Trees on the tundra: warmer climate might not favor prostrate *Larix* tree but *Betula nana* shrub growth in Siberian tundra (Lena River Delta)

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ABSTRACT

Tundra is primarily a habitat for shrub growth, not trees, but growth of prostrate forms of trees has been reported occasionally from the subarctic tundra region. In the light of on-going climate change, climate sensitivity studies of these unique trees are essential to predict vegetation dynamics and potential northward expansion of boreal forest tree species into tundra. Here we studied one of the northernmost *Larix* Mill. trees and *Betula nana* L. shrubs (72°N) from the Siberian tundra for the common period 1980-2017. We took advantage of the discovery of a single cohort of prostrate *Larix* trees within a tundra ecosystem, i.e., ca. 60 km northwards from the northern treeline, and compared climate-growth relationships of the two species. Both woody plants were sensitive to the July temperature, however this relationship was stable across the entire study period (1980-2017) only for *Betula nana* chronology. Additionally, radial growth of *Larix* trees became negatively correlated to temperatures during the previous summer. In recent period moisture sensitivity between *Larix* trees and *Betula nana* shrubs was contrasting, with generally wetter soil conditions favoring *Larix* trees growth and dryer conditions promoting *Betula nana* growth. Our study indicates that *Larix* trees radial growth in recent years is more sensitive to moisture than to summer air temperatures, whereas temperature sensitivity of *Betula nana* shrub is stable over time. We provide first detailed insight into the annual resolution on *Larix* tree growth sensitivity to climate in the heart of the tundra. The potentially higher *Betula nana* shrub resistance to warmer and drier climate versus *Larix* trees on a tundra revealed in our study needs to be further examined across habitats of various soil, moisture and permafrost status.

1. Introduction

Arctic is warming rapidly and the biomes are changing in a variety of ways. Specifically, expansion of trees into tundra in recent decades has been widespread, but not universal (Lloyd et al., 2003). Although warmer climate conditions are regarded as favorable for the development of northern tree habitats, different environmental factors and adaptation strategies may have variable effects in terms of the spread of individual species (Harsch et al., 2009; Kruse et al., 2020). In recent decades the boreal forest biome has shown both a tendency to increase vegetation greenness (greening) and a decrease in vegetation greenness (browning), testifying to the commenced process of its shift (Berner and Goetz, 2022). Commonly used variables such as growing season air temperature, permafrost occurrence and soil water content alone do not explain changes taking place in taiga and tundra ecotones (Maher et al., 2021). For example warm temperatures might impact woody plant

growth both positively and negatively, depending on local moisture availability on the tundra (Bjorkman et al., 2018; Buchwal et al., 2020; Myers-Smith et al., 2015). Moreover, despite physiological constraints, it is still unclear how far trees can spread northwards under warmer climate conditions from the world's largest forest, i.e., the boreal forest, also known as taiga.

Among boreal tree species *Larix* is indicated as the northernmost woody plant that has been reported to expand both in altitudinal (Devi et al., 2008; Kirdyanov et al., 2012; Shiyatov et al., 2005; Shiyatov and Mazepa, 2011) and latitudinal gradient (Esper and Schweingruber, 2004; Kharuk et al., 2005). Tundra is primarily a habitat for shrub growth, not for trees, but growth of prostrate *Larix* trees has been reported from the subarctic tundra in northern Siberia (Kruse et al., 2020). In general Siberian larch species cover broad biogeographical domain between the longitude of 70–179°E and latitude of 51–72°N (Abaimov 2010). Despite many studies being conducted on *Larix* trees at the

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northern limit of boreal forest in Siberia (e.g., Esper and Schweingruber 2004; Jacoby et al. 2000; Kharuk et al. 2019, 2006; Kirdyanov et al. 2003, 2020; MacDonald et al. 1998; Vaganov et al. 1999; Vaganov and Kirdyanov 2010), yet dendroclimatological studies on prostrate forms of larch trees growing within the tundra biome have not, to our knowledge, been performed. This is partially due to high inaccessibility of the area and satellite-derived remote sensing products being inadequate yet to capture single dwarf-like trees on the tundra. A previous study indicated that through seed dispersal prostrate forms of larch may grow at a 1–3 km distance from the maternal stand (Kharuk et al., 2006). Such trees represent probably one of the first succession stages of boreal tree species on a tundra, thus the analyzes of their radial growth response to climate is essential to understand vegetation change dynamics and treeline migration in response to on-going and projected climate change (Gonzalez et al., 2010). Insights on the climatic sensitivity of a treeline species and its dynamics over time have also the potential to detail our assessments of species recruitment and range extension of trees at the northern treeline (MacDonald et al., 2008).

In summer 2018, we encountered a prostrate form of larch trees, growing on the genuine treeless tundra (72°N) in the Lena River Delta, northern Siberia. We undertook this unique opportunity and performed comparative dendroclimatological analyzes between two co-existing species, i.e., one shrub and one tree species growing side-by-side in a subarctic tundra ca. 60 km northwards from the northern treeline. Our specific research questions are:

(1) What is the climatic sensitivity of two adjacent woody plant species growing in the subarctic tundra, i.e., one common boreal tree species and one common tundra shrub species?
(2) Is climatic sensitivity of the two co-occurring species changing under recent climate warming?

We hypothesized that radial growth of both species is positively related to summer temperature and that growth of both species is increasing under warmer climate. Tundra shrubs are known to be highly sensitive to climate (Buchwal et al., 2020; Myers-Smith et al., 2015) but studies on climate sensitivity of shrubs from East Siberia are not that common (e.g., Blok et al. 2011; Li et al. 2016). Thus, with this study we additionally aimed to filled that gap and characterize climate-growth response of *Betula nana*, a circum-arctic shrub species commonly studied in other parts of the Arctic (e.g., Bret-Harte et al. 2001; Buchwal et al. 2023; Gamm et al. 2018; Hollesen et al. 2015; Ropars et al. 2015).

2. Materials & methods

2.1. Study site and species sampling

In late August 2018 we sampled 17 prostrate trees of *Larix* Mill. (hereafter *Larix*) on the southern Kurungnakh Island (72°17'N, 126°08'E) located in the south-central Lena River Delta, northern Yakutia, Siberia (Fig. 1). Considering both current and projected *Larix* trees range distribution in northern Siberia (Tchebakova et al., 2005) all sampled individuals were most likely represented by *Larix dahurica*, also known as *Larix gmelinii* (Bobrov, 1972 cited in Abaimov, 2010). Kurungnakh Island belongs to the third main terrace of the Lena River Delta (Grigoriev, 1993), which is distributed in the southern delta as erosional Pleistocene Yedoma remnants. The trees were growing among dwarf birch shrubs within a subarctic tundra zone, ca. 8 km from the mainland at the westernmost channel of the Lena River Delta, classified as erect dwarf-shrub tundra (Walker et al., 2005). All trees were of ca. 30–40 cm height and were growing in a cohort, i.e., along frost cracks at distance of ca. 50 m. Each tree was of a creeping form with usually one main stem that grew vertically (Fig. 1D).

