**Title???  
- Climate response of coniferous trees in northern latitudes: longitudinal gradient from west to east**

**- Response of forest ecosystems to climate change beyond the Arctic Circle**

**- Influence of longitudinal climate gradient on larch and pine growth in the Arctic region**

**- Climate response of coniferous trees in the Arctic region: west-east gradient**

**- Regional differences in the climate response of coniferous trees in Arctic climate conditions**

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**Abstract**

Northern high-latitude ecosystems are experiencing rising temperatures, which are expected to alter the water balance and thermal dynamics of permafrost soils, consequently influencing the structure and functioning of plant communities. To investigate the response of these communities to environmental and climatic shifts, we employed dendroclimatic analysis based on the radial growth of trees. Here, we present findings from a study of four conifer species - *P. sylvestris., L. sibirica, L. gmelinii,* and *L. cajanderi* - sampled across six sites within the continuous permafrost zone of the Arctic Circle. We developed TRW chronologies and conducted correlation analyses with monthly climate variables, including temperature and precipitation, spanning the period from 1966 to 2021. Our results reveal that summer air temperature, particularly in June and July, is the primary factor limiting radial growth across all study sites. Sliding correlation analyses further indicate a strengthening influence of temperature anomalies on tree growth in recent decades, most notably in the context of rising mean daily temperatures. This trend suggests potential shifts in plant community structure and adaptive responses to emerging climatic conditions. Additionally, we observed that elevated summer temperatures correspond to enhanced radial growth, likely driven by improved photosynthetic activity and greater water availability amid permafrost thawing.

**Keywors:** Arctic, climate change, tree growth, tundra,treeline, permafrost, radial growth

**1. Introduction**

Over the past century, the Arctic has undergone unprecedented warming, at a rate nearly four times faster than the global average, with temperature increases exceeding 0.7°C per decade since the 1980s (Overland et al., 2019). This rapid climate shift has far-reaching consequences for local ecosystems and global climate dynamics, driving accelerated permafrost thawing, reduced snow cover duration, and alterations in carbon and hydrological cycles (Schuur et al., 2015; Frolking et al., 2006). A critical zone of transformation amidst these changes is the forest-tundra ecotone, the transitional boundary between tundra and boreal forests across northern Eurasia (Harsch et al., 2009). Observations indicate that tree line migration in this region has advanced northward at rates of up to 50 - 100 m per decade in response to warming (Esper & Schweingruber, 2004; Zhang et al., 2014). Even modest increases in mean annual temperatures can trigger significant shifts in woody vegetation distribution, structure, and function, influencing carbon sequestration, water balance, and biodiversity (Lloyd et al., 2002; Tchebakova et al., 2009; Bonan, 2008). In northern Russia and Finland, recent decades have witnessed notable vegetation dynamics, including the northward expansion of forest ranges, tree line migration, enhanced shrub growth, and localized declines in dominant conifer species (Zhang et al., 2014).

Dendrochronology, particularly dendroclimatology, provides a robust framework for reconstructing past climate and environmental changes with high temporal resolution (Vaganov et al., 1999; Kirdyanov et al., 2013). Tree-ring analyses enable the identification of species-specific responses to climatic drivers such as temperature, precipitation, and seasonal soil thaw depth, offering insights into growth-climate relationships across diverse ecological settings (St. George et al., 2010). In the northern regions, spanning from the Kola Peninsula to northeastern Yakutia, dendrochronological research has consistently highlighted summer temperature as the primary limiter of tree radial growth (Hughes et al., 2014). However, TRW signals can be modulated by non-climatic factors, such as soil nutrient availability or biological memory, necessitating complementary proxies like latewood density or isotopic analysis for more robust reconstructions (Fritts, 1976; Büntgen et al., 2020). Significant gaps remain in understanding how tree species respond to climate change along broad longitudinal gradients, particularly under varying permafrost conditions ranging from sporadic to continuous (MacDonald et al., 2015).

The forest-tundra ecotone of northern Eurasia supports a range of conifer species, including *Pinus sylvestris L.*, *Larix sibirica Ledeb*, *Larix gmelinii* (Rupr.) Kuzen and *Larix cajanderi Mayr*. Each species exhibits distinct ecological and physiological adaptations to the harsh subarctic environment. *P. sylvestris* is a widely distributed, drought-tolerant species capable of thriving in nutrient-poor soils and contributing significantly to regional carbon storage (Tchebakova et al., 2009). *L. sibirica*, a deciduous conifer, is highly resilient to extreme cold and drought, shedding its needles in winter to minimize water loss (Abaimov, 2010). *L. gmelinii* and *L. cajanderi*, dominant in eastern Siberia, are similarly cold-adapted but differ in their sensitivity to moisture availability and permafrost dynamics, with *L. cajanderi* often thriving in areas of continuous permafrost (Kirdyanov et al., 2013; Hughes et al., 2014). These species occupy a latitudinal range from 66°54′N to 71°57′N and an elevational gradient from 35 to 468 m a.s.l., experiencing mean annual temperatures from -0.48°C in western sectors to -13.28°C in the east, with summer (June - July) temperatures varying between 8.31°C and 13.09°C and annual precipitation declining from 547 mm to 210 mm along the longitudinal transect (data from nearby stations: Sodankyla, Kandalaksha, Salekhard, Khatanga, Chokurdakh, Ostrovnoye) (Table 1S).

Here, we investigate the climate response of four co-occurring conifer species - *P. sylvestris*, *L. sibirica*, *L. gmelinii*, and *L. cajanderi* - across six locations north of the Arctic Circle, spanning a longitudinal gradient from 27°E to 166°E. These sites, situated near weather stations such as Sodankyla (Finland) and Chokurdakh (Russia), reflect a climatic transition from milder, oceanic conditions in the west to the extreme continental climate of northeastern Siberia. Using TRW measurements, we analyze the spatiotemporal dynamics of radial growth in relation to key climate variables - temperature, precipitation, seasonal thaw depth, and snow depth - over the period from 1966 to 2021. This study aims to elucidate the moderating and enhancing roles of these climate factors, assess temporal shifts in growth - climate relationships, and evaluate species-specific differences in climate sensitivity.

