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# Age-dependent moisture response of conifers near their cold range limit

Jan Tumajer [a,*] , Grudd Håkan [b] , Jernej Jevšenak [c] , Andreas J. Kirchhefer [d] ,
Francesco Marotta [a] , Jiří Mašek [a] , Kiara Maria Nowatzki [e] , Nikolaus Obojes [f] ,
Markus Stoffel [g,h,i] , Václav Treml [a] , Jelena Lange [a,e]

[a] Department of Physical Geography and Geoecology, Faculty of Science, Charles University, Albertov 6, Prague 12843, Czech Republic
[b] Swedish Polar Research Secretariat, Abisko Scientific Research Station, Vetenskapens Väg 38, Abisko 98107, Sweden
[c] Department for Forest and Landscape Planning and Monitoring, Slovenian Forestry Institute, Večna pot 2, Ljubljana 1000, Slovenia
[d] Dendroøkologen A.J. Kirchhefer, Skogåsvegen 6, Tromsö 9011, Norway
[e] Institute of Botany and Landscape Ecology, University of Greifswald, Soldmannstraße 15, Greifswald 17487, Germany
[f] Eurac Research, Viale Druso 1, Bolzano 39100, Italy
[g] Climate Change Impacts and Risks in the Anthropocene (C-CIA), Institute for Environmental Sciences, University of Geneva, Boulevard Carl Vogt 66, Geneva 1205, Switzerland
[h] dendrolab.ch, Department of Earth Sciences, University of Geneva, rue des Maraîchers 13, Geneva 1205, Switzerland
[i] Department F.-A. Forel for Environmental and Aquatic Sciences, University of Geneva, Boulevard Carl Vogt 66, Geneva 1205, Switzerland

## ARTICLE INFO

## ABSTRACT

Growth dynamics of cold subarctic and subalpine forests are primarily sensitive to temperature, but growth responses may vary across regions or shift over tree ontogeny. Systematic assessments of spatial, interspecific, and demographic variation in temperature and moisture limitation of tree growth at cold distribution margins are essential for enhancing our understanding of how these ecosystems will evolve under climate regimes. To address this gap, we built a network of 22 tree-ring width chronologies from cold forests covering two regions (Fennoscandia, European Alps), three species (Pinus sylvestris, Pinus cembra, Larix decidua), and two age cohorts (45–100 and >150 years). We combined daily climate-growth correlations with the process-based Vaganov-Shashkin growth model to identify differences in critical growth factors between species and age cohorts. In addition, we assessed the coincidence of unusually wide and narrow tree rings with years of specific climatic anomalies. Although growing season temperature was the dominant growth-limiting factor, seasonal effects of water balance on tree growth were considerably large and varied systematically between regions, species, and particularly age cohorts. The growth of young P. sylvestris in Fennoscandia responded negatively to water balance and narrow rings coincided with wet years. In contrast, the growth of young P. cembra in the Alps was drought-limited. Old trees of all species and both age cohorts of L. decidua in the Alps showed limited sensitivity to water balance. The patterns of climate-growth responses in cohort chronologies based on tree age at the year of coring were similar to ontogenetic shifts of climate-growth responses if chronologies were based on the cambial age of individual rings. Our results stress the need to account for interspecific and demographic differences in sensitivity to climate in large-scale studies of cold forest ecosystems.

## 1. Introduction

Subarctic and subalpine forests dominated by cold-tolerating conifers represent biomes of global importance in terms of providing valuable ecosystem services and climate-biomass feedback (Gamfeldt et al., 2013). Being located at the latitudinal and upper margins of the current distribution of trees, respectively, these forests are highly sensitive to year-to-year meteorological variation and long-term climate change (Gauthier et al., 2015). Accordingly, growth series derived from their annual tree rings are usually strongly correlated with summer temperature due to the very short duration of the growing season and growth kinetics limited by cold conditions (Körner, 2021; Shishov et al., 2023). However, climatic sensitivity of boreal and subalpine conifers can show remarkable variation between regions (Lloyd and Bunn, 2007), species (Obojes et al., 2022), and individual trees (Wilmking et al., 2004). For example, significant soil moisture or air humidity

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* Corresponding author.
  *E-mail address:* tumajerj@natur.cuni.cz (J. Tumajer).

signals partly distorting the prevailing temperature signal of tree-ring chronologies have been observed from wet or dry regions of boreal and mountain forests (Girardin et al., 2024; Liang et al., 2014; Mirabel et al., 2023; Vaganov et al., 1999). Understanding these sources of variability in climate-growth responses should be deepened to better inform forecasts of future growth dynamics of cold forest ecosystems.

Boreal forests in Fennoscandia and the subalpine belt in the European Alps form cold limits of forest distribution in Europe with similar environmental conditions and prevailing temperature-sensitive tree growth (Körner, 2021). Due to different latitude and thus different intra-annual course of weather and daylength, patterns of climate-growth responses might substantially differ between these two regions. For instance, the two regions showed systematic differences in growth phenology, i.e., the timing of growth during the year (Mu et al., 2023), resulting in shorter periods of significant summer temperature-growth correlations in northern Europe compared to the Alps (Babst et al., 2013). Moreover, different coniferous species, each with distinct adaptation strategies, may respond differently to climatic stress including drought (Vitali et al., 2017), air freezing (Girardin et al., 2022), and soil freezing (Nicklen et al., 2021). Related to that, climate-growth responses may significantly differ between deciduous and evergreen conifers which frequently coexist in Alpine forests (Caccianiga et al., 2008; Obojes et al., 2022). Finally, the climatic sensitivity of tree-ring width series can vary between trees of the same species growing in the same region or even the same stand (Carrer, 2011; Wilmking and Juday, 2005). Growth decoupling among individual trees may reflect their social status and ontogenetic development (Carrer and Urbinati, 2004; Trouillier et al., 2019). Specifically, differences in the timing of the growing season between small and large trees may translate into different periods of cambial sensitivity to climatic conditions (Konter et al., 2016; Rossi et al., 2008).

High-elevation and high-latitude forests are characterized by a short, temperature-limited growing season which on average lasts three months at treeline (Körner, 2021). Potential moisture effects on tree growth are likely secondary and often short-term (Puchi et al., 2020; Tumajer et al., 2021), and might therefore be masked in correlations of annual tree-ring widths with monthly climatic data. This increases the need for approaches with daily temporal resolution to better understand sub-monthly climate-growth responses of cold-limited woody plants. This can be achieved by employing statistical approaches with daily instead of monthly climatic data (Jevšenak, 2019), sub-annual growth measurements instead of tree-ring width (Dobbert et al., 2022), or process-based models of wood formation with a high temporal resolution (Eckes-Shephard et al., 2022). Accordingly, sub-monthly approaches previously helped to identify short-term but significant periods with moisture control on radial growth in regions where monthly statistics suggest exclusively temperature-limited growth (Dobbert et al., 2022; Puchi et al., 2020).

In this study, we assessed climate-growth responses across 22 tree-ring width chronologies representing two major regions of cold forest ecosystems in Europe (Fennoscandia and the Alps), two stages of tree demography (young and old age cohorts), and three coniferous species with different ecological strategies (*Pinus sylvestris* L., *Pinus cembra* L., *Larix decidua* Mill.). We combined seasonal climate-growth correlations derived from daily meteorological data with the daily-resolved Vaganov-Shashkin process-based model of wood formation (VS-model; Vaganov et al., 2006) to characterize the intra-annual variation of growth-limiting factors for each chronology. We quantified the variation in climate-growth correlations between species and age cohorts. In addition, we assessed the synchronization of extremely wide and narrow tree rings with specific meteorological conditions (Jetschke et al., 2019). We hypothesized that all tree-ring width chronologies primarily respond to temperature due to the prevailing cold limitation of cambial activity (Körner, 2021). However, we expected to find signs of water-limited growth as well, and that growth responses to moisture would systematically vary between regions, species, and age cohorts. Specifically, we

assumed that young trees will be more sensitive to water balance due to their smaller stature and less developed root system compared to old and large trees. Moreover, we expected a stronger response of evergreen pines to winter and spring moisture compared to deciduous L. *decidua*.

