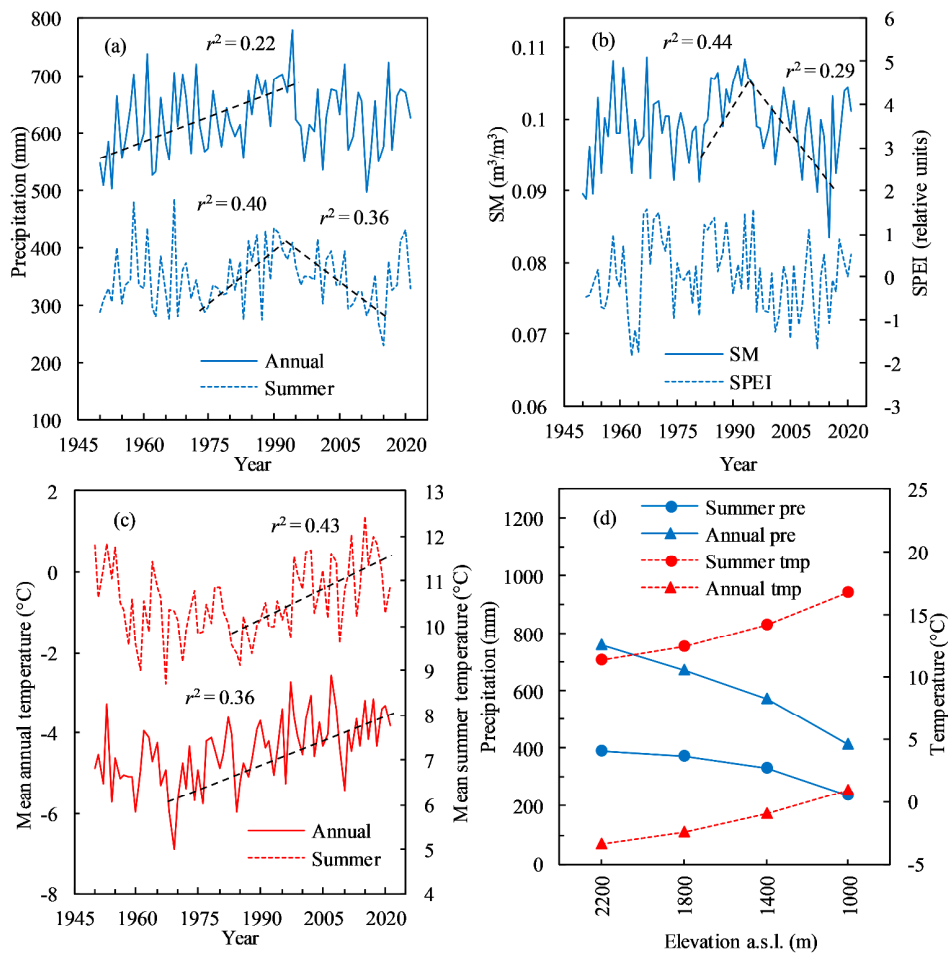


Fig. 2 (a-c) Temporal dynamic of climatic data (data averaged along the elevational gradient). (a) Precipitation, (b) summer soil moisture and drought index SPEI and (c) air temperature. (d) The patterns of mean summer temperature and mean annual temperature (tmp) and precipitation (pre) along the elevational gradient. Data averaged for the period 1950–2020. Trends are significant at $p < 0.05$. **Note:** the decrease in SPEI corresponded to the drought decrease.

seedlings with the age ≤ 30 y.

Ground cover within treeline, timberline and middle elevation was composed of *Betula nana* ssp., *Juniperus* sp., *Vaccinium vitis-idaea* L., *Spirea* sp., *Lonicera caerulea* L., *Salix* spp., *Carex* sp., *Bergenia crassifolia* L., *Dryas* sp., *Geranium* sp., *Anemone* sp., *Oxalis acetosella* L., *Empetrum nigrum* L., and moss and lichen species (e.g., *Cladonia rangiferina* L.). Within forest-steppe, ground cover was composed of *Salix* spp., *Caragana* sp., *Rhododendron* spp., *Cornus* sp., *Spiraea* sp., *Bupleurum* sp., *Vicia cracca* L., *Artemisia* sp., and gramineous species.

3.3 Remote sensing data

Forests area dynamic analysis was based on the MODIS-derived IGBP maps with a spatial resolution of 463 m (<https://lpdaac.usgs.gov/products/mcd>

[12q1v006](https://lpdaac.usgs.gov/products/mcd); Sulla-Menashe et al. 2019). We analyzed the dynamics of (1) deciduous needle leaf (i.e., forests with tree cover $>60\%$), and (2) woody savannas (i.e., a sparse forest with a tree cover of $30\%–60\%$). We calculated area changes (ΔS) as a difference between two basic periods: 2017–2019 and 2001–2003. The three-year period was used to decrease classification errors. Spatial analysis of the forested area was based on the GMTED DEM (<https://www.usgs.gov/coastal-changes-and-impacts/gmted2010>; spatial resolution ~ 250 m). We filtered out burned areas based on the MODIS MCD64A1 v.6.1 product (<https://lpdaac.usgs.gov/products/mcd64a1v061>). ESRI ArcGIS software was used in the remote sensing data analysis.