**2.** **Materials and methods**

*2.1. Study area and sampling*

This study was conducted across six localities along a longitudinal transect north of the Arctic Circle, spanning from northeastern Finland to northeastern Russia (27°E to 166°E; Fig. 1A). Four dominant conifer species within the forest-tundra ecotone were sampled: *P. sylvestris*, *L. sibirica*, *L. gmelinii* and *L. cajanderi*. Sampling targeted co-dominant trees at the following sites: Finland (**FIN**; 68°77′N, 27°15′E; 179 m a.s.l.) and Apatity on the Kola Peninsula (**APA**; 67°36′N, 33°2′E; 127 m a.s.l.) for *P. sylvestris*; Polar Urals (**PUR**; 66°54′N, 65°45′E; 125 m a.s.l.) for *L. sibirica*; Khatanga (**KHA**; 71°57′N, 102°40′E; 35 m a.s.l.) for *L. gmelinii*; and Chokurdakh (**CHO**; 70°30′N, 147°10′E; 71 m a.s.l.) and Bilibino (**BIL**; 68°02′N, 166°40′E; 468 m a.s.l.) for *L. cajanderi*. Between 18 and 35 trees were sampled per site (total n = 137) during the summers of using a 5-mm increment borer powered by an electric drill. Cores were collected at breast height (1.3 m), and tree height and diameter at breast height (dbh) were measured for sampled trees where data were available (Table S1). Tree characteristics varied across sites, with mean dbh ranging from 13.7 ± 5.2 cm in **KHA** to 36.6 ± 4.8 cm in **APA**, and mean height from 5.4 ± 1.2 m in **KHA** to 14.5 ± 1.7 m in **APA**. No dbh or height data were recorded for **FIN**. Average tree age ranged from 133 ± 35.9 years in **PUR** to 331.4 ± 118 years in **CHO**, reflecting differences in growth rates and site conditions (Table S1).

The study transect encompasses a broad climatic and ecological gradient within the forest-tundra ecotone, characterized by short growing seasons, low temperatures, and variable permafrost conditions. The westernmost sites (**FIN** and **APA**) lie near the upper limit of *P. sylvestris* distribution, featuring podzolic and peat-podzolic soils with high organic content and either absent or insular permafrost (active layer depth: 1 - 2 m). Central sites (**PUR** and **KHA**) transition to discontinuous permafrost (active layer: 50 - 100 cm), with mountain-tundra and tundra-gley soils. Eastern sites (**CHO** and **BIL**) are dominated by continuous permafrost (active layer: 30 - 60 cm), cryozems, and tundra-gley soils with low organic matter and limited microbiological activity. These soil and permafrost dynamics, coupled with rapid spring snowmelt and summer temperature variability, strongly influence water availability and tree growth across the transect.

Meteorological data were obtained from the nearest weather stations to each sampling site: Sodankyla (52 km from **FIN**), Kandalaksha (62 km from **APA**), Salekhard (58 km from **PUR**), Khatanga (7 km from **KHA**), Chokurdakh (2 km from **CHO**), and Ostrovnoye (48 km from **BIL**). Data were sourced from climexp.knmi.nl (**FIN**) and [www.meteo.ru](http://www.meteo.ru" \t "_blank) (Russian sites) for the period 1966 - 2021. Mean annual temperatures ranged from -0.48°C (**APA**) to -13.28°C (**CHO**), with June - July temperatures varying from 8.31°C (**CHO**) to 13.09°C (**FIN**) and annual precipitation decreasing from 547.48 mm (**APA**) to 210.40 mm (**CHO**) along the transect (Fig. 1B). Over the study period, mean annual temperatures exhibited a significant upward trend (*p <* 0.01) across all sites, with increases ranging from; June - September temperatures followed a similar pattern (Fig. 1C-D). The number of days with temperatures ≥5°C, marking the growing season, averaged 133 days in **APA** and 70 days in **CHO**, with significant increases of 44 - 52 days per decade in western and central sites (**FIN**, **APA**, **PUR**, **KHA**) and 11 - 29 days per decade in eastern sites (**CHO**, **BIL**) (Fig.S1).

The vegetation period across all sites is short (70 - 133 days), with *P. sylvestris* benefiting from persistent needles that enable photosynthesis during early spring warming, while the deciduous larches (L. sibirica, *L. gmelinii*, *L. cajanderi*) rely heavily on summer conditions for needle formation and growth. In western sites, the longer growing season and deeper active layer support greater moisture availability, whereas in eastern sites, delayed soil thawing and extreme cold constrain growth to a brief, intensive period.



**Figure 1.** Location and climate of the study area: (A) white dots show the location of sampling sites (**FIN**, Finland, **APA**, Apatity; **PUR**, Polar Ural; **KHA**, Khatanga; **CHO**, Chokurdakh; **BIL**, Bilibino). (B) Climate diagram for Sodankyla weather stations, Kandalaksha, Salekhard, Khatanga, Chokurdakh, Ostrovnoye for 1966 - 2021 period. (C) Average annual temperature trends for the periods 1966 - 2021 in the study areas. (D) Trends in average monthly temperature June-September for the period 1966 - 2021 in the study areas.