## 2. Material and methods

### 2.1. Study site and study species

The study was conducted at eight supposedly temperature-limited sites near the latitudinal and upper forest distribution limits: in five boreal forest stands in Northern Fennoscandia north of the Arctic Circle (Norway, Sweden, Finland) and three subalpine forest stands in the European Alps (Italy, Switzerland; Fig. 1). The topography in Fennoscandia is dominated by the Scandes mountain range in the north and west and flattens towards the Baltic Shield in the east. The climate is subarctic with cold winters and short mild summers (Figure S1). Due to oceanic climate and the North Atlantic Current, the coastal regions are considerably wetter than the inland and temperatures are milder in winter and cooler in summer. Accordingly, our sampling sites in Fennoscandia cover a prominent climatic gradient from the Atlantic coast with oceanic climate (VIK site: mean annual temperature 3.0 °C, total annual precipitation 1027 mm) over a dry inner-alpine valley in the Scandes (DIN, DIS; 0.8 °C, 324 mm) to the inland with rather continental climate (TOR, KEV: −1.4−−0.1 °C, 306–396 mm). The elevation of sites located in flat landscape or on gentle slopes spans between 155 and 460 m. Due to the flat surface, stagnant water in depressions was observed at some sites during the fieldwork, mainly at VIK and DIN.

The European Alps are a mountain range of alpine morphology uplifted by Paleogene tectonics. Climatic conditions show a pronounced shift with elevation from the Mediterranean or temperate climate at the foothills to the glacial environment above the snow line, with inner and higher ranges often being drier. Our sampling sites are located in relatively dry inner-alpine valleys of the Eastern Alps in the upper treeline ecotone in elevations between 2168 and 2265 m. Compared with Fennoscandia, sites in the Alps were located on significantly steeper slopes often covered by rocky fields and outcrops with shallow and dry soils. Mean annual climatic conditions of these sites (SCU, MAN, MAS) vary between 1.1–1.5 °C and 833–860 mm.

According to the dominant conifer species in these two regions, we studied the growth of *Pinus sylvestris* (Scots pine) in Fennoscandia and *P. cembra* (Swiss stone pine) and *Larix decidua* (European Larch) in the Alps. *Pinus sylvestris* is a widespread Palearctic conifer growing across entire Central and Eastern Europe and Northern Asia, reaching its northern distribution limit in northern Fennoscandia (Caudullo et al., 2017). It is an evergreen light-demanding species with a wide climatic niche tolerating both drought and cold stress (Ellenberg and Leuschner, 2010). By contrast, species ranges of evergreen *P. cembra* and deciduous L. *decidua* are mostly restricted to high mountain ranges in Central Europe (Alps and Carpathians; Unterholzner et al., 2024). Mixed stands of *P. cembra* and L. *decidua* dominate subalpine forests in the central part of the Alps in different successional stages, with L. *decidua* being able to colonize rocky, steep slopes with shallow soils. Under similar meteorological conditions, *P. cembra* tends to regulate stomatal conductance more compared to L. *decidua* (Anfodillo et al., 1998). Accordingly, montane *P. cembra* often shows a higher sensitivity to summer drought stress compared to coexisting L. *decidua* (Obojes et al., 2022).

### 2.2. Dendrochronological sampling and processing

Field sampling was performed during three campaigns in 2018 (KEV), 2022 (DIN, DIS, TOR, VIK, MAS, MAN) and 2023 (SCU). We targeted presumably cold-limited boreal forest stands with sparse canopy cover close to the northern distribution limit of *P. sylvestris* in Fennoscandia and mixed subalpine forests of *P. cembra* and L. *decidua* in the upper treeline ecotone in the Alps. We aimed to sample two age cohorts

**Fig. 1.** Map of the study regions in Europe (right) and distribution of individual sampling sites across Fennoscandia (top left) and the Alps (bottom left).

of young and old trees per site and species, and selected the respective trees based on assessment of tree size (stem diameter and height) and canopy shape. For young trees, we aimed to ensure a minimum cambial age of 45 years at coring height to allow for a meaningful period for climate-growth correlations. Only dominant (unsuppressed in case of young trees) healthy, straight trees without major mechanical damage (e.g., crown breakage, resin exudation, wounds) were selected for coring. We extracted two cores per tree at 1.3 m or lower above ground perpendicular to the slope using an increment corer. In total, 484 trees were cored. In addition, we measured basic dendrometric parameters of each sampled tree including diameter at breast height, total tree height, crown base height, and crown diameter.

Cores were air-dried, glued onto wooden supports, and smoothed using progressively finer sandpapers to improve the visibility of tree-ring borders. We scanned the cores using a standard flatbed scanner with a resolution of 1200–2400 dpi and measured tree-ring widths using CooRecorder software ver. 9.8.1. (Cybis Elektronik and Data AB; Maxwell and Larsson, 2021) and WinDendro ver. 2022c (Regent Instruments Inc.). The measurements were verified by visual and statistical cross-dating (Holmes, 1983). Cross-dated tree-ring width series from the same tree were averaged and the age of the tree was determined as the number of tree rings measured on the longer series. This approach provides a conservative estimate of actual tree age since we did not account for missing rings to the pith or below coring height. Trees were split into two cohorts based on this age estimation at coring height. Following the inspection of age histograms (Figure S2) and following previous studies (Carrer and Urbinati, 2004; Konter et al., 2016; Rossi et al., 2008), we defined 'young' trees as those having between 45 and 100 rings, while 'old' trees had >150 rings. From 484 trees cored, 168

and 229 were classified as young and old cohorts, respectively (Figure S2). The remaining trees did not fit into any age cohort, e.g., due to unexpected size-age relationship or large pith offsets of both cores, and were excluded from further analysis. The mean (minimum-maximum) replication of trees per site was thus 15.3 (6–26) and 20.8 (10–33) for young and old age cohorts, respectively. We used boxplots to compare mean values of dendrometric parameters between old and young trees. In addition, we calculated mean sensitivity (i.e., year-to-year variation in tree-ring width series) and mean inter-series correlation from the raw series for each of our sites and age cohorts.

We fitted a smoothing spline with a 50 % frequency cut-off at 40 years and used prewhitening to remove biological trends and autocorrelation from each tree-ring width series (Cook and Peters, 1981). Finally, we built 22 residual chronologies by bi-weight averaging of individual detrended tree-ring indices, resulting in a single chronology for each combination of site, species, and age cohort. To ensure stable sample depth of all chronologies over time, we trimmed them by the period 1975–2018 (KEV) or 1975–2020 (other sites). This period also agreed with the availability of station climatic data for the sites in Fennoscandia.