3.4 Dendrochronology analysis

The total sample size included cores from 213

trees. We glued each sample on wooden backing, planed it and treated it with a contrast-enhancing powder. Tree ring widths were measured using LINTAB 6 device (with the precision of 0.01 mm; Rinn 1996). Missing rings were detected by the cross-dating method. The quality of cross-dating was checked by COFECHA program. Age trend was eliminated by negative exponential or negative linear regression methods (by ARSTAN program). Standard and residual tree ring chronologies were generated for the four test sites along the elevation gradient (Fig. 1b). Standard chronologies are biweight robust mean values of indexed tree ring chronologies for the corresponding TP. Residual chronologies were generated from standard chronologies by eliminating autoregressive component. Tree-ring width chronology (in mm) is the proxy of the annual radial increment of the tree. We suggested a unitless growth index (GI) as the metric of the radial growth increment. GI is the normalized tree-ring chronologies with the average of 1.0. The dendroclimatic analysis was based on the residual chronologies. Samples for treeline ecotone included 43 larch and 40 Siberian pine trees. For the timberline ecotone, middle elevation belt, and forest-steppe ecotone sample sizes were 30, 31, and 69 larch trees, respectively.

3.5 Statistical analysis

We used StatSoft Statistica (<http://statsoft.ru>) and R 4.1.2 (<https://www.r-project.org>) software. We used a multiple linear and hierarchical multiple linear regression analysis. Multiple linear models were used to estimate the dependence of tree GI on the eco-climate variables. Before applying that analysis, we selected the main variables based on the preliminary correlation analysis. The best regression equations were found from the full set of possible regression equations with independent variables by applying the corrected Akaike information coefficient (AICc; Hurvich and Tsai 1989) and adjusted R^2 . We selected regression equations with statistically significant coefficients ($p < 0.05$) only estimated by t -statistic. Then, we applied the hierarchical multiple regression analysis in which an additional variable was added to the regression equation at each step of the analysis (Tabachnick and Fidell 2013). The hierarchical analysis provided estimates of explained dispersions for each variable. The piecewise regression analysis was used to detect breakpoints in the time-series of

larch and Siberian pine GI as well as in climatic variables dynamics (Ryan and Porth 2007).

4 Results

4.1 Climate variables dynamics

Values of precipitation and soil moisture are decreasing since c. 1995 until 2015 with the following increase. Trends in air temperature are positive since c. 1970 (annual) and c. 1985 (summer) (Fig. 2a-2c). The patterns of air temperature and precipitation distribution along the elevation gradient are shown in Fig. 2d.

4.2 Trees GI temporal dynamics vs. elevational gradient

Within the treeline ecotone, larch and Siberian pine GI increase were observed since ca. 2000 y (Fig. 3). In comparison with the reference (1980–1999) period, larch GI in the 21st century increased about 1.5 times middle elevations and up to 2.1 times in treeline ecotone. Siberian pine GI increase was about 2.9 times within treeline. Within middle elevations and forest-steppe, larch GI decreasing trend was observed since c. 2005, although median GI values within forest-steppe did not change. Notably that severe 2012 drought led to GI decrease both in treeline and forest-steppe ecotones (Fig. 3a, 3d), whereas within timberline and middle elevations drought influence was not significant (Fig. 3b, 3c).

4.3 Tree growth vs. climate variables

In the following analysis, we used the time interval 1990–2020, i.e., the period since the onset of significant GI changes (c. 1990; Fig. 3).

4.3.1 Treeline

Within the treeline, growth of larch and Siberian pine was increasing with summer temperature increase, whereas elevated April–May temperatures negatively influenced trees' growth (Figs. 4a and 5a). The latter living tissues' provocation by early spring warms with following on needles' and twigs' desiccation. Winter precipitation negatively influenced trees growth since increased accumulation and decreased growing period. Mid-summer (July)

precipitation was favorable for both species' growth. Similarly, increased soil moisture in mid-summer stimulated trees' growth (Figs. 4b, 4c and Figs.5b, 5c).

Larch GI dependence on the main variables described by equation 1:

$$GI_L = 0.5 \times T_{June} + 0.26 \times P_{July} + 0.37 \times SM_{July} - 0.08 \quad (1)$$

in which T_{June} , P_{July} , and SM_{July} are June temperature, July precipitation, and soil moisture ($p > 0.05$).

Adjusted $R^2 = 0.67$; the intercepted dispersion = 71%. Variables' inputs into intercepted dispersion: $T_{June} = 46\%$, $P_{July} = 11\%$, $SM_{July} = 14\%$. The unexplained dispersion in Eq. (1) and followed equations referred to variables with minor influence on the tree growth, including the potential CO2 fertilization effect.

Siberian pine growth dependence on the main variables described by Eq. (2):

$$GI_{SP} = 0.69 \times T_{JJA} - 0.41 \times T_{AM} - 0.01 \quad (2)$$

in which T_{JJA} and T_{AM} are the mean summer (June–August) and April–May temperatures ($p > 0.05$). Adjusted $R^2 = 0.77$, intercepted dispersion = 79%. Dispersion intercepted by variables: $T_{JJA} = 61\%$, $T_{AM} = 18\%$.

4.3.2 Timberline

Within the timberline, larch growth negatively correlated with April temperature and positively with temperature in June (Fig. 6a). Winter (November–February) precipitation had a negative influence on larch growth, whereas precipitation and soil moisture in July stimulated growth (Fig. 6b, 6c).