*2.2. Description of tree species*

*Pinus sylvestris*

*P. sylvestris* is one of the most widespread conifers of the boreal zone, occurring from Western Europe to Eastern Siberia (Adams et al., 2015; Bala and Chen, 2020; Boyden et al., 2012, Henttonen et al., 2017), growing in Norway, Sweden, Finland, and adjacent areas of Russia north of 65° N (northern Karelia and Murmansk Oblast). Its distribution often extends into the forest-tundra ecotone, where conditions become marginal for tree growth (Cook and Holmes, 1996; Devi et al., 2008). Morphologically, *P. sylvestris* is characterized by: evergreen needles, typically 4 - 7 cm long, persisting for several years (Esper et al., 2002; Grissino-Mayer, 2001); reddish - brown or brownish bark, often thicker at the base to provide protection from extreme temperatures and fires (Helama et al., 2012; Kharuk et al., 2008). Physiologically, *P. sylvestris* maintains year - round photosynthetic potential due to its robust needles (IPCC, 2021; Shiyatov, 2003). This may be advantageous during sudden warm spells in early spring, allowing trees to initiate photosynthesis before deciduous species have fully leafed out (Lloyd et al., 2005; Mann et al., 2009). However, Scots pine is limited by short, cool summers in arctic regions and typically shows a strong correlation with July temperatures (Kukarskih et al., 2017; Sidorova et al., 2010). In addition, moisture availability can sometimes limit growth, especially in well-drained soils on thin permafrost layers (Lawrence and Slater, 2005; Pastukhov and Kaverin, 2016). Cold adaptations include thickened bark, reduced needle surface area, and a vigorous root system capable of exploiting shallow nutrient layers (Bala and Chen, 2020; Romanovsky et al., 2010). *P. sylvestris* in northern Fennoscandia can often exhibit morphological plasticity, including multi - stemmed trunks and prostrate growth forms when exposed to extreme wind or snow loads (Timofeev et al., 2014; Walker et al., 2005).

*Larix sibirica*

*L. sibirica* is widespread in central and western Siberia, penetrating into mountainous and subarctic regions (Anchukaitis et al., 2012; Cerling, 1984; Devi et al., 2008). At the northern forest line, it forms sparse forests. It is the dominant species in the permafrost zone (Tchebakova et al., 2016).

Main characteristics include: the needles are deciduous, soft and bright green, appearing in spring and falling in autumn (Drobyshev et al., 2010; Esper et al., 2002); the cones are relatively small, ripening within one growing season (Hughes et al., 1999; Settele et al., 2014); The tree is capable of reaching considerable heights (up to 30 - 40 m) under optimal conditions, but growth is often stunted in the Polar Urals or near the Arctic tree line (Harsh et al., 2009; Haruk et al., 2006). This species is well adapted to a sharply continental climate with severe winters and a short growing season (Kharuk et al., 2010). Larch growth is positively correlated with summer temperatures, which is confirmed by studies in high and northern latitudes (Kirdyanov et al., 2020). Larch needles may be beneficial in extremely cold climates, as they reduce winter water loss (Mann et al., 2009; Rossi et al., 2008). The species invests heavily in rapid needle expansion once favourable temperatures are reached in early summer (Cook and Peters, 1981; Thomas et al., 2021). *L. sibirica* typically exhibits strong sensitivity to early summer (June) temperatures, which correlates with a short window for photosynthesis and cambial activity (Helama et al., 2009; Vaganov et al., 1999). Among larches, *L. sibirica* thrives on well - drained soils affected by permafrost, however it can be susceptible to root damage if the active layer depth is unusually shallow (Kukarskih et al., 2017; Smirnova et al., 2019). The species is known to form pure stands, but also coexists with other conifers or birch in mixed forests throughout the Urals (Sofronov et al., 2009; Zhang et al., 2021).

*Larix gmelinii*

Often called *Dahurian larch*, *L. gmelinii* occupies large areas of Eastern Siberia in the continuous permafrost zone, including regions with a sharply continental climate, where winter temperatures can drop below -50 °C (Anchukaitis et al., 2012; Ciais et al., 2013; Dai et al., 2020).

The main characteristics of this species are: tolerance to extreme cold: seedlings and adult trees can survive in areas of continuous permafrost, mainly due to a robust root system adapted to shallow, seasonally thawing soils (Friedlingstein et al., 2006; Kukarskih et al., 2017); Deciduous foliage: like other larches, it sheds its needles annually, minimizing winter drying and frost damage (Hughes et al., 1999; MacDonald et al., 2008); Morphological variability: *L. gmelinii* can have tall, straight trunks or more irregular formations depending on local soil and temperature conditions (Kharuk et al., 2008; Romanovsky et al., 2010). Phenologically, *L. gmelinii* is very sensitive to the timing of soil thaw and early summer temperatures *(Razumov et al., 2012; Sidorova et al., 2010*). Warmer June months can significantly improve growth rates due to an extended photosynthetic window (Cerling, 1984; Lawrence and Slater, 2005). However, intense temperature variability in continental Siberia can occasionally cause frost damage in late spring or early fall, affecting tree ring formation (Settele et al., 2014; Wilmking et al., 2005).

*Larix cajanderi*

Distributed primarily in northeastern Siberia (Yakutia, Chukotka), withstands some of the harshest climates on Earth (Kajimoto et al., 1999, DeGrandpre et al., 2011; Li et al., 2012; Lloyd et al., 2005). Its range covers areas such as Chokurdakh and Bilibino, where permafrost is continuous and the active layer is often limited to 30 - 60 cm (Pastukhov and Kaverin, 2016; Rogers et al., 2021; Thomas et al., 2021).

Distinguishing features include: high tolerance to extremely cold, dry winters and short, cool summers (Helama et al., 2012; Shiyatov, 2003; Sidorova et al., 2010); shallow root systems are well suited to thin active layers, allowing rapid uptake of meltwater and nutrients during the short growing season (Mann et al., 2009; Smirnova et al., 2019).

With a short growing season, *L. cajanderi* growth relies heavily on rapid soil thawing and access to water, with permafrost potentially acting as a water reserve during the summer months (Sugimoto et al., 2002).

In many regions of northeastern Siberia, *L. cajanderi* forms extensive larch-dominated forests, acting as an important carbon sink (Rossi et al., 2008; Schuur et al., 2015; Zhang et al., 2021). However, it remains highly sensitive to temperature fluctuations in June and July, showing radial growth variability related to annual weather conditions (Razumov et al., 2012; Romanovsky et al., 2010).