*2.3. Climatic data*

Climatic variables used in the analysis included daily minimum and maximum temperature and precipitation totals from 1st January 1975 to 31st December 2020. For all sites in Fennoscandia, we acquired daily climatic data from the nearest meteorological station (Table S1). The mean distance between the respective sampling site and the station was 20 km. For DIN and DIS sites, gaps in the local climatic series were filled

by linear regression from the second nearest station. To this end, we fitted linear regressions between temperatures measured at Dividalen (dependent variable) and Bardufoss (predictor) during the period of their overlap (Table S2). For the precipitation data, we fixed the intercept of the regression model to zero. For the alpine sites, given the significant climatic variability in complex alpine landscapes, we used data from the E-OBS ver. 28.0. gridded dataset with a spatial resolution of 0.1° (Cornes et al., 2018). We corrected the difference in elevation between the E-OBS grid centre and our sampling site by cokriging. Since the DIN-DIS (Fennoscandia) and MAN-MAS (Alps) site pairs were located close to each other, we used the same climatic series for both sites of the respective pair.

We calculated the mean daily temperature as the mean value of the daily minimum and maximum temperatures. To ensure consistency of statistical treatments of tree-ring width and climatic series, we removed trends from temperature and precipitation series by fitting a smoothing spline with a 50 % frequency cut-off at 40 years. It has been shown that removing trends from climatic series reduces risks of false or spurious climate-growth correlations, particularly if tree-ring widths were detrended with short spline, climate-growth correlations were calculated over short periods, and in areas with prominent trends in temperature including high latitudes and elevations (Ols et al., 2023). Daily detrended minimum and maximum temperatures were used to estimate potential evapotranspiration based on the Penman-Monteith formula (Allen et al., 2005). Finally, we determined daily values of climatic water balance as the difference between precipitation and potential evapotranspiration.

### 2.4. Statistical assessment of climate-growth responses

We applied three independent approaches to assess climate-growth responses for each chronology during the 1975–2020 period: seasonal climate-growth correlations based on daily climatic series (Jevšenak, 2019), a pointer year analysis (Jetschke et al., 2019), and the non-linear Vaganov-Shashkin process-based model of wood formation (Vaganov et al., 2006). Combining linear statistical methods, extreme year analysis, and non-linear process-based models was previously shown to be suitable to counterbalance limitations of each approach and to gain a better understanding of growth dynamics on sub-annual temporal scales (Jevšenak et al., 2021; Tumajer et al., 2023; Tychkov et al., 2019).

#### 2.4.1. Climate-growth correlations

We calculated linear climate-growth correlations between tree-ring width chronologies and seasonal climatic variables derived from daily climatic data (Jevšenak, 2019). To do this, we first calculated means of mean, maximum, and minimum temperatures and cumulative water balance for periods with a duration between 15 and 300 consecutive days (hereafter called 'season'). We allowed the seasonal window to partly overlap with the year before the tree-ring formation but its centre and end always occurred in the tree-ring formation year. For example, the first day of the earliest, shortest (15 days) season started on 24th December of the previous year (seven days before 1st January) and the first day of the earliest, longest (300 days) season started on 3rd August of the previous year (150 days before 1st January). Starting from here, seasons were calculated for each window length (15–300 days) and shifted by one day as long as the end of the season was located in the year of tree-ring formation. This way, we produced >80,000 seasons of mean, minimum, and maximum temperature and cumulative water balance for each study site. Next, we correlated each of these seasonal climatic variables with tree-ring width chronologies of the respective combination of site, species, and age cohort. Accordingly, climate-growth correlations were not calculated on climatic data in daily resolution but on seasonal climatic means derived from daily data not limited to calendar months. Since temperature directly affects water balance through potential evapotranspiration (Allen et al., 2005), partial correlations were used to control for the confounding effect of water

balance on correlations of temperature variables with tree-ring width chronologies. Similarly, we used mean seasonal temperature as a control variable in partial correlations of chronologies with water balance. Individual correlations and their significance levels were plotted as matrixes for a visual comparison of correlation patterns between age cohorts, species, and sites. In addition, we calculated the proportion of significant correlations for each season length between 15 and 300 days regardless of the timing of the season during the year. This was motivated by previous reports on shifts in the seasonal duration of significant climate-growth correlations between age cohorts (Konter et al., 2016).

In addition, we statistically quantified differences between the matrixes of climate-growth correlations using MANOVA (multivariate analysis of variance), a procedure that compares sample means across multiple dependent variables (Anderson, 2003). We used the correlation matrix as the dependent variable and tested for their variation between explanatory categorical variables of species and age cohort. We built two separate MANOVA models for correlation matrixes of mean temperature and water balance. For each model, we calculated partial eta-squared ($\eta_p^2$) as a relative measure of variance in climate-growth correlations associated with each categorical predictor, i.e., species and age cohort (Adams and Conway, 2014). The values of $\eta_p^2$ vary between 0 and 1 indicating low and high variation of climate-growth correlations explained by the given predictor, respectively.

#### 2.4.2. Climatic drivers of extremely narrow and wide rings (pointer years)

To analyse the level of synchronization between extreme meteorological conditions and unusually wide and narrow tree rings, we extracted seasonal climatic variables (mean, minimum, and maximum temperature, water balance) for the seasons that most strongly correlated with each chronology. Next, we identified pointer years with a tree-ring width of >1.75 x standard deviation narrower (negative pointer) or wider (positive pointer) than the long-term mean of the chronology (Jetschke et al., 2019). We compared mean values of the seasonal climatic variables in pointer years with the respective means up to two years before and after the pointer year. In doing so, we tested if the occurrence of the pointer years was synchronized with specific meteorological conditions (Lough and Fritts, 1987) and whether these conditions initiated lagged responses in tree-ring width chronologies (Klesse et al., 2022).

#### 2.4.3. Process-based modelling of wood formation

The VS-model is a moderately complex, sink-oriented process-based model of wood formation (Vaganov et al., 2006). Daily mean air temperature, precipitation totals, and site latitude are required inputs for the model. The VS-model simulates daily radial growth rates based on air temperature, soil moisture (calculated from precipitation and temperature), and photoperiod (calculated from site latitude). In the first step, the VS-model calculates partial growth rates of temperature and soil moisture which are nonlinearly dependent on the given climatic variable. The model weights daily contributions of temperature and soil moisture for tree growth assuming that the growth kinetics respond to the more growth-limiting climatic variable. Therefore, the key outputs of the model include a simulated unitless proxy for daily growth kinetics (integral growth rate) together with the dominant climatic limiting factor of the growth determined by partial growth rates (Fonti et al., 2022).

We calibrated the VS-model for each of 22 cohort chronologies independently. The calibration procedure reflected our initial hypotheses about the dominant control of temperature on tree growth with potential, variable growth responses to soil moisture. Accordingly, we performed model calibration in two steps. First, we identified optimal values of parameters defining temperature effects on tree growth assuming that soil moisture does not affect growth, i.e., soil moisture conditions are constantly optimal. During this step, we aimed to generate a set of temperature-response parameters inside realistic ecological intervals yielding the highest correlation between the

simulated chronology and the mean of old and young chronologies from the given site. In the next step, we fixed the temperature-response parameters to values calibrated in the first step and varied parameters of growth response to soil moisture and cambial phenology. The calibration resulted in two parameter sets yielding the highest correlations with each age cohort chronology per site. We used the Matlab implementation of the VS-model to generate 5,000 plausible combinations of parameters in both steps (Anchukaitis et al., 2020). Since the modelling period was too short for independent stationarity testing, we calibrated the model over the full interval 1975–2018 (2020) assuming the stationarity of the parameters during this short period (Tumajer et al., 2023). Based on model outputs, we plotted a matrix of simulated daily integral growth rates and their dominant climatic limiting factors for each site, species, and age cohort.