In order not to damage this unique tree population, we have limited our sampling to only selected individuals, i.e., trees were taken at a distance of 2-3 m apart. Since there were no other trees in that area we cannot exclude the fact that these were clonally reproduced plants (*cf.* Kruse et al. 2020). We have not detected belowground connections through the main roots between the sampled individuals, but horizontally spreading adventitious roots were observed. The mean stem-base
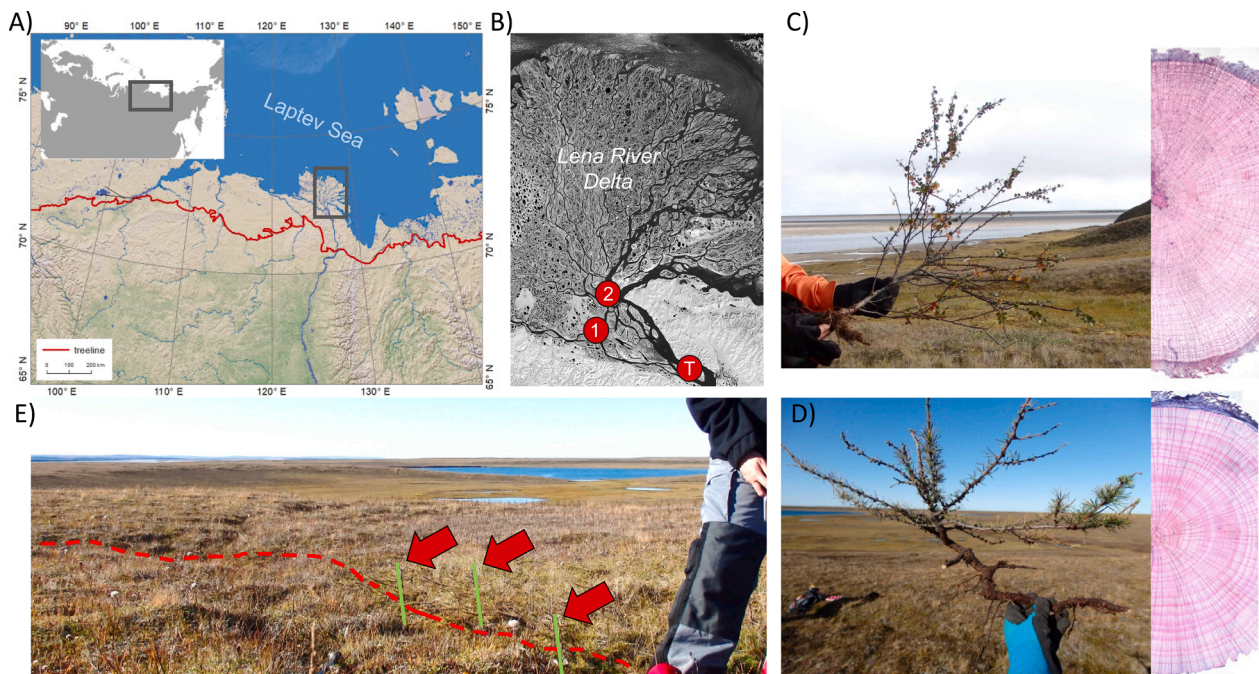

Fig. 1. (A) Study site location (grey rectangle) in the Lena River Delta, Siberia, ca. 60 km from the northern treeline (delineated in red after Walker et al. 2005); (B) prostrate *Larix* trees (1: Kurungnakh Island) and *Betula nana* shrubs (1, 2) sampling sites. One additional *Larix* tree was sampled on Tit-Ary Island (T). Morphology and growth rings overview of (C) *Betula nana* shrub and (D) *Larix* tree. (E) Overview of a prostrate *Larix* trees habitat in southern Kurungnakh Island; green vertical lines and red arrows indicate individual trees growing along the frost crack (red dashed line). An overview map (1A) was created using ArcGIS® software and shaded background relief by ESRI.

diameter of the *Larix* trees was 1.2 cm (max = 1.7; min = 0.7).

We cut and analyzed a total of 53 cross-sections from all the larches, including both above- (main branch) and below-ground (i.e., horizontally spread main stems) parts. Since below-ground parts appeared to be the oldest, we focused our serial sectioning (Kolishchuk, 1990) on the main stems (i.e., 83% of cross-sections studied). From two to five cross-sections per larch sampled at a mean interval of 10 cm were studied. Cross-dating of radial growth of these dwarf larches was performed using an additional larch tree sampled in 2019 on Tit-Ary Island, located ca. 40 km southeast from our main study site (Fig. A1 in Supplementary Material). Due to logistic constrains we were not able to sample more trees in that location. Fire scars were not observed in the *Larix* wood, but scars and traumatic resin ducts were spotted in a few individuals (Fig. A2 in Supplementary Material).

In order to compare climate sensitivity of dwarf larch trees with tundra shrubs, we sampled 50 *Betula nana* L. individuals. *Betula nana* (hereafter *Betula*) is one of the most dominant tundra shrub species in the area with a multi-stem architecture and canopy height up to ca. 40 cm. Shrubs were taken from two main locations in the Lena River Delta (Fig. 1B), including a plot sampled ca. 50 m away from the larch trees samples. Three shrubs were subjected to cross-dating and from all shrubs a stem-based cross-section was measured. After cross-dating, we excluded 13 shrubs because of low ($r < 0.2$) correlation with the master chronology. In the final *Betula* chronology 37 shrubs and 40 cross-sections were included (Table 1). All *Larix and Betula* sampling locations represented relatively well-drained low-slope environments.

Both *Larix* prostrate trees and *Betula* shrubs were growing on continuous permafrost, i.e., ground ice-rich Yedoma uplands (Morgenstern et al., 2013) with mean and maximum active layer thickness of 40 and 68 cm (as measured on 27th of August 2018), respectively. Mean annual temperature of the study area is -11.8 °C, with the mean February and mean July air temperatures of -31.9 and 9.2 °C as the coldest and the warmest months, respectively (period 2003–2018, meteorological data from Samoylov Island (Boike et al., 2019) located ca. 14 km from the main study site). The mean annual precipitation is 309 mm (period 1980–2018, Tiksi meteorological station data, KNMI Climate Explorer; (Trouet and Van Oldenborgh, 2013)). Mean snow depth is 30 cm (period 2011–2018, (Boike et al., 2019)).

Wood samples of both species were cut using a GSL-1 microtome, and all ring width measurements were performed on double-stained thin-sections (that is, with Safranin and Astrablue dyes) (Gärtner and Schweingruber, 2013). Each sample was photographed using an Olympus BX43 microscope (up to x40 magnification) and an Olympus CS30 digital camera. Single images were merged using Adobe Photoshop (Adobe Systems Incorporated, USA). Annual growth rings were measured using the manual path function in WinCell (Regent Instruments, Canada) along at least two radii on each cross-section. Cross-dating was first performed visually between cross-sections of an individual shrub, then between the shrubs. Next, cross-dating of all plants per species was verified using COFECHA (Grissino-Mayer, 2001; Holmes, 1983). We counted all missing rings at the plant level, and special attention was paid to continuously missing outer rings (CMOR;

Wilmking et al. 2012).

Raw chronologies (Fig. 2A, C) were calculated as arithmetic means using mean shrub/tree growth curves (i.e., after averaging all cross-sections from a single plant first). Standardized chronologies for both species (Fig. 2B, D) were produced using spline detrending of mean shrub/tree growth curves in the dplR package in R (Bunn et al., 2021). In order to assess the quality of each chronology the following descriptive statistics (Table 1) were computed: interseries correlations; the expressed population signal (EPS) that measures the reliability of the chronology based on interseries correlations and sample size (with EPS > 0.85 generally considered as a reliable value (Wigley, 1984)); sub-sample signal strength (SSS; Buras 2017; Cook and Kairiukstis 1990). In all consecutive analyzes we have used a mean standardized ring width (i.e., ring width index, RWI) for each calendar year and tree/shrub species population as a response variable.

2.2. Climate-growth relationships

Considering the common period (1980-2017) for both chronologies we ran bootstrapped correlation analyzes using monthly air temperature and precipitation ERA5-Land data (Muñoz-Sabater, 2019). The ERA 5-Land monthly climate data were obtained for the Kurungnakh Island ROI (Fig. A3B in Supplementary Material). Moving correlation analyzes were run for each chronology using ERA5 data for common period (1980–2017). For *Larix* we used a longer chronology timespan, i.e., for which the EPS was above 0.85 (period 1960–2017). Analyzes were performed in R (R Core Team, 2020) using the 'treeclim' package (Zang and Biondi, 2015). Additionally, we used the Standardized Precipitation and Evapotranspiration Index (SPEI), that helped us to assess the dryness of the study area climate. SPEI was computed for the period 1980-2017 using the R 'spei' package (Begueria and Vicente-Serrano, 2017; Vicente-Serrano et al., 2010) and CRU TS 4.02 data (Harris and Jones, 2019).