Larch growth dependence on the main variables described by Eq. (3):

$$GI_L = 0.57 \times T_{June} + 0.36 \times P_{July} + 0.26 \times SM_{July} - 0.05 \quad (3)$$

in which T_{June} , P_{July} and SM_{July} are June air temperature, July precipitation, and soil moisture ($p > 0.05$). Adjusted $R^2 = 0.86$, intercepted dispersion = 88%. Dispersion intercepted by variables: $T_{June} = 64\%$, $P_{July} = 20\%$, $SM_{July} = 4\%$.

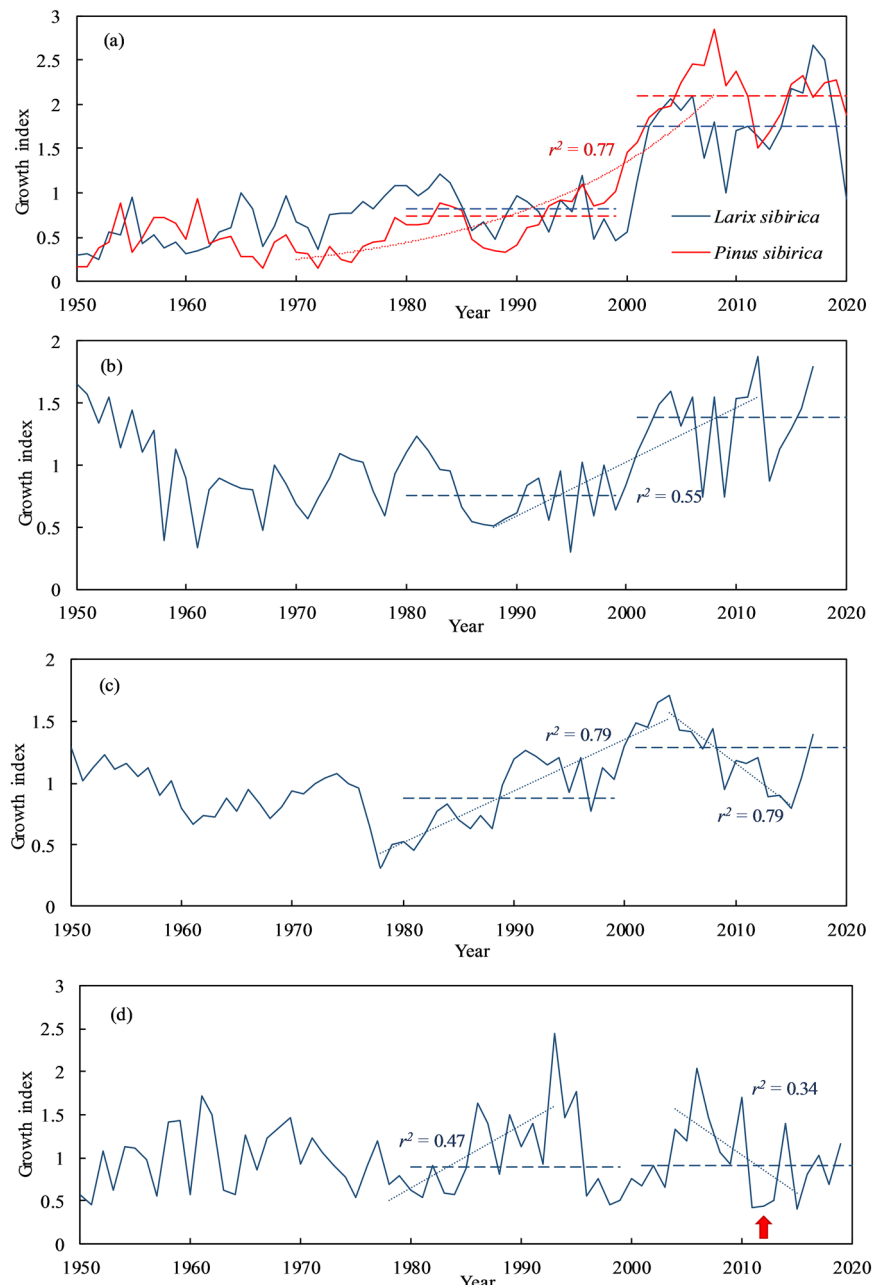


Fig. 3 (a) Larch and Siberian pine GI dynamics within treeline ecotone. (b–d): larch GI dynamics within (b) timberline (1900–2000 m), (c) middle elevations (1600–1700 m), and (d) forest-steppe (1100–1200 m). Dot lines ($p > 0.05$) indicated trends. Dash line indicated GI medians for the 1980–1999 and 2000–2020 periods. Severe drought year (2012) is indicated by arrow.