### 2.5. Cambial age chronologies

Our approach based on cohort chronologies reflected preferential sampling of young and old trees in the field and previous studies on age effects in climate-growth signals (Konter et al., 2016). However, since this method does not decouple tree age and tree size from time, it may fail to fully capture ontogenetical shifts in climate-growth responses (Trouillier et al., 2019). To test the robustness of our demographic approach, we compared the results based on age cohorts with the clustering of individual tree rings based on their cambial age. Since the latter approach requires large numbers of sampled trees from all cohorts (Trouillier et al., 2019), which were not available at site level, we pooled data per species for cambial age classification. Next, we created subsets of tree ring indices (detrended by spline with a 50 % frequency cut-off at 40 years) per species within specific intervals of cambial age including 45–100, 101–150, 151–250, and 251–470 years. We prewhitened and averaged all tree-ring indices within the same interval into cambial-age chronologies and subjected them to climate-growth correlations, pointer year analysis, and the VS-model in a similar way as for cohort chronologies.

Except for the calibration of the VS-model in Matlab, all statistical analyses were performed in R ver. 4.2.2. (R Core Team, 2022) using the packages 'dplR' (tree-ring detrending and chronology building; Bunn, 2008), 'dendroTools' (climate-growth correlations; Jevšenak and Levanič, 2018), 'fruclimadapt' (calculating water balance; Miranda, 2023), 'effectsize' ($\eta_p^2$; Ben-Shachar et al., 2020), and 'ggplot2' (producing charts; Wickham, 2009).

## 3. Results

### 3.1. Dendrometric parameters and chronology statistics

Trees classified as young had a lower mean height, stem diameter, and crown dimensions at all sites, which justifies our classification approach into the two age cohorts (Figure S3). Chronologies of young and old cohorts from the same site showed similar levels of sensitivity but inter-series correlation varied between cohorts in the Alps (Table 1). Regardless of the cohort, mean inter-series correlation and sensitivity peaked for L. decidua from the Alps followed by P. sylvestris from Fennoscandia and P. cembra from the Alps.

### 3.2. The effects of temperature and water balance on radial growth

Climate-growth correlations showed positive and significant effects of summer temperature on tree-ring width at most of our sites and for both age cohort chronologies (Fig. 2). Correlations were consistent regardless of whether mean, minimum, or maximum temperatures were considered (Figure S4). There was no distinct pattern in the strength of the correlation, either with respect to region, species, or age cohort. The highest temperature-growth correlations were found for old trees from the TOR site ($r = 0.66$–$0.70$, DOY 190–211). By contrast, DIS chronologies from Fennoscandia and the MAN and MAS P. cembra chronologies from the Alps showed the weakest correlations with temperature, but instead correlated more significantly with water balance. Peak temperature-growth correlations occurred during seasons with length between 15 and 60 days centred around the summer solstice. The majority of significant temperature-growth correlations occurred during short seasons of <150 days (Fig. 3). Significant correlations for seasons longer than 150 days were common mainly at sites with relatively higher mean annual temperature and presumably longer growing seasons (MAN, SCU, VIK), and for young age cohorts. Values of $\eta_p^2$ derived from MANOVA to quantify differences between species and cohorts in mean temperature-growth correlations equalled 0.19 and 0.29, respectively, indicating low explained variation (Table S3).

Correlations of cohort chronologies with water balance showed a distinct pattern according to tree age (Fig. 2). For old trees, correlations were mostly non-significant regardless of the region, site, or species. For young trees, correlations with water balance were often equally strong or stronger than with temperature. They were significantly negative for young trees from Fennoscandia except for VIK, and significantly positive

**Table 1**
Descriptive statistics of age cohort chronologies during the 1975–2018 (2020) period.

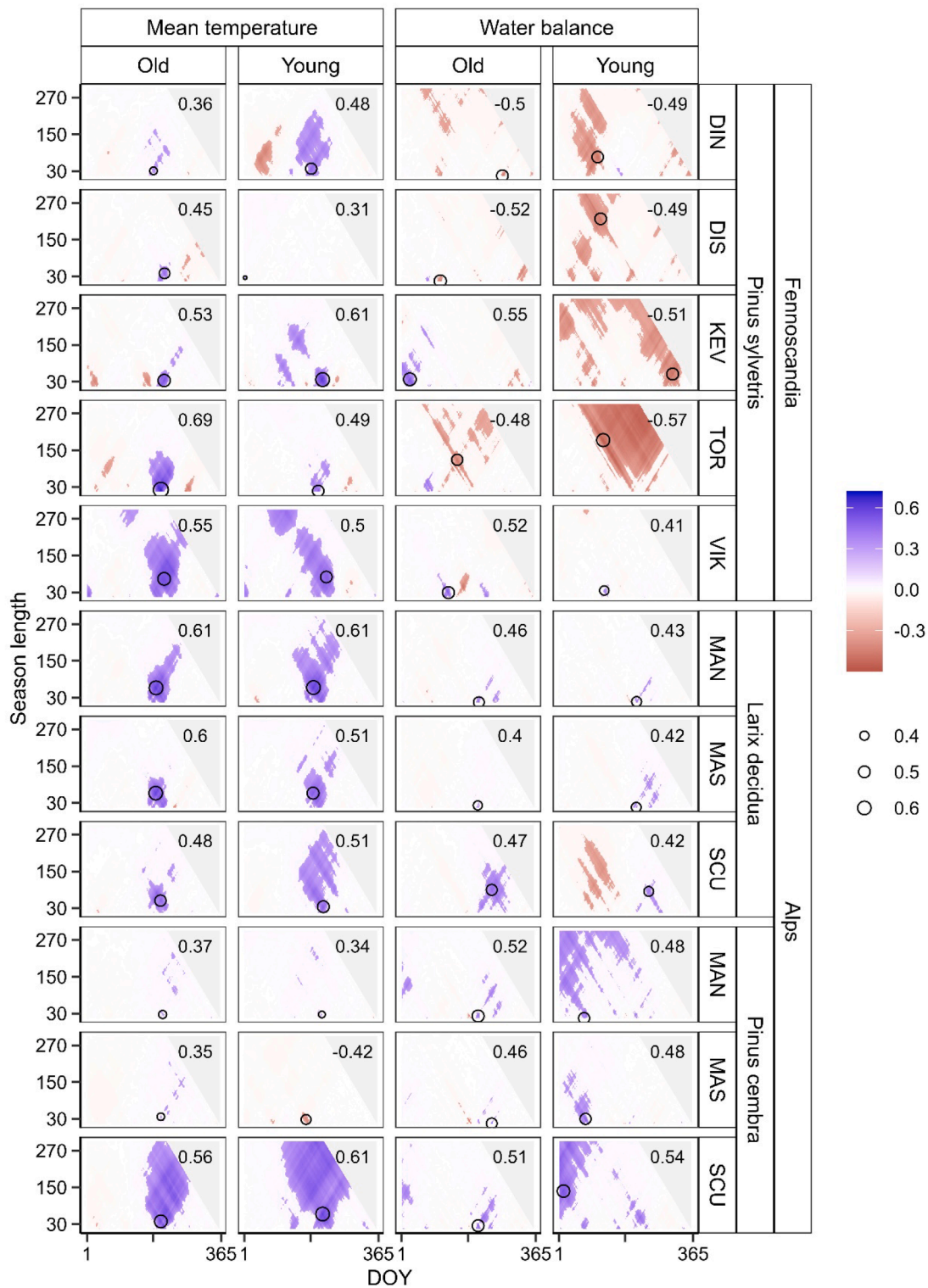| Region | Site | Full site name | Coordinates [N, E] | Elevation [m] | Species | Age cohort | Number of trees | Mean inter-series correlation | Mean sensitivity |
|---|---|---|---|---|---|---|---|---|---|
| Fennoscandia | DIN | Dividalen north-facing slope | 68.8345 19.5590 | 330 | Pinus sylvestris | Young | 19 | 0.34 | 0.19 |
| | | | | | | Old | 22 | 0.34 | 0.20 |
| | DIS | Dividalen south-facing slope | 68.8616 19.6084 | 460 | | Young | 21 | 0.44 | 0.17 |
| | | | | | | Old | 17 | 0.31 | 0.18 |
| | KEV | Kevo | 69.8336 27.1364 | 300 | | Young | 14 | 0.21 | 0.19 |
| | | | | | | Old | 32 | 0.26 | 0.22 |
| | TOR | Torneträsk | 68.2161 19.7630 | 380 | | Young | 21 | 0.39 | 0.18 |
| | | | | | | Old | 32 | 0.33 | 0.18 |
| | VIK | Vikran | 69.5236 18.7771 | 155 | | Young | 26 | 0.53 | 0.19 |
| | | | | | | Old | 33 | 0.56 | 0.19 |
| Alps | MAN | Mazia north-facing slope | 46.6978 10.6533 | 2265 | Larix decidua | Young | 14 | 0.42 | 0.20 |
| | | | | | | Old | 12 | 0.65 | 0.23 |
| | | | | | Pinus cembra | Young | 16 | 0.43 | 0.15 |
| | | | | | | Old | 10 | 0.31 | 0.15 |
| | MAS | Mazia south-facing slope | 46.7375 10.6788 | 2250 | Larix decidua | Young | 8 | 0.44 | 0.22 |
| | | | | | | Old | 18 | 0.57 | 0.23 |
| | | | | | Pinus cembra | Young | 6 | 0.25 | 0.19 |
| | | | | | | Old | 11 | 0.36 | 0.17 |
| | SCU | Scuol | 46.6966 10.3486 | 2168 | Larix decidua | Young | 9 | 0.26 | 0.21 |
| | | | | | | Old | 23 | 0.57 | 0.25 |
| | | | | | Pinus cembra | Young | 14 | 0.36 | 0.17 |
| | | | | | | Old | 19 | 0.27 | 0.17 |