Overall, these four species display distinct strategies - evergreen versus deciduous needles, differences in bark thickness and root system structure - that allow them to survive in one of the most challenging environments on the planet (Kirdyanov et al., 2013; Moiseyev et al., 2010; Pastukhov and Kaverin, 2016). *P. sylvestris* retains needles year-round, allowing early photosynthesis to occur during short-term spring warm spells. *L. sibirica, L. gmelinii* and *L. cajanderi* shed needles annually, making their growth more dependent on the current summer's climate conditions. Early summer temperatures are particularly important for needle formation and the initiation of radial growth.

*2.3. RW measurements and chronologies construction*

Collected cores were subjected to resin extraction using a Soxhlet apparatus with 96% ethanol for 72 hours to remove resinous compounds, following standard dendrochronological protocols (Cerrato et al., 2023). The cores were then air-dried, mounted on wooden supports, and polished with progressively finer sandpaper up to 1000 grit to enhance ring visibility. Polished cores were scanned at 3200 dpi resolution in RGB mode using an Epson Perfection V800 flatbed scanner (Epson, Japan), calibrated with an IT8 Calibration Target color card (Fuji), and processed with Silverfast SE software (LaserSoft Imaging, USA). Scanning was performed in a dark box to minimize external light interference (Agapova et al., 2024).

Tree-ring width (RW) was measured on digitized core images using CooRecorder version 9.3 (Cybis Elektronik & Data AB, Sweden). Narrow or missing rings, common in harsh Arctic conditions, were identified and cross-checked during visual cross-dating to ensure chronological accuracy. Individual RW series were visually cross-dated, and cross-dating accuracy was statistically verified using COFECHA (Grissino-Mayer, 2001). To remove age-related trends and non-climatic influences, raw RW series were standardized in ARSTAN (Cook & Holmes, 1996) by fitting a negative exponential or linear function, selected to account for juvenile growth trends and site-specific variability, producing standardized chronologies (Cook & Peters, 1981). Unlike residual chronologies, autocorrelation was retained to preserve biological memory effects relevant to permafrost-influenced growth dynamics. The quality and robustness of the resulting standardized chronologies were assessed using mean sensitivity (msx), expressed population signal (EPS), mean inter-series correlation (Rbar), and signal-to-noise ratio (SNR), calculated following Wigley et al. (1984). First-order autocorrelation (AC1) ranged from 0.30 to 0.75, reflecting significant growth memory, particularly in western sites (**FIN**, **APA**, **PUR**) with milder conditions (Table 1). The SNR for **CHO** was anomalously low (0.00), possibly due to limited series overlap or data processing artifacts, warranting further investigation.

**Table 1.** Statistical characteristics of standardized tree-ring width (RW) chronologies for the period 1966 - 2021 across six study sites.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Site** | **FIN** | **APA** | **PUR** | **KHA** | **CHO** | **BIL** |
| Mean Sensitivity (msx) | 0.25 | 0.25 | 0.40 | 0.55 | 0.44 | 0.44 |
| Expressed Population Signal (EPS) | 0.65 | 0.89 | 0.96 | 0.96 | 0.97 | 0.96 |
| Mean Inter-Series Correlation (Rbar) | 0.48 | 0.40 | 0.63 | 0.68 | 0.64 | 0.69 |
| Signal-to-Noise Ratio (SNR) | 2.75 | 4.40 | 31.29 | 25.63 | 0.0 | 29.40 |
| Autocorrelation order 1 (AC1) | 0.75 | 0.68 | 0.72 | 0.37 | 0.30 | 0.33 |

*2.4. Statistical analysis of climate relationships*

The climate sensitivity of RW standardized chronologies was evaluated using Pearson’s correlation analysis against monthly mean temperature and precipitation totals over the period 1966 - 2021, sourced from Berkeley Earth 1° gridded datasets (Rohde et al., 2013). Correlations were computed from September of the previous year to September of the current year to capture both prior- and current-year climatic influences on growth, with statistical significance tested at *p <* 0.05. The cumulative effect of climate was further assessed by testing consecutive monthly windows (e.g., May - June, June - July) to identify periods of strongest climate signal. Given the influence of permafrost dynamics, RW chronologies were also correlated with seasonal thaw depth data where available, to explore soil moisture effects.

To pinpoint precise temporal intervals of climate influence, daily moving correlations were calculated between RW indices and temperature data, highlighting peak sensitivity periods within the growing season. Temporal stability of these climate-growth relationships was analyzed using 30-year moving correlations with a one-year lag, implemented in the “treeclim” package (Zang & Biondi, 2015) within the R environment (R Core Team, 2022). This approach assessed shifts in climate signal strength and sensitivity trends over time.

Spatial stability and geographic extent of the temperature signal were evaluated through spatial field correlations between RW standardized chronologies and gridded air temperature data (Berkeley Earth 1° resolution) using the KNMI Climate Explorer ([https://climexp.knmi.nl/](https://climexp.knmi.nl/" \t "_blank)). Resulting correlation maps illustrate the spatial distribution and consistency of the temperature signal across the study region, providing insight into its variability over the 1966 - 2021 period.

**3. Results**

*3.1. Tree-Ring Width Chronologies*

Successful cross-dating was achieved for 137 trees across six sites along a longitudinal transect north of the Arctic Circle, including 35 *P. sylvestris* (**FIN**), 18 *P. sylvestris* (**APA**), 26 *L. sibirica* (**PUR**), 18 *L. gmelinii* (**KHA**), 20 *L. cajanderi* (**CHO**), and 20 *L. cajanderi* (**BIL**). The length of the standardized tree-ring width (RW) chronologies varied by site, ranging from 133 years (**PUR**, 1889 - 2021) to 331 years (**CHO**, 1690 - 2021), with a common analysis period of 1966 - 2021. Mean sensitivity (msx) ranged from 0.25 (**FIN**, **APA**) to 0.55 (**KHA**), reflecting moderate to high interannual variability, particularly in central and eastern sites with harsher climates. The expressed population signal (EPS) exceeded 0.85 at all sites except **FIN** (0.65), indicating robust chronologies for climate analysis, though **FIN** showed lower coherence. Mean inter-series correlation (Rbar) ranged from 0.40 (**APA**) to 0.69 (**BIL**), with higher values in eastern sites suggesting stronger synchrony among trees. Signal-to-noise ratio (SNR) varied widely, from 2.75 (**FIN**) to 31.29 (**PUR**), with an anomalously low value of 0.00 at **CHO**, likely due to limited series overlap or processing artifacts. First-order autocorrelation (AC1) of the standardized chronologies was highest at **FIN** (0.75), **APA** (0.68), and **PUR** (0.72), reflecting significant growth memory in western and central sites, and lowest at **CHO** (0.30) and **BIL** (0.33), consistent with permafrost-dominated conditions (Table 1).