Spatial correlations maps were computed between both chronologies and ERA5 mean monthly air temperatures (Muñoz-Sabater, 2019) using the Royal Netherlands Meteorological Institute (KNMI) Climate Explorer (Trouet and Van Oldenborgh, 2013), with a Monte Carlo approach to assess confidence intervals. Also, in order to assess which part of the growing season matters the most for both woody species radial growth, we ran correlations between chronologies and pentad mean temperatures, starting from May 5th till September 7th as a central day for respective pentads. For pentad means calculations we used daily air temperature data from Tiksi meteorological station obtained via Climate Explorer. Pearson's correlation coefficients were calculated for both species using current and previous year pentad mean temperatures. Additionally, the strength of the correlations between the two study species radial growth and pentad mean temperatures were investigated for early (1980–1998) and recent (1999-2017) periods, i.e., by splitting the main study period into two equal halves.

To examine moisture sensitivity of both species we computed moving correlations (for period 1980–2017) and simple linear regressions between standardized *Larix* and *Betula* chronologies and selected

Table 1

Descriptive statistics for *Larix* (top) and *Betula* (bottom) standardized (Spline) chronologies for the Lena River Delta. MS - mean sensitivity; Gini - Gini coefficient; AR(1) - first-order autocorrelation; r - mean (standard deviation) series intercorrelation; r.bt - average pairwise correlation between all series from various shrubs; snr - signal-to-noise ratio; EPS - expressed population signal; SSS - subsample signal strength.

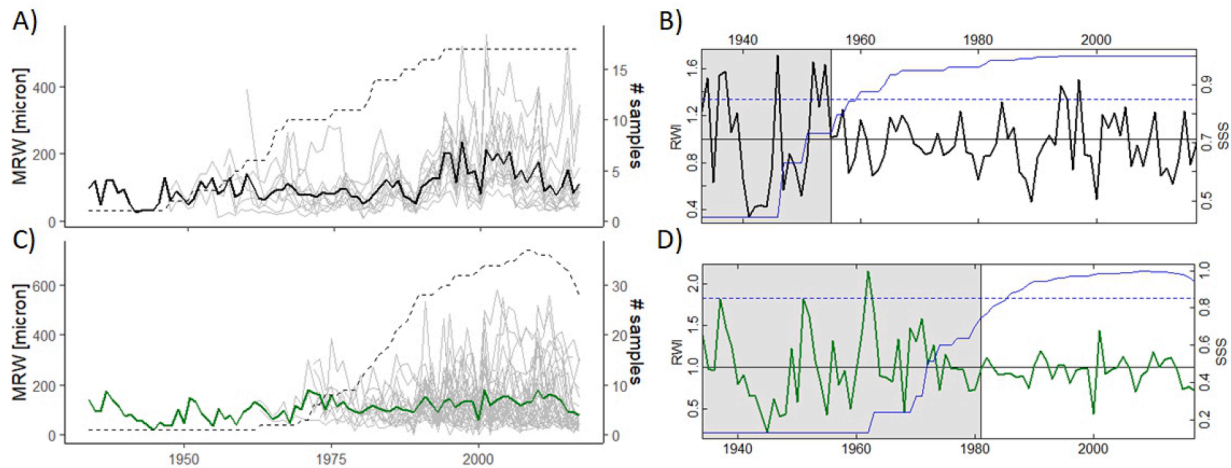| period	n. shrubs /trees	n. cross- sections	MS	Gini	AR(1) (sd)	R (sd)	r.bt	snr	EPS	sss
Larix (1960-2017)	17	53	0.389	0.211	0.159 (0.214)	0.572 (0.122)	0.413	9.63	0.906	0.973
(1980-2017)	17	53	0.39	0.213	0.144 (0.232)	0.698 (0.099)	0.478	14.67	0.936	0.995
Betula (1980-2017)	37	40	0.483	0.241	0.023 (0.226)	0.314 (0.189)	0.109	3.54	0.780	0.937

Fig. 2. Raw (A, C) and standardized (B, D) *Larix* (upper panel) and *Betula* (lower panel, green) chronologies. Sample depths are marked with dashed black lines (A, C). Subsample signal strength marked in blue line (B, D); cut-off period represented by low SSS marked in grey area (B, D). MRW - mean ring width; RWI - ring width index.

reanalysis and satellite-based products. Monthly equivalent water thickness (EWT) from the Gravity Recovery and Climate Experiment mission (GRACE) was obtained for the study region location (grid 72-73°N, 126-127°E) from the NASA GRACE Data Analysis Tool (https://grace.jpl.nasa.gov/data/data-analysis-tool/). GRACE EWT represents total terrestrial water storage anomalies from soil moisture, snow, surface water, as well groundwater (Landerer and Swenson, 2012), and EWT anomalies were recently used in climate-*Larix* growth studies in Siberia (Kharuk et al., 2019, 2015). EWT data are available (with gaps) since year 2002 and the accuracy of the EWT data is stated as up to 30 mm per month with spatial resolution $1° \times 1°$ (Long et al., 2014).

We further used the Moderate-resolution Imaging Spectroradiometer MODIS (i.e., 8-day MODIS Surface Reflectance product MOD09A1, 500 m grid cell resolution) satellite-derived time series (period 2001-2017) for spring snow cover anomalies in the Lena River Delta (Heim et al., 2022). Snow was approximated by the application of the Normalized Difference Snow Index NDSI: we binary-classified NDSI into "snow" and "snow free" by applying the global threshold of NDSI >0.4 representing a bright, and not wet snow-cover (Riggs et al., 2016, 2015), and thereby compiled annual raster matrices of the duration of spring snow-cover. To allow for quantitative interannual comparisons, we extracted the deviations per grid cell within a defined 'central Lena Delta' region of interest (ROI) (Fig. A3A in Supplementary Material), covering 4223 km^2 in the delta apex and surroundings.

For the Kurungnakh Island ROI (Fig. A3B in Supplementary Material), we extracted ERA5-Land (Muñoz-Sabater, 2019) volumetric soil water content (VSW) and soil temperature (ST) data back to 1980 with the application of the European Centre for Medium-Range Weather Forecasts (ECMWF) using the "reanalysis-era5-land-monthly-means" with a $0.1 \times 0.1°$ grid cell resolution (native resolution of 9 km). VSW (expressed in $m^3 * m^{-3}$) representing the volume of water in soil layer 1 (0–7 cm, the surface is at 0 cm), layer 2 (7–28 cm) and layer 3 (28–100 cm) were used. Soil temperature data (ST; converted from Kelvin to Celsius) for the respective layers were also acquired. ERA5-Land data were downloaded via Copernicus Climate Data Store (https://cds.climate.copernicus.eu). Since correlations between *Larix* chronologies and soil-related variables were not stable over time (Figs. A4 and A5, Supplementary Material) we focused on simple linear regressions for a recent period (i.e., 1999–2017), which also overlapped with the period covered with GRACE data. Additionally, correlations between both chronologies and GRACE data were performed for each month separately (Figs. A11 and A12, Supplementary Materials). In the Results section only significant simple linear regressions between both

chronologies and GRACE data are shown.

3. Results

3.1. Chronology and climate characteristics

Mean age of *Larix* and *Betula* individuals was 51 (min = 25, max = 86) and 34 (min = 11, max = 85) years, respectively. The correlation between *Larix* and *Betula* chronology was significant for the common period (1980-2017; r = 0.38; p = 0.017), but not for the recent period (1999-2017, r = 0.40; p = 0.088). There was significant correlation (r = 0.40, p = 0.012) between raw *Larix* chronology from our study site and the raw *Larix* growth series from Tit-Ary for the common period (1980-2017) (Fig. A1 in Supplementary Material).

Mean ring widths for *Larix* and *Betula* raw chronologies were very similar and equaled 0.129 and 0.125 mm (period 1980–2017), respectively. Missing rings (i.e., missing in one part of the plant, but present in at least one cross-section from that plant) were present in six (35%) *Larix* trees and nine (24%) *Betula nana* shrubs. Maximum amount of CMORs found at the plant level was 11 and 8 in *Larix* and *Betula*, respectively. Cross-dating between various parts of the *Larix* trees was crucial since the difference between adjacent plant parts in terms of age was up to 25 years.