**Fig. 2.** Matrixes of climate-growth correlations between tree-ring width chronologies and seasonal mean temperature (left column) and water balance (right column) for each site, species, and age cohort for the period 1975–2020 (2018 for KEV). Seasons are of 15–300 consecutive days in length (y-axes) and results are plotted on the day of the year (DOY) which is in the centre of the respective season (x-axes). Non-significant correlations ($p > 0.05$, $|r| < 0.294$) are not shown. The circles indicate the most significant correlation for a given chronology, with the respective correlation coefficient provided in the top-right corner. The size of the circle scales with the absolute value of the most significant correlation. For correlations with minimum and maximum temperatures, see Figure S4.

for *P. cembra* trees from the Alps. *Larix decidua* showed mostly non-significant correlations with water balance. Significant correlations with water balance often encompassed seasons longer than 200 days (Fig. 3). For water-balance correlations, MANOVA yielded $\eta_p^2$ values of 0.57 and 0.09 for species and age cohorts, respectively (Table S3). This

indicates the high variation in the correlation coefficient between species.

Our pointer year analysis identified 83 extremely wide or narrow rings in the tree-ring width chronologies of both cohorts (Figure S5). Wide tree rings in Fennoscandia were associated with positive anomalies
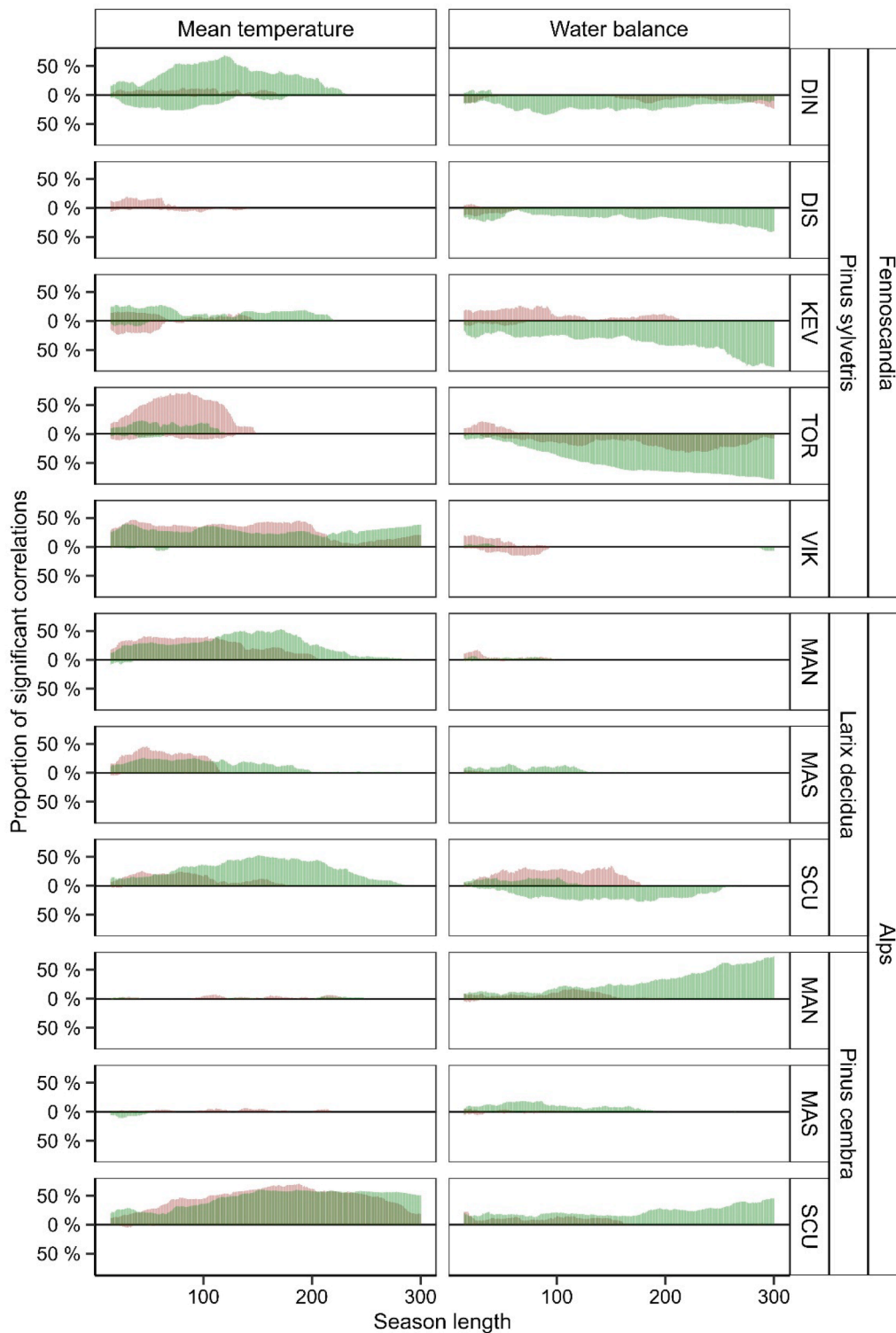
**Fig. 3.** Proportion of significant ($p < 0.05$) correlations of chronologies with mean temperature and water balance for periods with a duration between 15 and 300 consecutive days for young (green bars) and old (brown bars) trees. Bars above/below solid line at 0 % represent positive/negative correlations.

in mean and minimum temperatures, but not with maximum temperatures, for both young and old age cohorts (Fig. 4, S6). However, these years with above-average temperatures were followed by narrow rings in old trees, i.e., tree growth benefited from warmer temperatures in the year of growth but not in the subsequent year. Narrow rings in young trees occurred during wet years in Fennoscandia. In the Alps, wide rings in *P. cembra* coincided with wet years particularly in old trees.