Correlations between chronologies revealed regional patterns. The highest positive correlation occurred between **FIN** and **APA** (r = 0.59, *p <* 0.01), attributed to their proximity, shared species (*P. sylvestris*), and similar northwestern Eurasian climates. A moderate correlation was observed between **BIL** and **CHO** (r = 0.42, *p <* 0.01), reflecting their geographic closeness and common species (*L. cajanderi*). Sites with different larch species (**PUR** **- KHA**) showed a weak positive correlation (r = 0.25, *p <* 0.01), likely due to overlapping climatic influences despite ecological differences between *L. sibirica* and *L. gmelinii*. Negative correlations were noted between eastern and western sites (**CHO** - **PUR**, r = -0.43; **CHO** - **FIN**, r = -0.39; *p <* 0.01), indicating divergent growth responses across the transect (Fig. S2).

The RW chronologies reveal distinct growth patterns across the transect, driven by regional climatic gradients and species-specific responses. *P. sylvestris* at FIN and APA, located in the milder western part of the transect, shows stable growth with a recent increase, likely benefiting from Arctic warming. In contrast, Larix species at PUR, KHA, CHO, and BIL exhibit greater variability and generally lower RW, reflecting the more extreme conditions of the central and eastern Arctic. The post-2010 stabilization in RW across most sites, except FIN and APA, may indicate increasing limitations on growth, such as moisture stress or permafrost degradation (Fig. S3).

*3.2. Climate-growth analysis*

The climate sensitivity of standardized RW chronologies was assessed using Pearson’s correlation analysis against monthly temperature (Fig. 2) and precipitation (Fig. 2) data for 1966 - 2021. Results for residual chronologies are provided in the Supplement (Fig. S3,). Summer temperatures positively influenced RW across all sites, with species- and site-specific differences in timing and magnitude. At **PUR** (*L. sibirica*), **KHA** (*L. gmelinii*), and **BIL** (*L. cajanderi*), RW showed strong correlations with June temperature (r = 0.54, 0.43, 0.41, respectively; *p <* 0.01), and a weaker signal at **CHO** (*L. cajanderi*; r = 0.24, *p <* 0.05), reflecting temperature limitation in continental climates. In contrast, western sites **FIN** and **APA** (*P. sylvestris*) exhibited significant correlations with July temperature (r = 0.35, 0.41; *p <* 0.01), consistent with milder conditions delaying peak growth sensitivity. At **CHO**, prior autumn (September - October) and March temperatures negatively affected RW (r = -0.30 to -0.35; *p <* 0.05), suggesting a lagged influence of cold-season conditions.



**Figure 2.** Correlation coefficients of tree ring width with temperature.

Moving daily correlations showed a positive influence of mid-summer temperatures (June 23 - July 10) in all study areas (Fig. 3A). However, when moving from west to east along the northern profile, an increase in the maximum correlation coefficients is noted, as well as their shift to earlier dates. The seasonal dynamics of the influence of temperatures demonstrates a decrease in the significance of July temperatures and an increase in the influence of June temperatures on the variability of tree growth indices. In the western regions (**FIN, APA**), where Scots pine grows, the effect of July temperatures is weaker (DOY 191 and 190; r = 0.43 and 0.41; *p* ***<*** 0.01) compared to other locations where larch grows: the central sites **(PUR**, **KHA**), where the correlation coefficients reach a maximum (DOY 174 and 181; r = 0.65 and 0.67; *p* **<** 0.01), and the eastern sites of **CHO** and **BIL** (DOY 183 and 176; r = 0.56 and 0.54, respectively; *p* **<** 0.01). Analysis of the effect of precipitation did not reveal a significant long-term effect on the radial growth of trees at any of the study sites (Fig. 3A).



**Figure 3.** Sliding correlation coefficients (A and B) between standard tree-ring width indices and climate data (temperature and precipitation).