Evaluation of overall growing conditions for both woody plants revealed that summer air temperature in the study area has significantly increased over the common period 1980–2017 (Fig. 3A). Changes in summer precipitation sums were not significant for the common period, but the amount of precipitation has declined in recent years (Fig. 3B). Statistically significant increase in the dryness of the study area climate, as expressed by significant decline of the Standardized Precipitation and Evapotranspiration Index (SPEI, averaged for three-months period) has been observed for July-September (Fig. 3C).

3.2. Climate-growth relationships

Radial growth of *Betula nana* chronology (1980-2017) was positively related to July temperatures (r = 0.53; confidence intervals (CI) = [0.26:0.70]) (Fig. 4). Positive correlation between *Larix* chronology and mean July temperatures was not significant (r = 0.23; CI = [-0.05:0.48]) for entire study period (1980-2017; Fig. 4A) and moving correlation analyzes revealed that this relationship was only significant for a middle part of the study period (Fig. 5A). In addition, *Larix* chronology was negatively correlated with July temperatures from the previous year (r
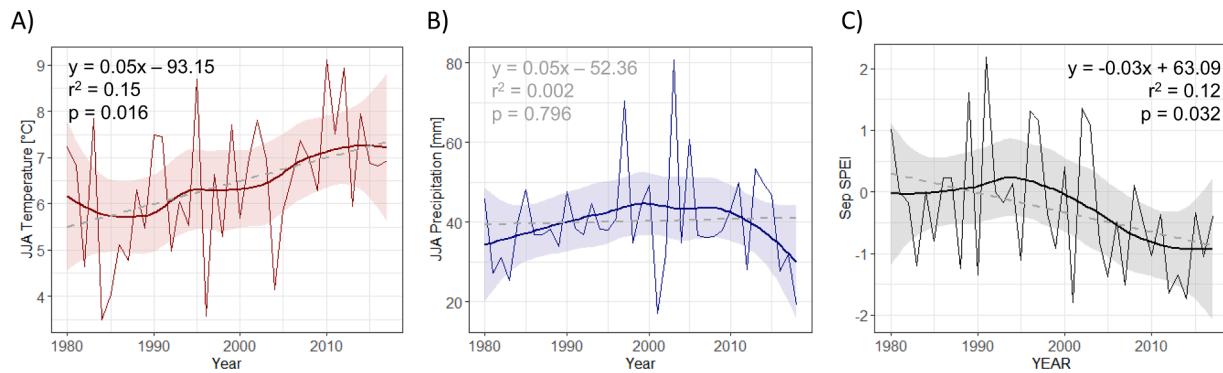
Fig. 3. Study site climate (1980–2017): (A) summer (June-July-August; JJA) air temperature and (B) precipitation (source: Tiksi meteorological station); (C) July-to-September Standardized Precipitation Evaporation Index (SPEI). Significance of linear models marked in black font.
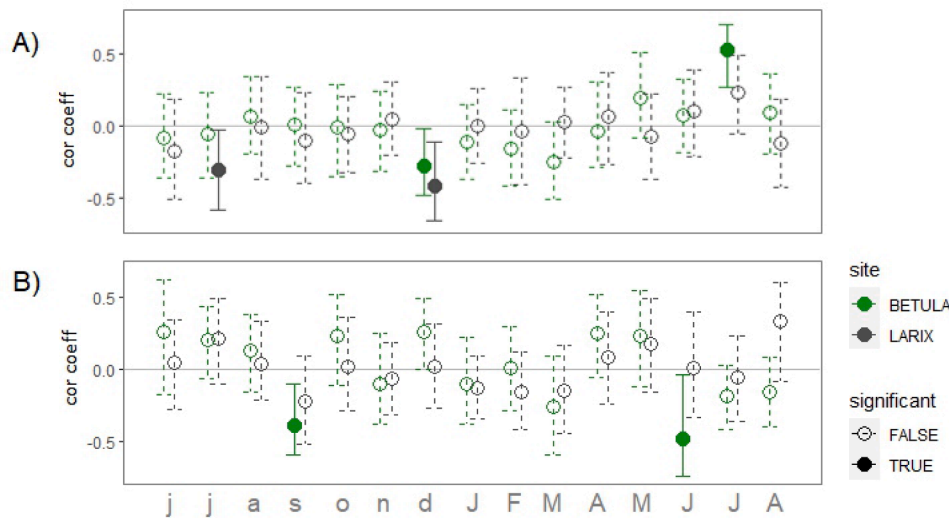

Fig. 4. Bootstrapped correlation coefficients between standardized *Larix* (black) and *Betula* (green) chronologies (i.e., ring width index) from the Lena River Delta and A) air temperature and B) precipitation ERA5 data for the common period (1980–2017). Significant coefficients ($P < 0.05$) together with associated confidence intervals (at the level of 95%) are marked with solid lines and filled dots. Monthly climatic variables include previous year (small letters, from June) to current year (capital letters, to August).

= -0.31; CI = [-0.59:-0.03]) (Fig. 4A) but this relationship has emerged only in recent years (Fig. 5A). In contrast, *Betula* shrubs were not sensitive to previous summer temperatures and their sensitivity to July temperature of the current year was stable for the entire study period (Fig. 5B).

Also both chronologies were negatively correlated with previous December temperatures (*Betula*: r = -0.28; CI = [-0.48:-0.02]; *Larix*: r = -0.42; CI = [-0.66:-0.11]). Whereas, relationships with precipitation were negative for *Betula* chronology for previous September (r = -0.39; CI = [-0.59:-0.09]) and current June (r = -0.48; CI = [-0.74:-0.04]).

Larix chronology was positively correlated with only one pentad mean air temperatures (July 2–6), whereas *Betula* was positively correlated with almost all pentad mean temperatures in July (Fig. 6). Correlations for recent period (1999–2017) were both positive (for end June) and negative (end May) for *Larix* chronology, and only positive for *Betula* chronology (July and August). Both chronologies were negatively correlated with selected pentad mean air temperatures. The strongest negative correlations were found in a recent study period for previous year pentad mean temperatures, i.e., between July 12–16 and June 17–21 and *Larix* and *Betula* chronologies, respectively.

Spatial correlation analyzes performed in three selected time steps revealed consistent positive growth response of *Betula* chronology to current July temperature in the upper Lena and Lena Delta region (Fig. 7B). In contrast, negative correlation between *Larix* chronology and previous July air temperature for the Lena Delta and Laptev Sea region has increased in recent period, while the correlation with current July temperature has been weakening (Fig. 7B). Relationship between

Betula chronology and previous July temperature was insignificant.

Negative correlation between *Larix* chronology and previous summer temperatures were supported by a positive relationship between previous July EWT (GRACE, period 2002–2017) and standardized *Larix* chronology (slope = 0.02, r^2 = 0.33; p = 0.042) (Figs. 8A and A11). Correlations for raw *Larix* chronology were even stronger and significant for both previous June and July EWT (Fig. A6 in Supplementary Material). In contrast, standardized *Betula* chronology was negatively related to current June EWT (slope = -0.01, r^2 = 0.37; p = 0.036) (Figs. 8B and A12). *Larix* growth was positively related to June VSW (slope = 3.301, r^2 = 0.26; p = 0.026), whereas *Betula* was negatively related to July VSW (slope = -2.586, r^2 = 0.47; p = 0.001). Relationships with soil temperature were also opposite between the two species, i.e., negative for *Larix* (for June ST; slope = -0.062, r^2 = 0.25; p = 0.029) and very positive for *Betula* (slope = 0.063, r^2 = 0.50; p = 0.0007) (Fig. 8). Correlations between spring snow cover anomalies and both chronologies were non-significant (Fig. A7 in Supplementary Material).