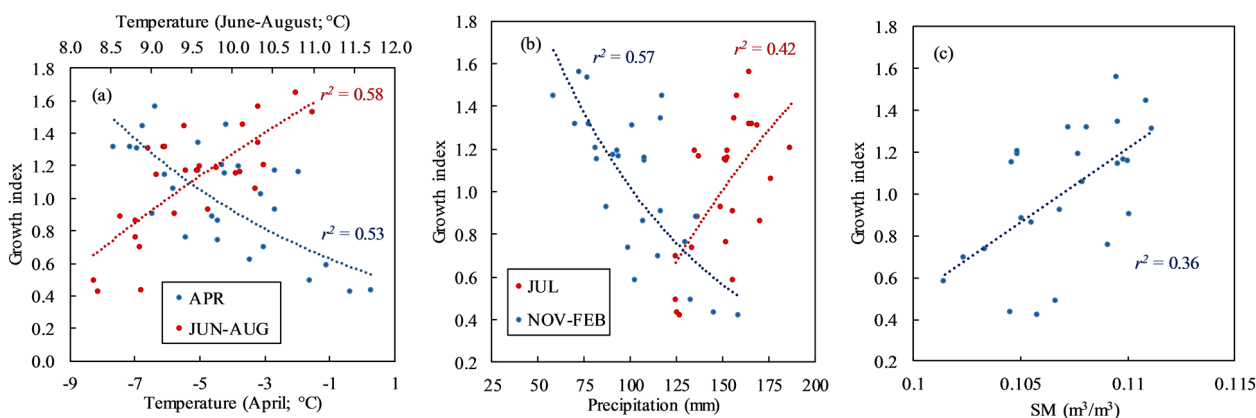


Fig. 4 (a) In the treeline ecotone, the larch GI negatively correlated with April air temperature, whereas correlation with summer temperature was positive. (b) The larch GI positively correlated with July precipitation, whereas winter (November–February) precipitation negatively influenced the GI. (c) The GI positively correlated with July soil moisture (SM). SM was measured in volumetric units (m³ of water within m³ of soil; section 3.1). Hereafter the analyzed period was 1990–2020.

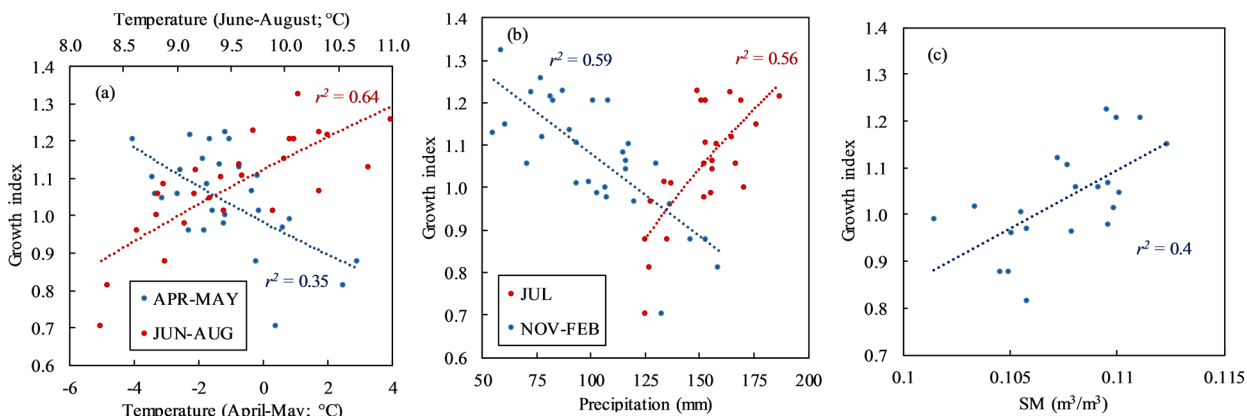


Fig. 5 (a) Siberian pine GI in treeline ecotone negatively correlated with April–May temperatures, whereas the correlation with summer temperature was positive. (b) July precipitation increased GI, whereas winter (November–February) precipitation negatively influenced GI. (c) GI positively correlated with soil moisture in July.

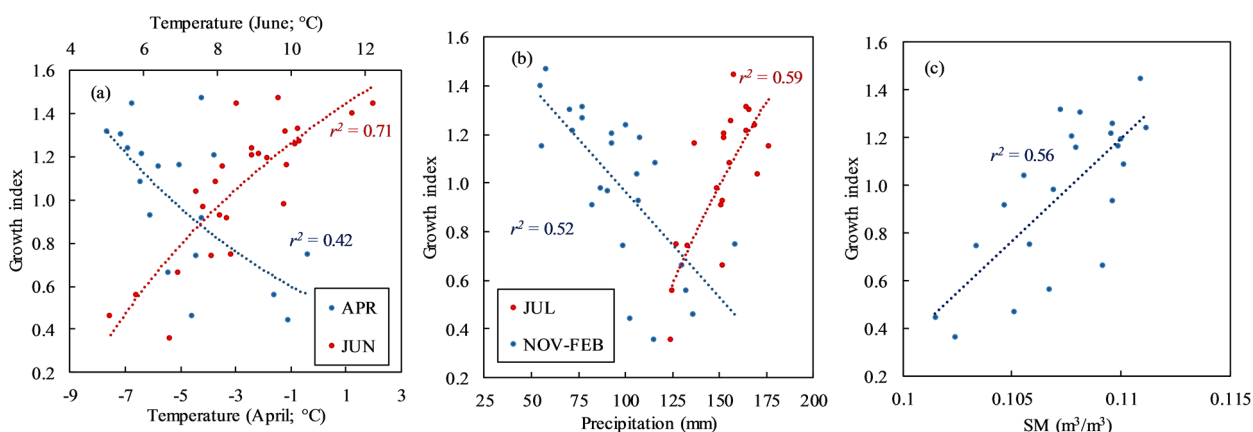


Fig. 6 (a) Larch GI in timberline negatively correlated with April temperature and positively with June ones. (b) Larch GI negatively correlated with winter (November–February) precipitation, whereas precipitation and soil moisture in July (c) stimulated growth.