Climate-growth correlations of species-pooled chronologies based on

the cambial age of tree rings had similar patterns as those of site-specific cohort chronologies (Figure S7a). Temperature-growth correlations of cambial-age chronologies peaked for short seasons in the middle of summer. Correlations with water balance were mostly negative in *P. sylvestris*, non-significant in *L. decidua*, and positive in *P. cembra*, and faded toward older cambial age in both pines. Pointer-year analysis of cambial-age chronologies was affected by low replication of pointer years. However, the dependence of extreme tree-rings on climate overall
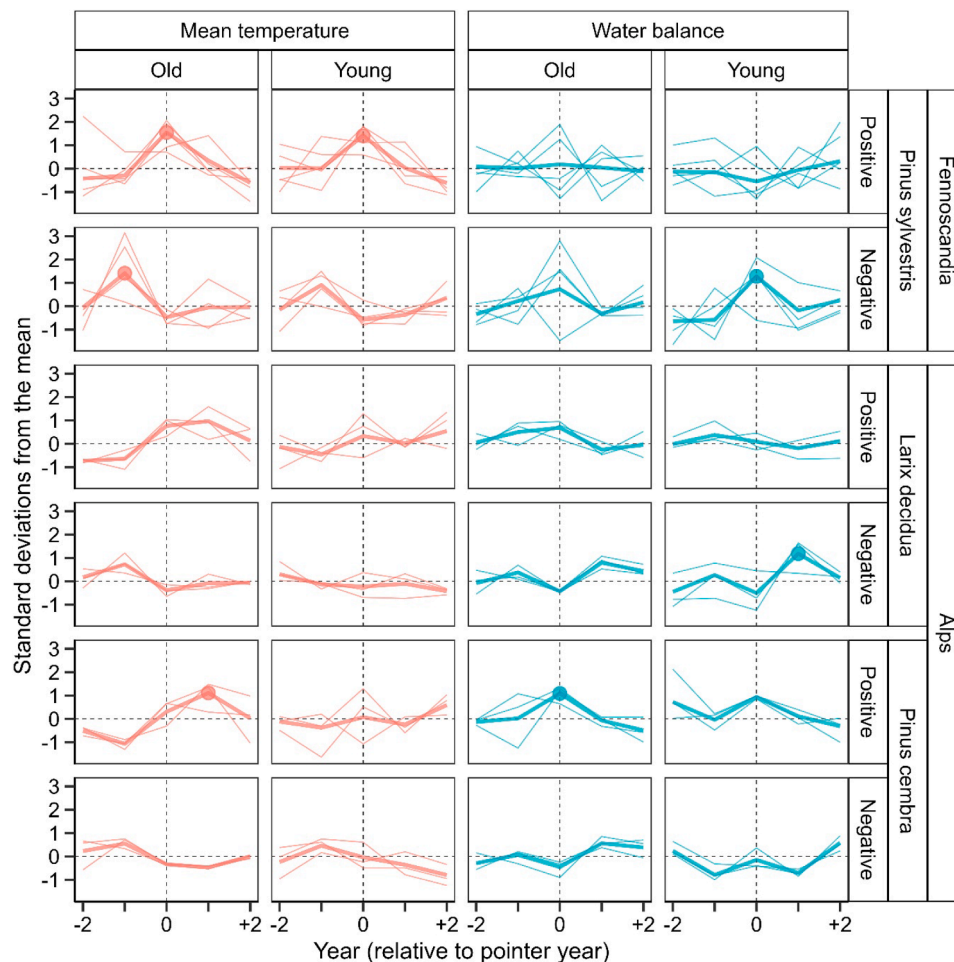
**Fig. 4.** Anomalies of mean temperature and water balance in pointer years (0 on the x-axis) and two years before and after the pointer year expressed as standard deviations from the mean. Only mean temperature and water balance seasonal variables that correlate the most with each chronology are shown (see circles in Fig. 2). Thin lines represent individual sites, bold lines depict the mean across all sites. Climatic variables were z-transformed before plotting to remove between-site differences in mean climatic conditions. Filled circles highlight mean anomalies of climatic variables exceeding 1x standard deviation from their mean. Pointer years were defined as ring widths deviating for >1.75x standard deviation from the long-term mean (1975–2020). For anomalies of minimum and maximum temperatures during pointer years, see Figure S6.

agreed with similar results based on cohort chronologies (Figure S7b).

### 3.3. Growth-limiting factors derived from the VS-model

All chronologies simulated by the VS-model significantly ($p < 0.05$) correlated with the cohort chronologies, thus indicating a good model fit (Figure S8). The simulations helped to refine systematic differences in seasonal climatic limitation of the growth between regions and species (Figs. 5, S9). According to the model, temperature was the primary growth-limiting factor at all sites, but some sites and species had periods of optimal (SCU, *L. decidua*), drought-limited (MAN, MAS, *P. cembra*), or moist-limited (TOR, KEV) growth. For both *Pinus* species, the simulated partial growth rate of soil moisture dropped below the partial growth rate driven by temperature in specific parts of the growing season, i.e., the model predicted that moisture was more growth-limiting than temperature. This manifested as seasonal summer drought stress for *P. cembra* in the Alps but spring growth limitation by soil moisture oversaturation for *P. sylvestris* in Fennoscandia. Differences in the intensity of moisture limitation between age cohorts were less systematic compared to linear climate-growth correlations. The VS-model simulations for species-specific cambial-age chronologies confirmed age-dependent growth limitation by high soil moisture for *P. sylvestris* and age-dependent drought effects on the growth of *P. cembra* (Figure S10). All calibrated parameters of the VS-model are listed in Tables S4 and S5.

### 4. Discussion

Our results confirmed a prevailing temperature control on radial growth of subarctic and subalpine trees near the latitudinal and elevational treeline, respectively (Körner, 2021). Additionally, we found frequent and simultaneous effects of water balance on growth, but these effects were by far more pronounced for the young age cohorts and both *Pinus* species. Notably, wet conditions promoted the growth of young *P. cembra* in the Alps but limited the growth of young *P. sylvestris* in Fennoscandia resulting in the synchronization of extremely narrow rings with moist years at our high-latitude sites. Below we discuss possible drivers and consequences of the observed variability in climate-growth responses including age effects, species adaptations, and between-site environmental differences.