4. Discussion

4.1. Temperature sensitivity

In contrast to a previous study from the nearby treeline region (MacDonald et al., 1998) the *Larix* chronology from Kurungnakh Island in the Lena River Delta, 60 km north of treeline, was negatively correlated with previous summer temperatures, especially in the recent years. In fact, negative correlation between *Larix* chronology and previous July
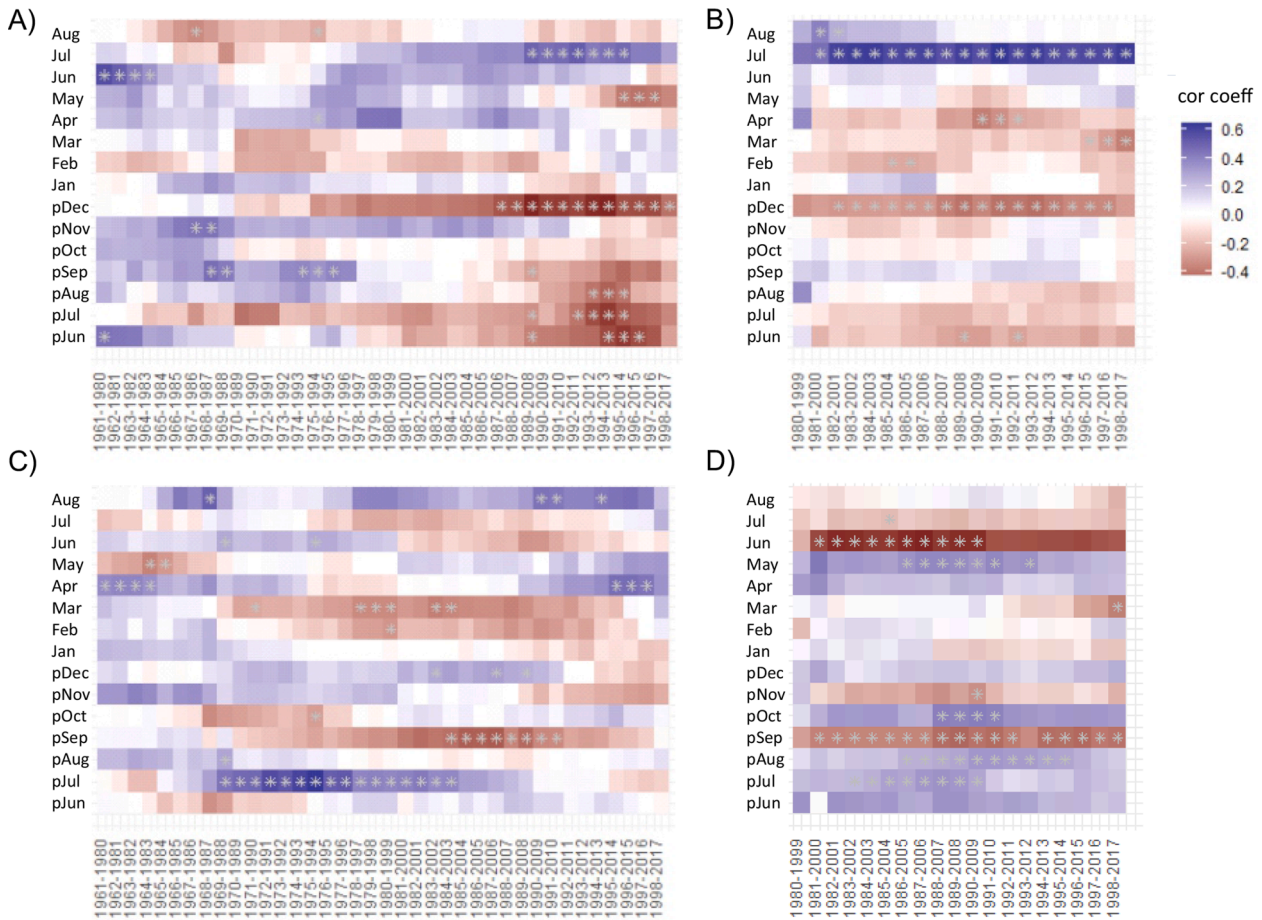
Fig. 5. Moving correlation coefficients between standardized *Larix* (A, C) and *Betula* (B, D) chronologies from the Lena River Delta and air temperatures (A, B) and precipitation (C, D). Significant coefficients (*P* < 0.05) are marked with asterisks. Monthly climatic variables include previous year (small letters, from June) to current year (capital letters, to August). Climate data source: ERA5.
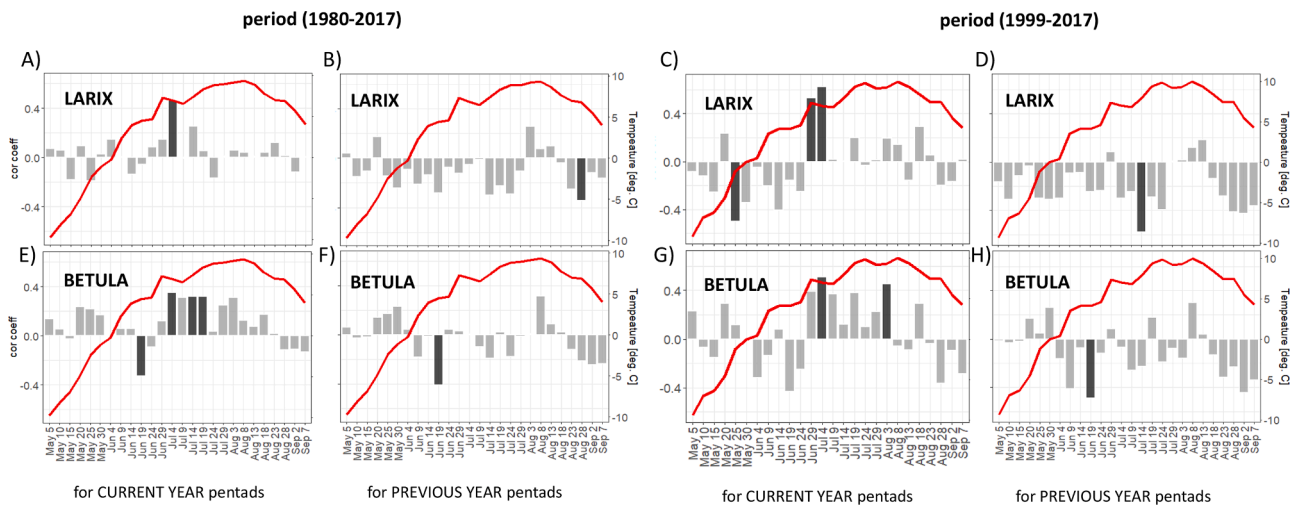

Fig. 6. Correlations between current (A, C, E, G) and previous year (B, D, F, H) pentad's mean air temperatures and standardized *Larix* (upper panel) and *Betula* (lower panel) chronologies from the Lena River Delta for the entire (1980-2017) and recent (1999-2017) study period. Temperature data source: Tiksi meteorological station. Mean pentad temperatures for the study periods are marked in bold red line. Significant correlations are marked with black bars.

temperature was stronger than positive correlation to current July temperature for the common period (1980–2017), which might be indicative for a potential drought stress. In contrast, a prominent role of current summer temperature on *Larix* growth was indicated previously