4.3.3 Forest-steppe

Within the forest-steppe, the larch GI is strongly dependent on the moisture availability at the beginning of the growing period (May–June) (Fig. 7d). Precipitation in the September–April period also positively influenced larch growth (Fig. 7b). Similarly, air drought decrease (indicated by SPEI) led to the larch GI increase (Fig. 7c).

Larch growth dependence on the main climate variables described by Eq. (4):

$$GI_L = 0.41 * SM_{MJ} + 0.42 * SPEI_{June} - 0.08 \quad (4)$$

in which SM_{MJ} and $SPEI_{June}$ are May-June soil moisture and June SPEI ($p < 0.05$). Adjusted $R^2 = 0.62$, intercepted dispersion = 65%. Dispersion intercepted by variables: $SM_{MJ} = 58\%$, $SPEI_{June} = 7\%$. Thus, the major variables that limit larch growth within the forest-steppe are the soil and atmospheric moisture content.

During the time interval 2000–2020 versus the reference period (1980–1999), larch growth dependence on the soil moisture shifted to the earlier

dates (up to late April). A minor increase in GI sensitivity to moisture was also observed in the end of the growing period (Fig. 8). That shift referred to the combined effect of decreased SM with elevated air temperature in the 21st century (Fig. 2b, 2c).

4.4 Seedlings

Within the treeline ecotone, seedlings recruitment (both number and health status) was successful. Within timberline (i.e., closed larch stands), seedlings recruitment was poor. Within forest-steppe ecotone, seedling and sapling density was low. Meanwhile, within burns (elevations 1200–1400 m) seedlings reached 20000 stems/ha (Fig. 9, Table 1).

4.5 Forest area dynamic along the elevational gradient

Since the 2000-s, the forest area was increased with elevation increase. Area increment increase was

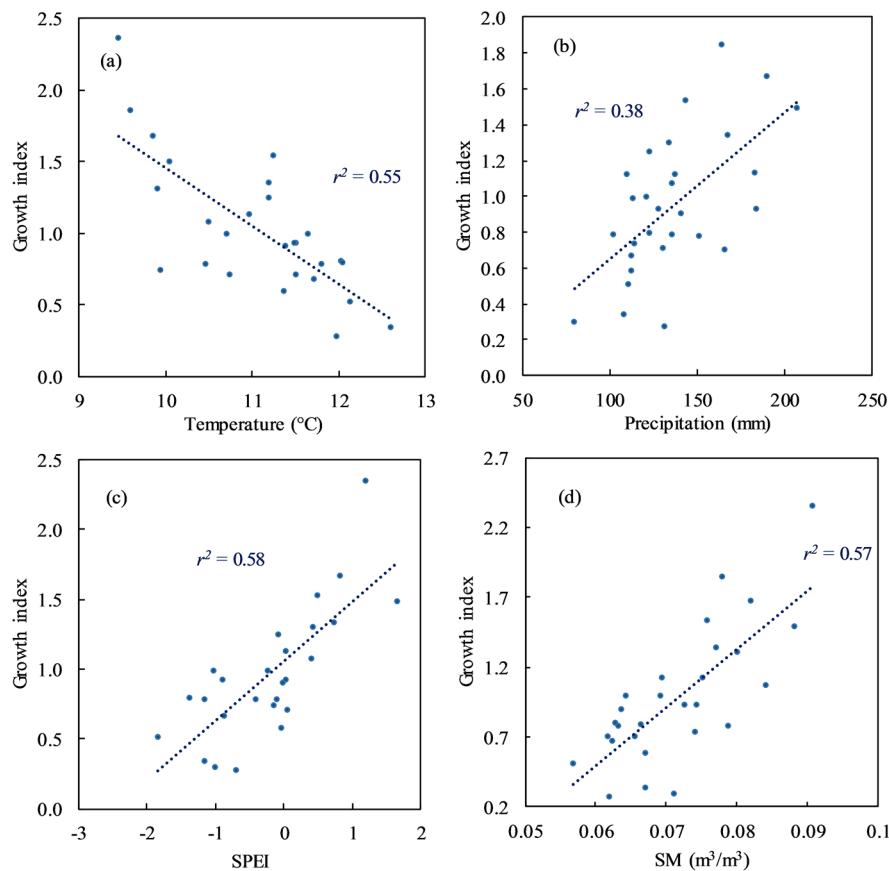


Fig. 7 (a) In forest-steppe, the larch GI negatively correlated with April–August temperature. (b) Larch GI positively correlated with September–April precipitation. The larch GI positively correlated with atmospheric (c; June SPEI) and soil moisture (d; May–June).