*3.3. Temporal stability of temperature signals*

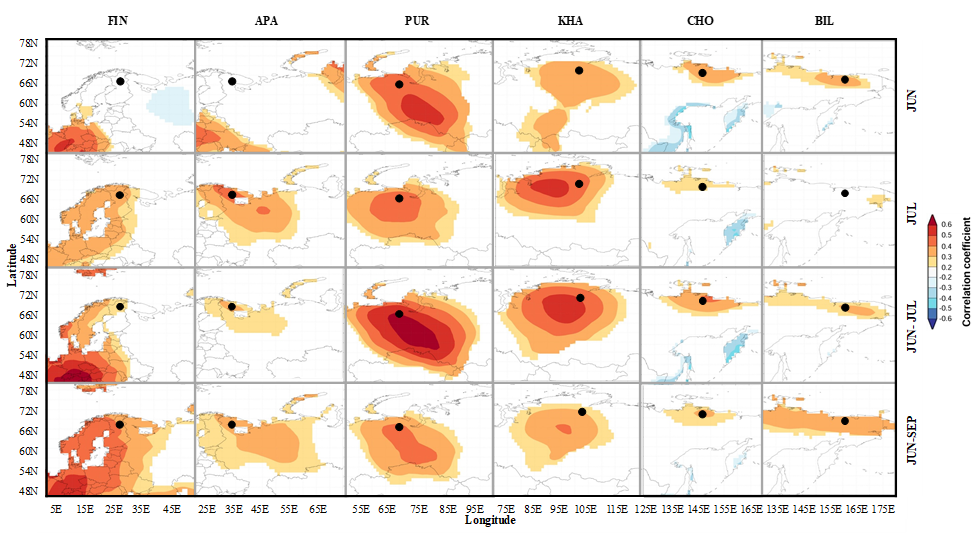
Thirty-year moving correlations with a one-year lag revealed temporal instability in temperature responses across most sites (Fig. 4). At **FIN** and **APA**, correlations with July temperature increased from the late 1970s to the early 1990s (r = 0.45 - 0.50; *p <* 0.01), followed by a slight decline (r = 0.35 - 0.40; *p <* 0.05) post-1990s. June - September temperatures showed similar trends, peaking at r = 0.50 (p < 0.01) in the 1980s. In contrast, **PUR** and **KHA** exhibited a gradual decrease in June - July temperature sensitivity, with **PUR** dropping from r = 0.60 (1966 - 1995) to r = 0.45 (1992 - 2021; *p <* 0.01) and **KHA** showing a marked decline post-1990s (r = 0.65 to 0.40; *p <* 0.01). **CHO** displayed a weakening temperature signal across all summer months, becoming insignificant (r < 0.20; p > 0.05) after 1980, while **BIL** showed an increasing trend, with June - July correlations rising from r = 0.40 (1966 - 1995) to r = 0.55 (1992 - 2021; *p <* 0.01). These shifts highlight dynamic climate-growth relationships over recent decades.



**Figure 4.** Sliding correlations (25-year window with 1-year step) of tree-ring widths with June, July, June-July, June-September temperatures for the total period 1966 - 2021.

*3.4. Spatial stability of temperature signals*

Spatial field correlations with Berkeley Earth 1° gridded temperature data for 1966 - 2021 underscored regional differences in temperature signal strength (Fig. 5). **FIN** and **APA** showed weak and localized correlations, strongest in July (r = 0.40; *p <* 0.01) and June - September (r = 0.40; *p <* 0.01), confined to northwestern Eurasia (65° - 70°N, 20° - 40°E). Central sites **PUR** and **KHA** exhibited robust and extensive correlations, particularly for June - July temperatures (r = 0.60 and 0.50; *p <* 0.01), spanning central Siberia (60° - 75°N, 60° - 120°E), with **PUR** showing the highest signal strength. Eastern sites **CHO** and **BIL** displayed weaker, more restricted correlations, peaking at r = 0.30 (p < 0.05) for June - July and June - September, centered over northeastern Siberia (65° - 75°N, 140° - 170°E). These patterns reflect stronger temperature limitation in central sites compared to western and eastern extremes.



**Figure 5.** Spatial field correlations between June, July, June - July and June - September mean temperatures (Berkeley 1°) and tree-ring widths for the period 1966 - 2021. Black dots indicate the locations of sampling sites.

**Discussion**

Our findings demonstrate that summer temperature serves as the primary climatic driver of radial growth across all studied sites, with pronounced regional and species-specific variations along the west-east gradient in northern latitudes. Western stands of *P. sylvestris* exhibit a stronger response to July temperatures, whereas eastern larch-dominated sites show heightened sensitivity to June conditions. These patterns align with previous dendroclimatic studies in northern Russia and Fennoscandia, which consistently identify summer warmth as a key limiting factor for tree growth in cold environments (Vaganov et al., 1999; Kirdyanov et al., 2013; Hughes et al., 1999). Precipitation, while secondary to temperature, exhibits variable and site-specific effects, reflecting the complex hydrological dynamics of permafrost-dominated ecosystems and the physiological tolerances of the studied species.

The monthly correlation analyses reveal distinct temporal windows of temperature sensitivity, closely tied to the physiological traits of the studied species. In western sites (e.g., **FIN**, **APA**), where permafrost is absent or discontinuous, *P. sylvestris* radial growth correlates most strongly with July temperatures. As an evergreen conifer, *P. sylvestris* maintains year-round needles, enabling earlier photosynthetic activity and a prolonged growing season in milder climates with deeper active layers (Kirdyanov et al., 2024c; Rossi et al., 2009). In contrast, at central (**PUR**, **KHA**) and eastern (**CHO**, **BIL**) sites with continuous permafrost, Larix spp. exhibit peak sensitivity to June temperatures, driven by their deciduous nature and the need for rapid foliage deployment (Sidorova et al., 2012; Zhou et al., 2021). Daily correlations reinforce this, showing a westward-to-eastward shift in peak temperature response from July to mid-June, reflecting continentality and permafrost constraints (Lloyd et al., 2005).

Precipitation responses, though less dominant, reveal intriguing patterns that merit closer examination. Across most sites, precipitation exerts a weak or negative influence on radial growth, consistent with the notion that water availability is rarely limiting in permafrost-dominated regions due to sufficient snowmelt (Vaganov et al., 1999; Bykov et al., 2023). However, positive signals emerge at **APA** and **BIL**, suggesting localized moisture deficits or favorable hydrological conditions in specific years. At **APA**, a western site with discontinuous permafrost, the deeper active layer and higher annual precipitation likely enhance soil moisture retention, benefiting *P. sylvestris*. This species, with its deeper root system and conservative water-use strategy, can exploit available water to sustain photosynthesis into July, particularly during dry spells (Rossi et al., 2009; Körner, 2012). Conversely, at **BIL**, an eastern site with continuous permafrost, the positive precipitation signal may reflect episodic rainfall alleviating shallow thaw limitations, temporarily boosting Larix spp. growth by supplementing snowmelt-derived moisture (Sugimoto et al., 2002).