in a broad spatial scale. This includes, positive correlation found between both June and July temperatures and *Larix sibirica* chronology in the Polar Urals (Kukarskih et al., 2018) or *Larix gmelinii* chronologies in the (south) Taimyr Peninsula (Vaganov and Kirdyanov, 2010). Also, a
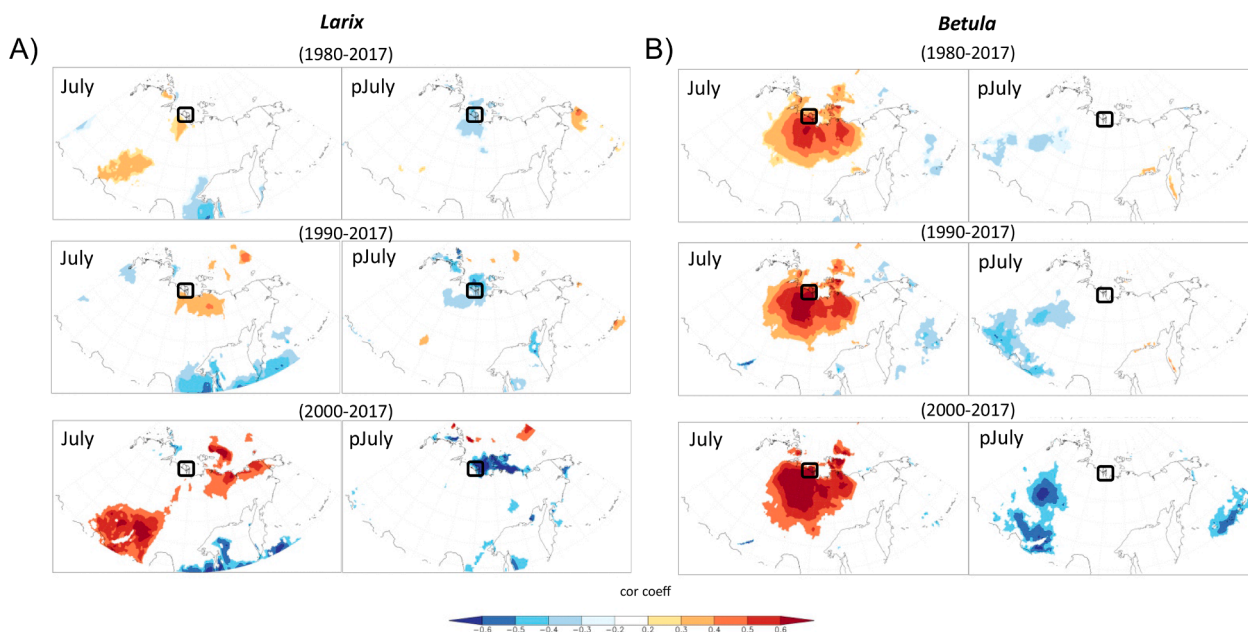
Fig. 7. Spatial correlation analyzes between (A) standardized Larix and (B) *Betula* chronologies and mean July and previous July (pJuly) temperatures (source: ERA5) for period 1980–2017 (upper panel), 1990-2017 (middle panel) and 2000–2017 (lower panel). Bold black square indicates the study area, Lena River Delta. Only significant ($P < 0.1$) correlations are shown.

recent study from central Siberia (Kirdyanov et al., 2020) revealed, for the similar common period (1980-2009), a positive correlation between *Larix gmelinii* chronology and June temperature, and a positive correlation with July precipitation. Considering positive relationship between *Betula nana* growth and July temperature revealed in our study site, most of the previous studies indicated a positive relationships between *Betula nana* growth and summer temperatures Arctic-wide (e.g., Buchwal et al. 2023; Hollesen et al. 2015; Ropars et al. 2015). Only one recent study, performed in western Greenland, have highlighted negative relationships between *Betula nana* growth and summer temperatures (Gamm et al., 2018).

But prostrate *Larix* trees in our study responded differently than *Betula* shrubs to warmer and drier climate that was recorded recently in the central Lena River Delta. Starting from about year 2000 *Larix* growth is less sensitive to July temperature and more sensitive to moisture conditions (Fig. A4 in Supplementary Material). In contrast, negative correlations to soil moisture conditions together with positive correlations to air and soil temperatures for *Betula* chronology are stable across the entire study period (1980-2017) (Fig. A4 in Supplementary Material). Previously, the loss of thermal response in *Larix* ring widths since the 1970s was reported for trees from the Taimyr region in northern Siberia (Jacoby et al., 2000). The weakening of radial growth-temperature relationships was also recently observed for *Larix sibirica* chronology in the southern part of the Polar Urals (Kukarskih et al., 2018). The fact of decreasing temperature sensitivity in boreal tree species is well-described and dated for the period of the 1960s (Briffa et al., 1998; D'Arrigo et al., 2008). A recent synthesis effort highlighted that a similar phenomenon is already observed in the shrub chronologies from the dry arctic tundra regions near the end of the 20th century (Buchwal et al., 2020), which coincides with the timing of decreasing *Larix* sensitivity to summer temperature in the central Lena River Delta. Thus, with this study we might provide the first indication of decreasing temperature sensitivity in *Larix* trees from the tundra, where growth constraints due to a warmer and drier climate might emerge later than within the boreal zone/taiga.

Interestingly, the weakening of the summer temperature signal in our *Larix* chronology was captured only when using monthly temperature data (Fig. 5). The correlations between pentads mean temperatures for recent period (1999–2017) revealed that positive correlation

between *Larix* and summer temperature is still present, but is related not only to July but also end of June temperatures (Fig. 6). Also, in contrast to *Betula, Larix* chronology in a recent period (1999–2017) was not positively correlated with pentads characterized by the highest mean air temperatures, i.e., in beginning of August. In general, the highest positive correlation between *Larix* and mean pentad air temperatures was found for a short time window between July 2-6 (period 1980–2017) and between June 27 - July 6 (period 1999–2017). As expected for a tundra region, these time windows are much shorter and also appear later in the growing season than early summer temperatures (June 6 to July 17) that appeared to be positively correlated with *Larix cajenderi* from the treeline area in northern Yakutia (Hughes et al., 1999) or two selected *Larix* spp. chronologies from the northern treeline closest to our study area (June 17 to July 11) (Kirdyanov et al., 2003). The importance of positive temperatures in the early part of the growing season is probably still the major factor controlling cambial cell division and radial growth of *Larix* (Antonova and Stasova, 1997; Kirdyanov et al., 2003) but high temperatures and associated lack of moisture become stressors during the latter part of the growing season in our study area. In order to properly capture the dynamics in temperature sensitivity of woody plants growth in high latitudes, where growing season length is short and variable (Park et al., 2016), we recommend using pentads mean or daily temperatures in future studies.