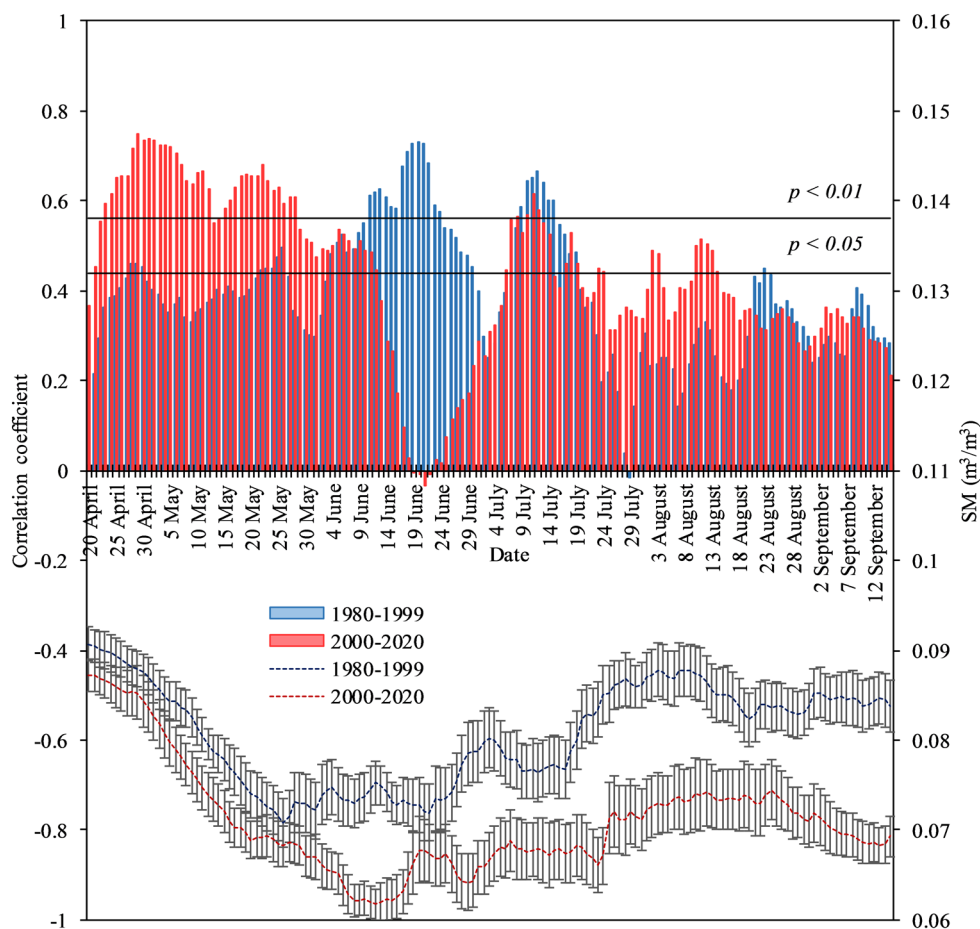


Fig. 8 Larch GI daily correlations with soil moisture shifted from June to the late April-May days. Compared periods: 1980–1999 (1, blue) and 2000–2020 (2, red). The lower chart shows SM (m^3/m^3) dynamics during 1980–1999 (3, blue) and 2000–2020 (4, red). During the latter period, SM content decreased (Fig. 2b).

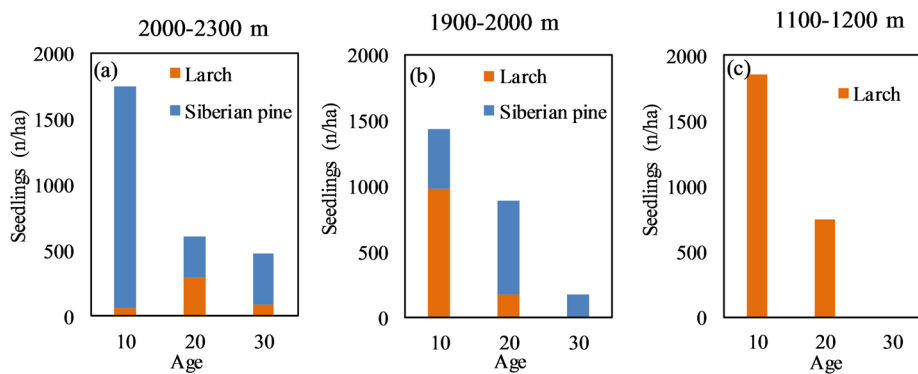


Fig. 9 Larch and Siberian pine seedlings at different elevation belts: (a) 2000–2300 m; (b) 1900–2000 m; (c) 1100–1200 m.

observed in the direction from the forest-steppe to high elevation with the followed on decrease within the treeline limit (2100–2300 m) (Fig. 10b). Maximal growth increment (>+50%) was observed within the 2000–2100 m elevation belt. In the low elevations (<1400 m) forested area changes were negligible.

5 Discussion

Climate change within West Sayan Mountains resulted in different consequences for trees' growth within highlands and lowlands. Warming led to larch GI increase in the humid highlands, whereas within

moisture-limited forest-steppe GI stagnated or even decreased during recent years (Fig. 3). Thus, during 2000–2020 versus similar reference period, larch GI increased 1.5–2.2 times in the treeline, timberline, and middle elevations, whereas within forest-steppe ecotone larch growth was stagnated. A high GI increase (2.8 times) also shows Siberian pine within treeline ecotone. Similarly, the larch-covered area within the low elevation belt stagnated. Moreover, a minor increment drop was observed at elevations 1200–1300 m due to wildfire events (Fig. 10). Whereas with elevation increase, the forested area gradually increased with maximal increment (c. +50%) within the 2000–2100 m elevation belt. Followed on growth drop occurred within the treeline limit, the zone of extremely harsh habitat (Fig. 10).