### 4.1. Temperature-growth responses

As expected, we observed significant positive temperature-growth correlations during the growing season, with the correlation peak centred around the summer solstice at most sites of our network and for both age cohorts. Subarctic and subalpine coniferous forests are characterized by cold climates limiting the duration of the growing season and the rate of wood formation with the growth peak and thus correlation strength often synchronized with day length (Rossi et al., 2006).
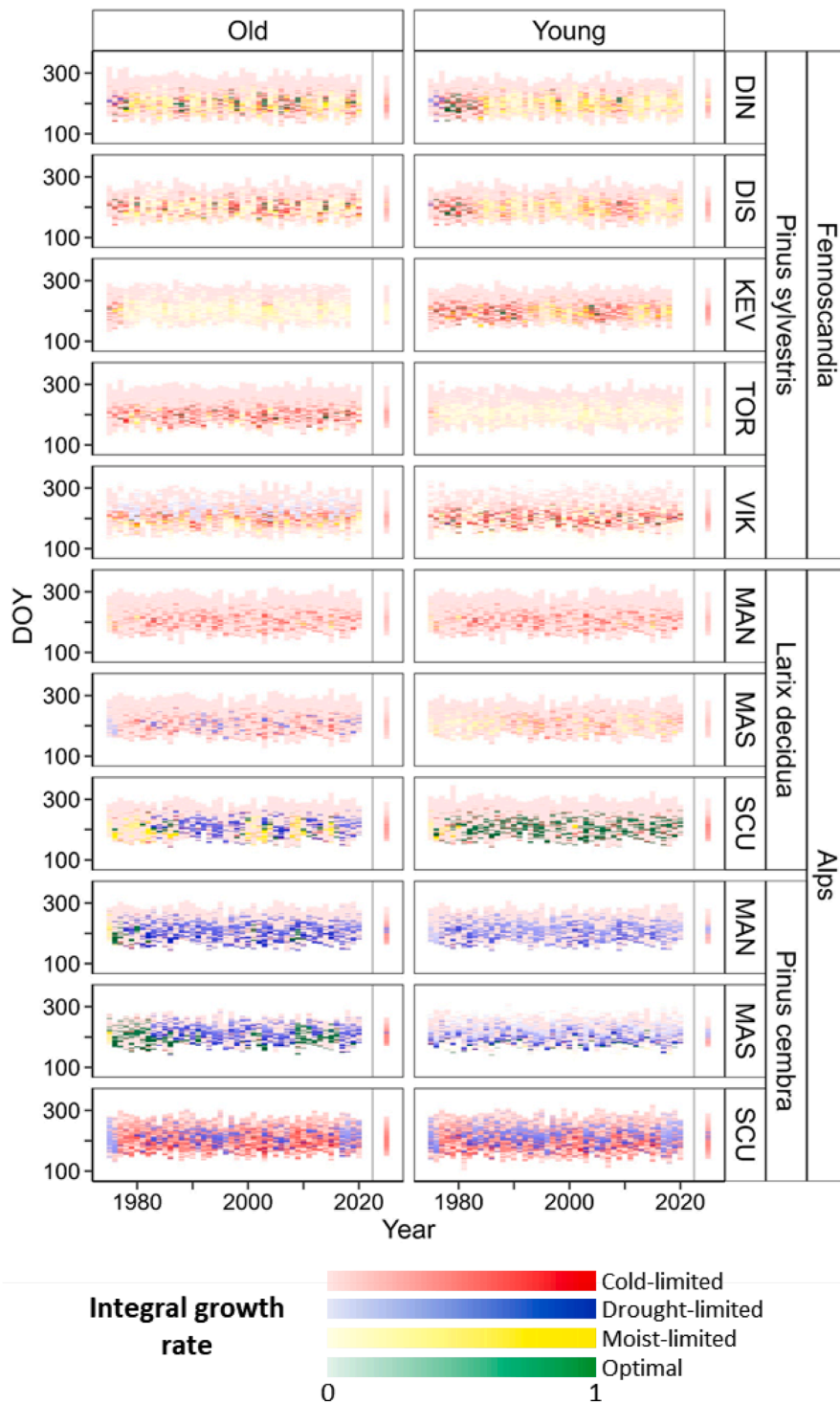
**Fig. 5.** Matrix of the dominant growth-limiting factors (colours) and the strength of the respective integral growth rates (colour intensity) for each day (DOY) from 1st January 1975 to 31st December 2020 as derived from the VS-model. The value of integral growth rate represents a unitless proxy for the rate of wood formation with 0 indicating cambial dormancy or quiescence and 1 indicating the physiological maximum of wood formation rate. The additional column on the right of each matrix shows mean daily integral growth rates and the most frequent limiting factor over the entire period of the simulation.

Naturally, our results are in line with previous research in Fennoscandia (Hartl et al., 2021) and mountain forests (Ponocná et al., 2016), and studies showing a significant coherence of tree-ring width chronologies with instrumental temperature records (Büntgen et al., 2006; Grudd, 2008). Notably, our observed low values of $\eta_p^2$ from MANOVA comparing temperature-growth correlations confirm the low variation in temperature signals between chronologies from different species and age cohorts.

Prominent exceptions to this pattern were the MAN and MAS *P. cembra* sites (Mazia, Alps), as well as the DIS site (Dividalen, Fennoscandia), where positive correlations with summer temperature were weak or absent. Plausible explanation for the MAS site could be related to a relatively large gap between the site elevation (realized treeline) and the potential treeline isotherm due to historical grazing (Obojes

et al., 2022). While the potential treeline represents a global cold margin of tree existence (Körner, 2021), cambial activity tends to be less sensitive to summer temperatures below the potential treeline (Camarero et al., 2021). In addition to site conditions, weak temperature signals in *P. cembra* cohort chronologies from MAS can be attributed to limited tree replication, although both cohorts showed a high mean inter-series correlation (Table 1). At the MAN site, temperature-growth correlations could have been masked by dominant moisture limitation due rocky microsite with potentially low soil water holding capacity and fast drainage associated with a steep slope. Dry local climate with very low precipitation in the continental inner-alpine valley could contribute to weak temperature-growth correlations in DIS site (Kirchhefer, 2005).

### 4.2. Age-dependent and species-specific growth responses to water balance

The growth response to water balance showed systematic variation between regions, species, and age cohorts. These differences were visually apparent from the correlation matrixes and were confirmed by high values of $\eta_p^2$ for the species derived by MANOVA. While correlations with water balance were mostly non-significant for old trees, they were mostly significant for young trees of both *Pinus* species. Interestingly, young trees experienced both strong positive (*P. cembra* in the Alps) and strong negative (*P. sylvestris* in Fennoscandia) effects of water availability on radial growth. This divergent response to water availability of pine growth between regions was consistent with the outputs of the process-based model and was independent of detrending of climatic data performed in our study (Figure S11). Young and small pines might have less developed root systems potentially exacerbating drought sensitivity in Alpine sites (Mašek et al., 2021; Rozas et al., 2009). By contrast to flat landscape prevailing in our sites in Fennoscandia, high-mountain environments are often covered by steeper slopes and shallow and rocky soils with limited water holding capacity. This agrees with systematically higher values of soil drainage coefficient leading to faster soil moisture depletion calibrated by the VS-model in the Alps compared with sites in Fennoscandia (Table S5; parameter Λ). Accordingly, moisture availability was shown as an important predictor of recent treeline shifts in seasonally dry mountains, particularly through its effects on seedling and sapling establishment (Elliott and Petruccelli, 2018; Liang et al., 2014; Sigdel et al., 2018) and growth phenology (Ren et al., 2018). Moisture demands of young trees might, therefore, contribute to lagged responses of some mountain treelines to climate warming (Fajardo and McIntire, 2012; Harsch et al., 2009).

Snow accumulation and melting may play a considerable role for both positive and negative effects of water availability on growth observed in our study, as the window of significant correlations with water balance often starts early in the year (Harvey et al., 2020). Accordingly, prominent variation of partial growth rates to soil moisture simulated by the VS-model can be linked to the spring period of snow melting and its effect on seasonal growth dynamics (Figure S9). Excessive snow may delay the timing of growth onset at high latitudes by cooling the stem base preventing spring nocturnal radial growth (Flynn et al., 2025), altering soil temperature in spring, which is an important predictor of radial growth during the first part of the growing season (Sanmiguel-Vallelado et al., 2021), or by soil waterlogging (Francon et al., 2024). By contrast, high snow cover might reduce local drought in drier mountain microsites (Hagedorn et al., 2014). Ongoing and future changes in winter precipitation may therefore play crucial roles in the growth of woody plants both in Fennoscandia (Mathisen and Hofgaard, 2011) and in the Alps (Carrer et al., 2023). We found a lack of moisture signals in the tree-ring width chronologies of L. *decidua,* possibly due to its anisohydric response to summer drought stress (Obojes et al., 2022) and its deciduousness preventing the exposure of needles to winter conditions.