In contrast to *Larix* trees in our study area, the strength of a positive correlation between *Betula nana* shrubs and July temperature has increased over recent period (Fig. 5B). This might indicate, together with a negative correlation found between *Betula nana* growth and June precipitation, that birch shrubs enhanced their growth in the warmer and drier conditions (Fig. 3) of the study area. Moreover, we found that *Betula nana* growth was positively related to the number of days with the mean daily temperature >14.9 °C, which was not the case for *Larix* dwarf trees (Fig. A8 in Supplementary Material). However, *Betula* shrubs growth seems to be hampered by warm temperatures in the early growing season (June 17–21), which is most likely related to early spring frost events. Overall, the highest correlations to mean daily temperatures for our *Betula* chronology were found in the first part of July for entire study period, which is similar to the period revealed for this species in northeast Siberia (Indigirka lowlands, 70°N) (Blok et al., 2011). However, in contrast to the studies conducted in the Indigirka
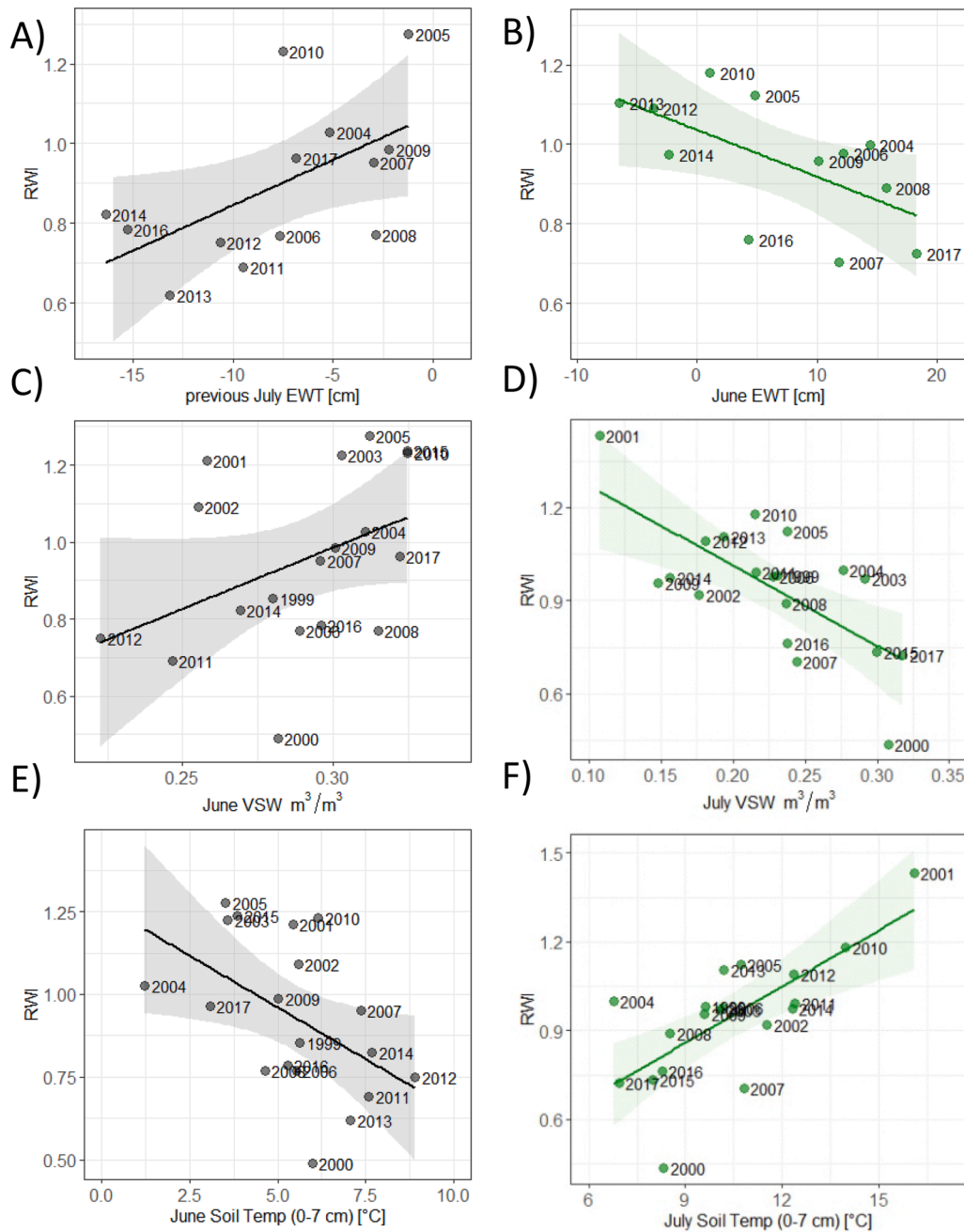
Fig. 8. Relationships between standardized *Larix* (A, C, E; black) and *Betula* (B, D, F; green) chronologies and (A, B) equivalent water thickness (EWT; source: GRACE, period 2002-2017), (C, D) volumetric soil water (VSW, source: ERA5-Land; period 1999-2017), (E, F) soil temperature (source: ERA5-Land; period 1999–2017) in the Lena River Delta.

lowlands (Blok et al., 2011; Li et al., 2016) we did not find any positive relationship with current or previous summer precipitation and *Betula* growth in the Lena Delta River tundra region. This fact might further strength the notion that *Betula* radial growth in our study region is not currently limited by moisture availability and its growth is mainly driven by warm summer temperatures which is in line with the studies conducted in other tundra locations (Buchwal et al., 2023; Hollesen et al., 2015; Ropars et al., 2015). We should however indicate that under continuously warmer and drier conditions *Betula* growth might also be constrained by lack of moisture, which was shown recently, for example in western Greenland (Gamm et al., 2018).

4.2. Moisture sensitivity

The weakening of a positive July temperature signal in *Larix* chronology recorded in recent years coincided with an increasing negative impact of previous summer temperatures (Fig. 5A). Combined analyzes between various moisture sources and *Larix* radial growth in a recent period revealed that its growth is promoted by higher soil moisture conditions recorded both in current and previous growing seasons. *Larix* trees studied on the tundra, similar to larch forests on permafrost, have shallow root systems formed within a shallow seasonal thaw layer (Kharuk et al., 2021), thus favorable moisture conditions in the upper soil layer are crucial for their growth. Positive relationships between *Larix* growth and hydrothermal conditions of soils has been formerly indicated in Siberia region (Fedorov et al., 2007; Nikolaev & Fedorov,

2004). Particularly, the importance of soil moisture condition during the autumn of the previous growing season was highlighted (Nikolaev et al., 2009), which is in accordance with our results. Also positive relationships between *Larix* tree growth and both previous and current year soil moisture conditions were found in eastern Siberia (Tei et al., 2013). On the other hand positive relationship between moisture and tundra shrub growth is already well-described across Pan-Arctic region (Bjorkman et al., 2018; Myers-Smith et al., 2015) indicating specifically an increasing role of soil moisture for shrub growth across the tundra biome.

Our results are similar to the analyzes performed recently by Kharuk et al. (2019) in Putorana Plateau (northern Siberia, 67°N) where *Larix* tree growth was found to be stressed by drought. However, the negative effect of warming on *Larix* growth in that location was indicated in the mid-1990s, which is ca. a decade earlier than in our study area. Also, we might assume that positive correlations found in our study between *Larix* growth and soil moisture (expressed by EWT) are not as strong as in Kharuk et al. (2019), since the onset of warming and water deficit stress might have started later in the tundra then in the northern boundary of the taiga region. Recent studies provide further confirmation on the importance of moisture as a controlling factor of larch growth in Eastern Siberia (Sato and Kobayashi, 2018) with both too dry and too moist (associated with floods) conditions hampering larch growth. Negative correlations to growing season temperatures and an increasing drought stress are also well-described for *Larix gmelinii* radial growth from permafrost degradation areas in northern China (Chen et al., 2022).

Water storage in the discontinuous permafrost area of the central Lena River basin was reported to have increased for the period 2002–2010 (Velicogna et al., 2012), but our study site located in the continuous permafrost zone is actually characterized by rather decreasing water equivalent thickness (Fig. A9 in Supplementary Material). Spring snow depths are decreasing in the Lena River Delta (Fig. A10 in Supplementary Material) and timing of snow melt in some recent years was reported already in late April/early May (Heim et al., 2022), which limit potential meltwater availability for tree growth on a tundra but also expose plants to frost damage in early part of the growing season. In fact, we have not found any frost rings in *Larix* wood, but mechanical damage, including scars and traumatic resin ducts formed right at the beginning of an early wood formation was observed (Fig. A2 in Supplementary Material). Also, probably due to unstable snow regimes observed in recent decades, we have not found significant relationships between *Larix* growth and timing of snow melt, which was previously indicated from the forest-tundra zone in Siberia (Kirdyanov et al., 2003; Vaganov et al., 1999).

Although reanalysis soil and snow data for high latitudes has to be treated with caution (Cao et al., 2020), the correlations with ERA5-Land-derived data have collectively demonstrated that the direction of relationship between *Larix* chronology and moisture turns to be positive in recent years (about after year 2000 till present). In contrast, *Betula* chronology was negatively correlated to moisture and preferred warmer soil conditions (Figs. 8 and A5 in Supplementary Material). It is probably too early to indicate a drought-induced growth limitation in prostrate *Larix* trees in our study location, considering that positive correlation to June (especially at the pentad level) is significant, but an increasing role of moisture conditions for this species growth should be acknowledged. Thus, similarly for *Larix* growth in central Siberia (Sidorova et al., 2009), with our study we provide the first indication of water shortage for larch growth in the subarctic Siberia.

In our study we lack a physiological explanation of the weakening temperature signal in our *Larix* chronology, but it is clear from our analyzes that such a phenomenon is not present in *Betula* chronology, i.e., shrubs growing exactly at the same geographical location. In contrast to temperature, moving correlations between *Larix* chronology and monthly precipitation in our study area were insignificant (Fig. 5C), which in our opinion might indicate the limitation of reanalyzed

precipitation data in terms of quality for high latitudes (Drobot et al., 2006). Also, precipitation itself might not adequately represent the amount of moisture available for plant growth on the tundra, which probably relies more on snow melt and the active layer thaw water source. For example, a positive relationship between depth of ground thawing and *Larix* growth was revealed previously in Taimyr Peninsula (Kharuk et al., 2006). We lack thaw depths measurements for our *Larix* site in a long term, but future studies on radial growth limitation of this species should monitor active layer depths and associated soil moisture across and between the growing seasons.