Negative precipitation signals, more common across the gradient, indicate that excess moisture can hinder growth, particularly in Larix spp. Their shallow root systems, adapted to cold and poorly drained soils, are prone to waterlogging, which reduces oxygen availability to roots and suppresses cambial activity (Bocharov, 2009; Kirdyanov et al., 2024a). This physiological vulnerability contrasts with *P. sylvestris*, whose deeper roots and greater tolerance for wet conditions mitigate such effects, explaining its weaker negative response to precipitation (Vaganov et al., 1999). In continuous permafrost zones (e.g., **CHO**, **BIL**), high surface runoff and limited infiltration due to frozen subsoils further decouple precipitation from growth, as water remains unavailable to roots despite abundant inputs (Sugimoto et al., 2002; Turetsky et al., 2010). These findings align with observations in other high-latitude systems, where excess moisture from snowmelt or summer rains often offsets precipitation’s potential benefits (Bykov et al., 2023).

The secondary role of precipitation contrasts sharply with water-limited ecosystems like the forest-steppe, where radial growth strongly tracks rainfall (Arzac et al., 2021; Tabakova et al., 2020). In our study area, snowmelt provides a baseline moisture supply, reducing dependence on summer precipitation and amplifying temperature’s dominance. However, the timing and intensity of rainfall matter: early-season excesses (June) may exacerbate waterlogging in Larix spp., while late-season deficits (July) could stress *P. sylvestris* in western sites if snowmelt reserves deplete. This species-specific sensitivity to precipitation underscores the interplay of hydrology and physiology, with permafrost acting as a filter that modulates water availability (Lawrence and Slater, 2005).

The moving correlation analyses reveal temporal instability in temperature sensitivity, with declines since the 1980s at some sites (e.g., **CHO**) linked to regional warming (Overland et al., 2019; Smirnova et al., 2019). Precipitation sensitivity, though generally weak, shows a non-significant upward trend in July at eastern sites, hinting at an emerging shift in hydric balance (IPCC, 2021). This trend may reflect increasing evapotranspiration demands as temperatures rise, potentially depleting soil moisture reserves in shallow permafrost soils (Turetsky et al., 2010). For Larix spp., this could amplify waterlogging risks if permafrost thaw increases surface water pooling, while *P. sylvestris* might face greater reliance on rainfall in western sites as snowmelt timing shifts earlier (Romanovsky et al., 2010). These subtle changes suggest that precipitation’s role, though minor now, could grow under future warming, particularly if permafrost degradation alters drainage patterns.

The interplay of temperature and precipitation responses highlights species-specific adaptations to permafrost environments. *P. sylvestris* thrives in milder western sites with extended seasons, while Larix spp. exploit brief early-summer windows in the east. Warming may shift the forest-tundra ecotone, but precipitation’s evolving role could complicate these dynamics. Enhanced moisture deficits or excesses, driven by permafrost thaw, could disproportionately affect Larix spp., limiting their upward expansion, while *P. sylvestris* may gain from improved drainage in western sites (Kharuk et al., 2010; Schuur et al., 2015). Long-term monitoring of precipitation-growth relationships is critical, as hydrological shifts could reshape forest structure and carbon cycling in northern latitudes (Bonan, 2008; Shiyatov, 2003).

**Conclusion**

This study underscores the pivotal role of summer temperature as the primary driver of radial growth for *P. sylvestris* and Larix spp. across a longitudinal gradient in northern latitudes, affirming its status as a key limiting factor in permafrost-dominated environments (Anchukaitis et al., 2012; Vaganov et al., 1999). Our results reveal distinct species-specific responses, with *P. sylvestris* in western sites showing peak sensitivity to July temperatures and Larix spp. in eastern sites responding most strongly to June warmth. These differences reflect physiological adaptations - evergreen persistence versus deciduous rapid deployment - and are modulated by local variations in permafrost extent, active layer depth, and microclimatic conditions. Such heterogeneity highlights the importance of considering species traits and site-specific factors in assessing climate impacts on high-latitude forests.

Precipitation, while secondary to temperature, exerts a variable and often minor influence on radial growth, consistent with the dominance of snowmelt-derived moisture in these ecosystems (Bykov et al., 2023). Rare positive signals at sites like **APA** and **BIL** suggest that localized soil permeability and rainfall timing can occasionally enhance growth, particularly for *P. sylvestris*, which tolerates wetter conditions better than Larix spp. However, negative responses predominate, likely due to waterlogging constraints in shallow permafrost soils, emphasizing that excess moisture may limit rather than promote growth in this region. The muted role of precipitation contrasts with water-limited systems and underscores the unique hydrological dynamics of the study area.

The temporal instability of climate-growth relationships, particularly the declining temperature sensitivity since the 1980s at some sites, points to adaptive responses to regional warming. Warmer conditions may alleviate thermal constraints, particularly for Larix spp. in eastern sites, potentially promoting upward or northward shifts in their distribution limits (Shiyatov, 2003). Conversely, *P. sylvestris* could expand in western areas with milder climates, altering forest composition and succession dynamics. These shifts carry significant implications for carbon storage, albedo, and hydrological cycles, though their realization depends on mitigating factors such as permafrost thaw and extreme weather events (Bonan, 2008; Schuur et al., 2015).

Overall, this study confirms that temperature governs radial growth across the gradient, with species-specific and site-specific nuances shaping the magnitude and timing of responses. Precipitation’s limited role may increase under future warming as permafrost degrades, warranting further monitoring. These insights enhance our understanding of forest responses to climate variability and provide a foundation for predicting ecosystem trajectories under ongoing change in northern latitudes.

