



Linking crown transparency to xylogenesis: histological signatures of tree vitality in *Pinus sylvestris* L. and *Juniperus communis* L.

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Received: 18 November 2025 / Accepted: 13 June 2026 / Published online: 20 June 2026
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Abstract

Key message Increased crown transparency delays the onset and shortens the duration of xylogenesis, resulting in reduced tracheid production in *Pinus sylvestris* and *Juniperus communis*. In understory *J. communis*, peak tracheid production occurred significantly later than in dominant *P. sylvestris*.

Abstract Ongoing climate warming threatens the integrity of mountain forests by diminishing tree vitality, increasing susceptibility to pathogens, and accelerating mortality. A loss of tree vitality is reflected in increased crown transparency (CT), which is particularly evident in forests experiencing drought conditions. In this study, we examined the timing and dynamics of xylogenesis in *Pinus sylvestris* L. and co-occurring *Juniperus communis* L. across three CT classes at a drought-prone site (959 m a.s.l., Tyrol, Austria). Throughout the 2024 growing season, xylogenesis in both species (n=20 each) was monitored using microcore sampling at weekly (*P. sylvestris*) and three-week (*J. communis*) intervals. We tested whether increasing CT affects radial growth and xylem phenology. Specifically, we assessed whether increased CT delays the onset and shortens the duration of xylogenesis. Our results show that xylogenesis in *P. sylvestris* started 9–13 days earlier than in *J. communis*, and the inflection point in *J. communis* occurred 10–20 days later than in *P. sylvestris*. Increasing CT was associated with reduced tracheid production and basal area increment, and consistently delayed the onset and shortened the duration of xylogenesis. These findings demonstrate a tight coupling between CT and stem growth, highlighting that CT constrains wood formation.

Keywords Wood formation phenology · Crown defoliation · Drought stress · Microcoring · Histological analysis

Introduction

Prolonged periods of drought and heat pose a serious threat to forest ecosystems, frequently leading to declining tree vitality and increased mortality. Physiological indicators of stress include crown thinning (Camarero et al. 2015), reduced photosynthetic capacity (Granier et al. 2007; Reichstein et al. 2007; Zang et al. 2012), and diminished

wood production (Galiano et al. 2011; Eilmann et al. 2011; Camarero et al. 2015). These declines are often accompanied by heightened vulnerability to biotic agents, such as pathogens and parasitic plants (Dobbertin et al. 2007; Wermelinger et al. 2008; Gomez-Gallego et al. 2022).

The loss of photosynthetically active tissue may limit carbon availability and modify allocation patterns, potentially impacting root functioning and the tree's capacity for recovery (Galiano et al. 2011). Persistent drought can shift the balance between carbon assimilation (source) and metabolic demand (sink). While photosynthesis is typically reduced, maintenance respiration and other sinks may respond differently, so non-structural carbohydrate pools may either decline or, if sink activity is more strongly limited than source, temporarily increase (Körner 2003; Eilmann et al. 2010). Changes in the balance between carbon supply and demand can affect resilience to further stress and, depending on source–sink dynamics, may increase the risk of mortality. As a compensatory response, trees often invest in deeper rooting systems to access more stable water

Communicated by DeMicco

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sources (Ericsson et al. 1996; Puhe 2003; Ye et al. 2019; Sun et al. 2024), which is reflected in shifts in the shoot-to-root ratio (Waring 1987; Chen et al. 2021). Morphologically, drought stress may also result in shortened needles and increased crown transparency (CT)—traits that may reflect both adaptive adjustment and declining vigour (Solberg 2004; Dobbertin et al. 2010). However, the interpretation of increased CT remains debated: it may reflect functional adaptation to water scarcity or signal structural damage and incipient dieback (Dobbertin 2005; Dobbertin et al. 2010; Sánchez-Salguero et al. 2012). Nevertheless, CT is widely accepted as a retrospective indicator of past stress exposure and an effective proxy for the tree's physiological condition (Dobbertin 2005; Gričar et al. 2009; Eilmann et al. 2013).