Considering the maximum age of the studied *Larix* trees, this population of trees was established in the 1970s which overlaps with the phase of tree population increase at the northern treeline designated previously and favored by an increase in annual and summer temperatures (Esper and Schweingruber, 2004). However, we indicated that in recent years the temperature itself is not the main driver for *Larix* growth and that the importance of available moisture for prostrate tree growth on a tundra is increasing.

4.3. One larch cohort: limitations and future prospects

We have to acknowledge that only one cohort of prostrate *Larix* trees was investigated in our study, thus results might be site-specific and constrained by local conditions (Kirdyanov et al., 2013). Moreover, most likely our *Larix* trees sample pool represents clonally reproduced individuals (Kruse et al., 2020), thus they might not adequately represent an ecosystem-wide climate growth response of prostrate *Larix* trees within the northern Siberia tundra belt. Despite these obvious limitations, we undertook probably the first comparative dendroclimatological study between prostrate *Larix* trees and adjacent tundra shrub species in the isolated from the mainland the Lena River Delta region. What might be recognized as a potential violation of dendrochronological method (i.e., studying clones, and not independent individual trees) is actually an adaptation strategy of these one of the northernmost growing trees, lowering the risk of extinction under changing climate conditions (Kruse et al., 2020). And with our study we provide a detailed insight into the annual resolution on tree growth sensitivity to climate in the heart of the tundra.

Our results show that prostrate *Larix* trees growing within an upland tundra in the subarctic Siberia are more prone to water deficit stress than co-existing shrub species *Betula nana*. Our results highlight that in contrast to *Larix* trees, *Betula nana* shrub species seem to be better adapted to changing climate conditions, which under current climate change indicates both warmer and drier conditions (during both summer and dormant season). Specifically, we show that prostrate *Larix* tree growth on the Siberian tundra is limited in recent period mainly by moisture conditions of both previous and current year. Thus, with a warmer climate we might expect limited expansion of that species within the tundra in contrast to well-adapted tundra shrubs. Recent assessment have documented that increases in larch cover in northern Siberia are generally small compared to changes in shrub cover and that latitudinal expansion of larch is likely to require centuries (Frost and Epstein, 2014). Also, in contrast to a previous study performed in northern West Siberia (Miles and Esau, 2016) our results suggest that larch trees growth on a tundra might not be characterized by increased productivity. Future studies should aim to integrate remote sensing and both shrubs and trees dendrochronology to better assess the current state of prostrate tree growth and their future state, including potential increase in a tree height, within the forest-tundra ecotone. Previous studies performed on shrubs in northwestern Eurasian tundra (Forbes et al., 2010; Macias-Fauria et al., 2012) have manifested great potential of such integrative approach in vegetation modelling. In contrast to *Larix* trees, northward shrub migration and colonization of new tundra grounds is currently well-documented and highlighted by transition from low erect to tall shrubs (Bjorkman et al., 2018). We hypothesize that under favorable moisture conditions prostrate larch trees might

continue to expand at the local level forming small successional patches, similar to the one described in this study. However greater expansion at the landscape level might be hampered by the fact that predominant reproduction type for prostrate *Larix* trees is clonal by short distance spreading ramets (Kruse et al., 2020). Further, we hypothesize that lateral spread of both *Betula* shrubs (Bret-Harte et al., 2001) and *Larix* trees via adventitious shoots (Bonga and Pond, 1991) is expected to not only support their survival on the tundra, but also to claim new ground incrementally. Far range *Larix* seeds dispersal by river channels, strong winds or through animal migration should be also considered and examined.

Examples of dwarf *Larix* trees within a Siberian tundra belt (i.e., outside of the northern treeline) are probably not that uncommon, since the boreal forest (taiga) - tundra ecotone is the world's largest and stretches for over 13,400 km (Ranson et al., 2004). Recent studies (Kharuk et al., 2006; Wieczorek et al., 2017) have described numerous observations on prostrate forms of larch trees formed sometimes in clusters in the Ary-Mas forest (i.e., in the zone between 72°02'N and 72°40'N latitude), i.e., in southern Taimyr Peninsula and at the Khatanga River. Also, observations of dwarf, shrub-like forms of *Larix* trees from Pyasina River (71°N) and Lukunskaya River (72°40'N) on the western and eastern Taimyr Peninsula, respectively, have been previously indicated (Abaimov 2010; Jacoby et al., 2000). Among the northernmost occurrences of larch trees in so called 'near-tundra forests' Isaev et al. (2010) indicated also Olenyok River (72°37'N) and Tit-Ary Island (72°N), south to the Lena River Delta. To establish accurate projections of northward larch expansion we need systematic measurements of *Larix* prostrate trees between the sites. With this study we showed that shrub-like forms of *Larix* trees can be found even in the heart of the Lena River Delta, and most likely more clusters of this species are present on a tundra. Thus, future studies should focus on comparative studies between these remote locations to accurately assess climatic sensitivity of prostrate *Larix* trees beyond the latitudinal treeline.

We recommend, that such studies should implement quantitative wood anatomy analyzes, which are broadly applied to larch chronologies from the northern treeline and Siberian interior (Bryukhanova et al., 2013; Panyushkina et al., 2003). Future studies should include the measurements of latewood cell parameters and density, which often encode other climatic signals than tree ring widths alone (Vaganov and Kirdyanov, 2010). Also, if the extraction of available amount of cellulose per annual growth ring could be positively resolved, isotopic analyzes could be applied to prostrate *Larix* trees from the tundra, similarly like for trees in the Siberian north (Sidorova et al., 2009). Implementation of both wood anatomy and isotopic studies might significantly contribute to a mechanistic explanation of potential drought-induced growth limitation of prostrate larch trees on a tundra. The advantage of shrubs over trees might also resides in potentially shorter period of wood formation, which was recently shown at the alpine treeline (Treml et al., 2019), and designates a valuable prospect in future tundra studies.

In order to predict future growth of *Larix* trees in the Siberian Arctic, we need more studies from habitats represented by a wide range of soil and permafrost conditions (Hagedorn et al., 2020; Kirdyanov et al., 2013). Since many *Larix* individuals in our study had desiccated or damaged uppermost shoots (which was not the case for *Betula* samples), future research should also investigate the effect of dormant season conditions, including the effects of wind and frost on prostrate *Larix* tree growth on the tundra. Also, the effects of herbivores, should not be neglected. Most importantly, we should assure that future prostrate trees sampling will not damage the habitat and allow the tree population to grow further.

5. Conclusions

Our study showed that prostrate *Larix* trees can be found beyond the northern treeline on the island in the central Lena River Delta. Climate-growth relationship analyzes revealed that climatic sensitivity of these trees is not stable over time, with weakening sensitivity to July temperature in recent years and increasing importance of moisture availability for *Larix* radial growth. In contrast to *Larix* trees, radial growth of the adjacent tundra shrub species *Betula nana* was positively related to July temperature across the entire study period with no signs of potential moisture stress at least at the current stage.

Our study suggests that prostrate *Larix* trees on the tundra, as the most northward-spread and probably the most cold-resistant tree species in the Northern Hemisphere, are currently threatened not by cold but rather dry conditions during summers. Notably, the mean age of *Larix* individuals from our study area was much younger than in previous studies conducted at the Siberian treeline, which might indicate that the cohort of trees studied represents the early succession stage of boreal trees within the tundra biome threatened by warmth-induced harsh conditions in recent period. Comparison studies of trees vs. shrubs radial growth in boreal forests are just emerging (Yang et al., 2022) and collectively with our tundra-specific study indicate potentially higher shrub resistance to a warmer and drier climate.

Data availability

The mean growth curves (i.e., raw series) for individual shrubs/ trees and standardized chronologies for each species are available at The International Tree-Ring Data Bank (ITRDB): Larix (https://www.ncei.noaa.gov/access/paleo-search/study/38187); Betula (https://www.ncei.noaa.gov/access/paleo-search/study/38186).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2023.109543.

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