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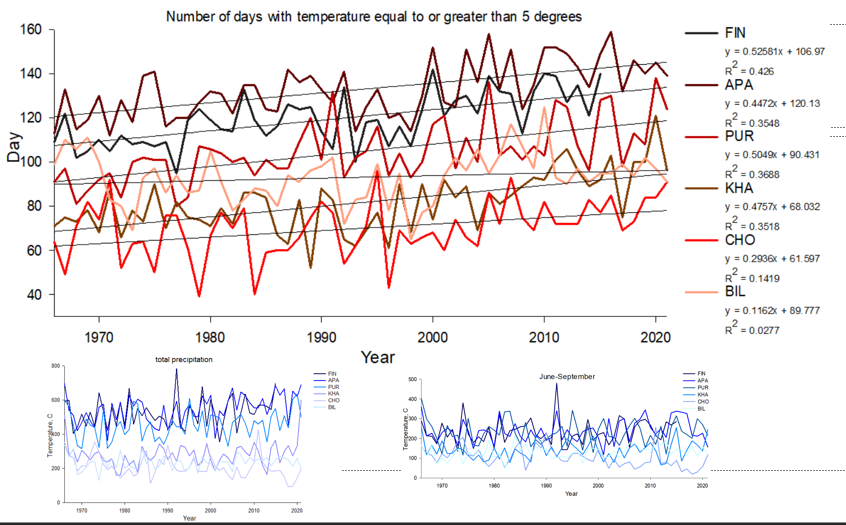
**Supplements**

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| Species | Pinus sylvestris | Pinus sylvestris | Larix sibirica | Larix gmelinii | Larix cajanderi | Larix cajanderi |
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**Table S2.** Characteristics of sampled trees across six study sites for the period 1966 - 2021.

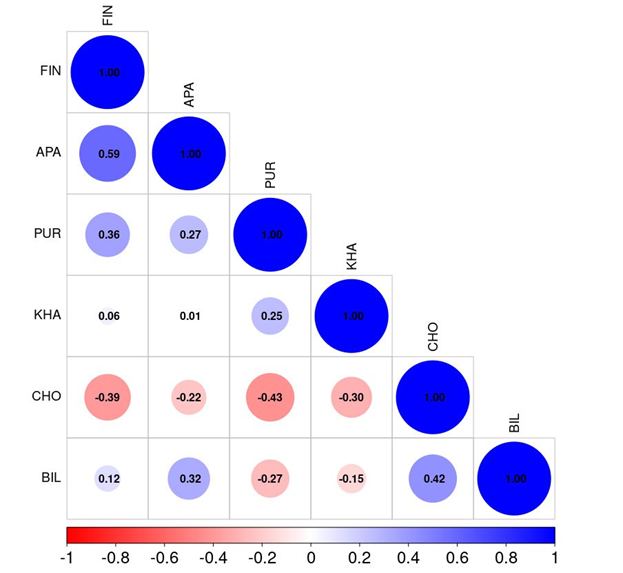
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| --- | --- | --- | --- | --- | --- | --- |
| Site | FIN | APA | PUR | KHA | CHO | BIL |
| No. trees | 35 | 18 | 26 | 18 | 20 | 20 |
| Average age of trees (years) | 162 ± 59.4 | 263 ± 73.6 | 133 ± 35.9 | 300 ± 36.7 | 331.4 ± 118 | 163 ± 22 |
| Mean dbh (cm) | - | 36.6 ± 4.8 | 15.3 ± 4.2 | 22.3 ± 1.9 | 13.7 ± 5.2 | 16.9 ± 5.0 |
| Mean tree height (m) | - | 14.5 ± 1.7 | 9 ± 1.9 | 11.7 ± 2.2 | 5.4 ± 1.2 | 9.12 ± 1.2 |





**Figure S1.** Number of days with temperature equal to or above 5 °C.

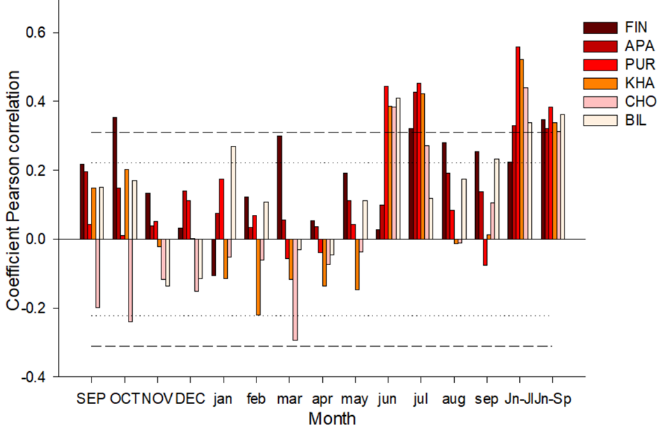
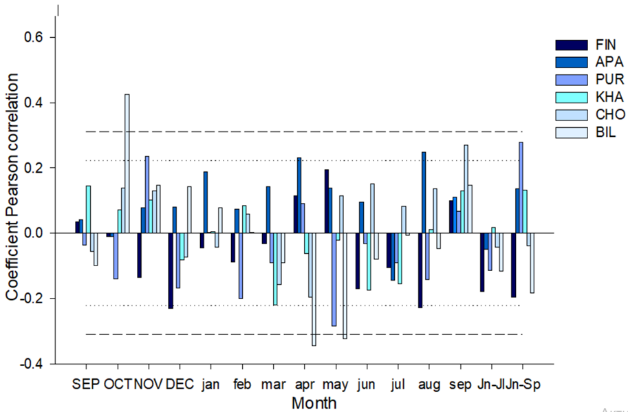
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**Figure S2.** Correlation matrix of tree ring widths between study areas.



**Figure S3.** Tree-ring width indices for the period 1966 to 2021.

А  B 

**Figure 2.** Coefficients of paired (A and B) correlations of tree-ring width with temperature and precipitation

**Table 1** - Characteristics of trees

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | **FIN** | **APA** | **PUR** | **KHA** | **CHO** | **BIL** |
| Number of trees | 35 | 18 | 26 | 18 | 20 | 20 |
| Average age of trees (years) | 162 ±59,4 | 263 ±73,6 | 133±35,9 | 300±36,7 | 331,35±118 | 163±22 |
| Mean dbh (cm) |  | 36.6 | 15.3 | 22.3 | 13.7 | 16.9 |
| Mean tree height (m) |  | 14.5 | 9 | 11.7 | 5.4 | 9.12 |
| Average tree ring width (mm) | 0,98+0,12 | 0,98+0,14 | 0,95+0,3 | 0,95+0,29 | 0,98+0,29 | 0,98+0,11 |
| Active soil layer deep (cm) | ? | ? | ? |  | 14 | ? |