Within treeline and timberline, trees' GI was mostly dependent on the June and summer air temperatures. Although precipitation within treeline and timberline were sufficient (c. 800 mm), trees GI indicates dependence on the soil moisture in July. That was attributed to low soil water capacity since trees grow mostly on the convex steep slopes with shallow rocky well-drained soils underlined by bedrocks (Appendix 1). Wintertime precipitation negatively influenced trees' growth due to the delay in the growing period. Thus, within treeline and timberline, soil moisture was sufficient for trees' growth with the exception of soil moisture in July (Fig. 4c, 5c, 6c). A similar larch growth pattern was described for the alpine ecotone within the northern part of the Altay-Sayan region (Petrov et al. 2015, 2021).

Notable non-intuitive negative correlations of larch and Siberian pine growth with spring (April–May) air temperatures. That phenomenon was attributed to the cambium activity provocation by early spring warms with the followed desiccation and

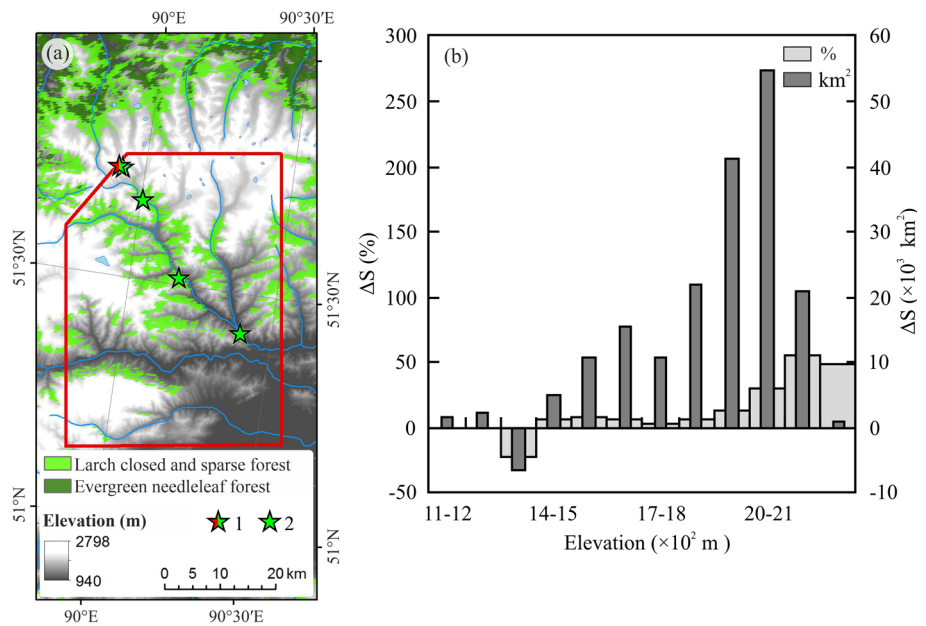


Fig. 10 (a) The elevational transect boundary is shown by the red line. Stars corresponded to test sites in Fig. 1b. The upper transect part approximated the watershed boundary. (b) The forested area increments along the elevation. Increments (ΔS) were calculated as a difference ((1) in %, or (2) in km²) between 2017–2019 and 2001–2003. ΔS gradually increased along the elevation and decreased at the treeline limit (>2100 m).

damage by late frosts. Thus, the number of days with $T > 0^{\circ}\text{C}$ in April occurred for about a decade. Meanwhile, trees' bark temperatures on the stem's sunlit side may exceed ambient temperature up to $+20^{\circ}\text{C}$ (Sakai 1966), i.e., increasing the warming effect. Therefore, spring warms provoked cambium and photo-system activity, whereas soil water is still not available. That caused a "physiological drought" with consequent desiccation and mortality of needles and twigs (Appendix 2a-2c, 3a,3b). To the point, trees' photo-system located not only within needles, but also within the bark and even young twigs' stem (Kharuk et al. 1994).

Within the forest-steppe, the larch GI was strongly influenced by soil and atmospheric moisture content. Within the forest-steppe ecotone, the elevated air temperatures on the background of precipitation stagnation (Fig. 2a) lead to a decrease in available moisture. Thus, the seasonal onset of larch growth limitation by soil moisture shifted from June to late April–May (Fig. 8). Limitation by SM was indicated also by GI dependence on the moisture stored in the soil in the previous growing period (Fig. 7b). Notable that acute droughts decreased trees growth not only within the forest-steppe ecotone, but also within the precipitation sufficient treeline

ecotone (Fig. 3a,3d). Meanwhile, within timberline and middle elevations, drought influence was not significant. That paradox is explained by low snow accumulation within the treeline due to snow blowing, whereas closed stands facilitated snow accumulation. In addition, in the treeline shallow well-drained rocky soils had a low water capacity. Larch trees (*L. gmelinii*) growth decrease and even mortality was reported in Mongolia (Li et al. 2007; Juříčka et al. 2020) and northern China (Zhang et al. 2018), and that phenomenon was attributed to the permafrost degradation. Within our study larch growth dependence on the permafrost influence was hardly possible since within lower elevations permafrost not occurred. Within treeline and timberline permafrost occurred sporadically; meanwhile the seasonal thawing depth is about 3.0 m and underling bedrocks located at 0.5–1.5 m depth.