Demographic and species-specific differences in moisture sensitivity have significant implications for future dynamics of cold forest ecosystems. For instance, they might translate into differential responses of high latitude and high elevation forests to climate warming (Harsch et al., 2009). In seasonally dry mountains, treeline shifts might be increasingly decoupled from temperature due to the moisture demands of seedlings amplified by the high intensity of competition among young treeline cohorts (Sigdel et al., 2024). By contrast, the growth of woody plants in cold and humid sites might temporarily profit from both reduced moisture and increased temperature. Moreover, different moisture sensitivity of conifers forming mixed stands, mainly in the stage of saplings and small trees, might lead to disproportional upward and northward shifts under future climate (Obojes et al., 2022; Sigdel et al., 2024). Monitoring of seedling establishment and growth of young trees is essential to understand temporal variation in treeline dynamics in warmer and drier climate (Fajardo and McIntire, 2012).

### 4.3. Variation in the season length of significant climatic signals

Significant climate-growth correlations for long seasons were more common for young trees compared to old trees. This can be a consequence of shifts in the growing season over the lifespan of the tree. A larger tree size can delay the onset of the growing season due to a thicker bark and the later release from frost-driven stem shrinkage (Zweifel and Häsler, 2000), longer basipetal flow of phytohormones from the needles' primordia to the stem base (Aloni, 2007), or higher exposure of the apical meristem to cooler air masses (Körner, 2021). Consequently, old individuals usually experience a shorter growing period at the stem base compared to young trees (Rossi et al., 2008), which might be reflected by the slightly shorter seasons of significant climate-growth correlations of old trees in our study. By contrast, young trees with earlier growth onset are more exposed to snow effects in the spring or soil moisture availability at the end of summer.

The seasonal window length with significant climate-growth correlations differed not only between age cohorts but also between sites. Significant temperature-growth correlations mostly occurred for short seasons of <150 days with the peak correlations often between 15 and 60 days mainly in Fennoscandia. The prevalence of short seasons with significant temperature-growth correlations agrees with studies from high latitudes correlating tree-ring widths with climatic data (Andreu-Hayles et al., 2020; Hartl et al., 2021) and intra-annual wood formation monitoring (Buttò et al., 2019; Francon et al., 2024). This suggests that the direct effects of temperature on tree growth in the summer determined a substantial part of the annual tree-ring width in regions with short growing seasons, such as most of our Subarctic sites (Körner, 2021). In contrast, significant temperature-growth correlations across long seasonal windows were detected at several sites in the Alps (mainly SCU) and our oceanic site in Fennoscandia (VIK) with warmer springs and autumns and thus presumably longer growing seasons.

The short window of significant temperature-growth correlations observed for the old cohort in Fennoscandia underlines the suitability of long boreal tree-ring chronologies for multicentennial summer temperature reconstructions (Esper et al., 2016). However, we showed that the window length of the temperature signal of young trees might substantially differ from old trees. This challenges regional extrapolations of climatic signals derived from long boreal chronologies initially built for paleoclimate reconstructions (Babst et al., 2018). Our results highlight the strong existing discrepancy between optimal sampling strategies for the research in the fields of paleoclimatology (targeting old trees with strong climatic signals) and ecology (covering all age cohorts with different seasons of climatic sensitivity in demographically complex stands) in cold coniferous forests (Nehrbass-Ahles et al., 2014).

### 4.4. Pointer years and their synchronization with meteorological anomalies

Extreme growth reductions or releases were partly synchronized with anomalies in seasonal climatic variables in Fennoscandia but less in

the Alps. The prevailing limitation of cambial activity by low temperatures in Fennoscandia resulted in the formation of wide rings in years with above-average mean and minimum temperatures during summer. The occurrence of wide rings in synchrony with minimum, but not maximum, summer temperatures may be a consequence of the diel stem growth cycle and the dependence of growth rate on nocturnal rather than diurnal conditions (Zweifel et al., 2021). Moreover, extreme growth reductions occurred in years with above-average water balance, mainly for young trees. As discussed in the previous chapter, this might be a consequence of the negative effect of high snow loads in Fennoscandia mainly on small trees (Vaganov et al., 1999). It remains to be tested whether and to what extent such conditions impede absolute growth and persistence of young trees at high latitudes in Fennoscandia and thus hamper potential forest shifts (but see Mathisen and Hofgaard, 2011). Interestingly, old trees in Fennoscandia formed narrow rings following a warm year. Given the low productivity of the boreal forests, the growth might be reduced in a year following an exceptionally wide ring due to the depletion of carbohydrate storage pools into wood, needles, or seeds. Accordingly, trees close to the cold limit of their species range often form narrow tree rings in years with abundant production of cones or fruits (Hacket-Pain et al., 2018) which are initiated by multiannual sequence of climatic conditions favouring seed development (Roland et al., 2014; Tumajer and Lehejček, 2019). The lower synchronization of pointer years and best-correlating seasonal climatic variables in the Alps might be due to the longer growing season (Mu et al., 2023) and associated lower dependence of annual wood formation on meteorological conditions around the summer solstice. Moreover, some of narrow rings observed in chronologies of L. *decidua* might have been caused by non-climatic drivers including outbreaks of defoliating insects (Saulnier et al., 2017).

## 5. Summary and conclusions

Our results highlight covariance between tree-ring widths from northern boreal and subalpine forests with seasonal temperatures and water availability, the latter being particularly important for young pine trees at our sites. While summer temperature was the dominant growth-limiting factor for most sites as expected, correlations with water balance differed significantly between regions, species, and age cohorts. We observed strong negative correlations of moisture with growth for young *P. sylvestris* trees in Fennoscandia where years with abundant moisture coincided with unusually narrow rings. By contrast, young but not old individuals of *P. cembra* growing in our Alpine sites were drought-limited as indicated by positive correlations between tree-ring width chronologies and water balance. Chronologies of old trees generally showed a stronger correlation with temperature and neglectable correlations with water balance. Our results imply both demographic and interspecific divergence in responses to ongoing climate change because different age cohorts and species might profit or suffer from changes in temperature, precipitation, and evapotranspiration to a different extent. In particular, special attention should be paid to the ecological consequences of variable moisture sensitivity of cold forest stands with heterogenous species composition, including future shifts in species composition. Accounting for heterogenous climate-growth responses in structurally diverse forests during sampling campaigns is needed to better inform forecasts of future forest growth at cold distribution margins and draw a more differentiated picture of tree growth responses to climate changes.

## CRediT authorship contribution statement

**Jan Tumajer:** Writing – original draft, Formal analysis, Data curation. **Grudd Håkan:** Writing – review & editing, Data curation. **Jernej Jevšenak:** Writing – review & editing, Formal analysis. **Andreas J. Kirchhefer:** Writing – review & editing. **Francesco Marotta:** Writing – review & editing, Data curation. **Jiří Mašek:** Writing – review & editing,

Data curation. **Kiara Maria Nowatzki:** Writing – review & editing, Data curation. **Nikolaus Obojes:** Writing – review & editing, Data curation. **Markus Stoffel:** Writing – review & editing. **Václav Treml:** Writing – review & editing, Data curation. **Jelena Lange:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization.

## 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.

## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2025.110634.

## Data availability

Data will be made available on request.

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