Larch seedlings occurred throughout all southern megaslope, whereas Siberian pine seedlings occurred within highlands only, i.e., within the elevations with sufficient precipitation. Seedlings recruitment was successful mainly within the treeline ecotone and at the timberline edge (Table 1, Fig. 9). Both species' seedlings was mainly healthy. Larch and Siberian pine seedlings was located mostly within micro depressions, whereas on the convex slopes seedlings was rare (Appendix 2). Siberian pine seedlings were also found within bushes, whereas larch seedlings, on the contrary, were rarely found within shrubs since is a highly light-sensitive species. Thus, shrubs (*Betula nana* L. mostly) competed with tree species for a better habitat. It was known that warming in mountains entailed seedlings uphill migration (e.g., Lenoir et al. 2008; Kharuk et al. 2010, 2021c; Petrov et al. 2021). In the windy treeline habitats, trees uphill migration occurred mostly in the form of trees' clusters (so-called "hedges"; Appendix 3). Once established, hedges promote positive feedback, i.e., wind-protection, snow accumulation, and soil formation that facilitated further seedlings' establishment (Holtmeier 2009; Kharuk et al. 2021c).

Within closed stands, seedlings recruitment was poor since larch is a shade intolerant species. In addition, dense ground cover within closed stands limited seed germination. Larch seedlings recruitment as well as old larch forests' regrowth were regularly facilitated by wildfires which burn out on-ground cover and improve regime of insolation (Kharuk et al. 2021a). Opposite to larch, shade-

resistant Siberian pine seedlings were also observed within closed larch forests that would be located even far from mother-trees. Siberian pine dissemination provided mostly due to nutcracker bird (*Nucifraga caryocatactes* L.) activity.

Warming within treeline caused a krummholz (Siberian pine mostly) transformation into upright forms. That phenomenon onset was indicated by the strong GI increase at c. 1990 (Appendixes 2, 3). The krummholz physiognomy transformation was widely observed in Siberia, as well as in Scandinavian and North American mountains (e.g., Kullman and Kjallgren 2006; Holtmeier 2009). Meanwhile, larch grows upright even in sites where Siberian pine was still krummholz. As the leader in cold-resistance, this species occupied higher elevations in comparison with Siberian pine (c. >20 m uphill).

Within the forest-steppe ecotone, the seedlings density was low (Fig. 9c). In that zone, growth of even drought-resistant larch was limited by available moisture. Moreover, soil moisture within the forest-steppe significantly decreased during recent decades (Fig. 8). Observed larch growth reduction with potential larch southern retraction coincided with predicted and observed larch species response to changing climate. Larch trees and stands growth increase alongside with larch migration into cold alpine tundra is similar with the phenomenon of larch northward migration (Kharuk et al, 2006, 2010, 2015a; Mamet et al 2019).

As mentioned above, wildfires are considered as an important factor that supported larch dominance in some habitats (e.g., Kharuk et al. 2021a). Light-sensitive larch hardly regenerated under the mother canopy, whereas within burns seedlings usually abounded. Thus, within burns seedlings exceeds 25,000 seedlings/ha (Table 1, Fig. 9). There were also some evidences of larch seedlings downhill migration (Kirpotin et al. 2021). However, warming-induced wildfire probabilities increase in Siberia periodically burned out larch seedlings within the forest-steppe with consequent slow-down of larch downhill migration. However, that issue was still poorly investigated and needs future studies.

Drought-resistant larch is a potential substitute for the precipitation-sensitive Siberian pine and fir species that experienced increasing decline and mortality within the southern lowland part of its range (Kharuk et al. 2021b). The latter supported hypothesis of northward shift of the boreal forests'

southern boundary in the lowlands due to moisture constraints in the future climate (Pachauri et al. 2014). However, in a warming climate larch itself experienced radial growth stagnation or even radial growth decline within the lowlands' southern range of this species, within the transition between Siberian taiga and Mongolian forest-steppes. The continuous warming (scenario RCP4.5, RCP6.0) threatens the transformation of sparse larch forests within lowlands into steppe communities.

6 Conclusion

We concluded that soil moisture, in combination with elevated air temperature, were the major drivers that influenced larch and Siberian pine growth within the southern megaslope of the West Sayan Mountains. We found that warming increased larch and Siberian pine growth within treeline and timberline ecotones, i.e. within elevations with sufficient precipitation, whereas within forest-steppe larch growth stagnated or even decreased during recent decades. Within treeline and timberline, trees' growth was mostly stimulated by the summer temperature, whereas spring temperatures negatively influenced growth due to living tissues' activation

with the followed on desiccation and the late frosts' damage. Within the forest-steppe ecotone, larch growth was mostly dependent on soil moisture. Significant SM decrease during recent decades shifted larch dependence on moisture to the early dates. Seedlings recruitment was successful within treeline and timberline zones, whereas within forest-steppe it was poor. The results obtained indicated that the current climate warming leads to stagnation or even a decrease in larch growth within low elevations at the southern range of that species in Siberia. In combination with a poor seedlings recruitment, that threatens transformation of the open lowland larch forests into steppes communities. Meanwhile in the highlands warming facilitates larch and Siberian pine growth and the forested area increase.

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