Against this backdrop, the present study examines how CT influences radial growth in two co-occurring conifers—*Pinus sylvestris* L. and *Juniperus communis* L.—at a drought-prone submontane site in the Eastern Alps. Both species co-occur in the montane *Erico-Pinetum sylvestris* vegetation type, typically occurring on shallow, skeletal soils of carbonate origin on south-facing slopes in inner-Alpine dry valleys such as the Upper Inn Valley near Mieming (Mucina et al. 1993). Scots pine populations in this region frequently experience growth decline and partial dieback under recurrent drought. Dendrochronological evidence from nearby areas indicates that *P. sylvestris* is particularly sensitive to spring drought, exhibiting pronounced reductions in radial growth (Oberhuber et al. 1998; Oberhuber and Kofler 2000), a pattern also observed across southern Europe under intensifying climate stress (Carnicer et al. 2011). In contrast, information on drought-related growth response of *J. communis* in the study region remains limited. Although Beikircher and Mayr (2008) suggest that structural traits may facilitate efficient water transport under dry conditions, the dynamics of radial growth in *J. communis* under drought-prone environments remain poorly understood.

To address this knowledge gap, we conducted intra-annual wood anatomical analyses by repeatedly collecting microcores at high temporal resolution throughout the growing season 2024, enabling us to quantify the relationship between CT and xylem formation in both species. CT was classified into three classes and related to parameters describing cambial activity and xylem formation. Specifically, we assessed whether higher CT is associated with reduced annual xylem production, reflected in smaller radial increments and fewer cells per radial file. Additionally, we investigated how CT influences the timing and duration of xylem formation, while accounting for potential effects of growth form (tree vs. shrub). Based on the evidence that drought stress limits radial growth in *P. sylvestris* (Oberhuber et al. 1998; Oberhuber and Kofler 2000) and on the

presumed structural adaptations of *J. communis* under dry conditions (Beikircher and Mayr 2008), we hypothesised that (i) increasing CT, which reflects past stress impacts on tree functioning (Dobbertin 2005; Gričar et al. 2009; Eilmann et al. 2013), is associated with lower annual xylem production, reflected in both reduced radial increment and fewer cells per radial file. Furthermore, given that drought stress is known to constrain cambial activity and shorten the growing season in conifers (Gruber et al. 2010; Swidrak et al. 2014), we hypothesised that (ii) the onset of xylem formation is delayed and its duration shortened in individuals with high CT compared with low-CT individuals.

Materials and methods

Study species

Pinus sylvestris L. (Pinaceae) and *Juniperus communis* L. subsp. *communis* (Cupressaceae; hereafter *J. communis*) are two widely distributed, light-demanding woody species with Eurosiberian and Eurasian ranges, respectively. Both exhibit broad physiological tolerance to temperature and soil moisture variability, reflecting their wide ecological amplitude and low site specificity (Ellenberg et al. 1991; Landolt et al. 2010). Despite these shared traits, the species differ markedly in growth dynamics and physiological strategies. *J. communis* frequently develops a characteristic upward-twisting stem architecture (“tension growth”, “Spannrückigkeit”). These forms are typified by pronounced longitudinal ridges and deep furrows along the stem surface. Such structural features are indicative of irregular radial growth, potentially reflecting heterogeneity in cambial activity. Growth phenology also diverges substantially between species. In *P. sylvestris*, primary growth—particularly shoot and needle elongation—is largely confined to spring (Richardson 2004). In contrast, *J. communis* may sustain shoot growth well into late autumn or early winter, depending on environmental conditions (Ninot et al. 2025). This environmentally responsive growth suggests a high degree of phenological plasticity in *J. communis*. Such flexibility becomes particularly evident under contrasting climatic conditions: in Arctic regions, warming enhances growth rates during the short growing season, whereas in Mediterranean areas, an earlier onset of cambial activity often coincides with reduced summer growth due to increasing drought stress (Tumajer et al. 2021). At the hydraulic level, *J. communis* displays remarkable stability across elevations and genetic provenances, suggesting a conserved water-use strategy that operates independently of local climatic conditions (Unterholzner et al. 2020). As an anisohydric species, *J. communis* maintains stomatal conductance and gas exchange even at

very low water potentials (down to -6 MPa) (Zweifel et al. 2009), which supports ongoing carbon assimilation but increases vulnerability to xylem embolism and may delay post-drought recovery (West et al. 2008). Moreover, the species requires relatively high temperatures and low atmospheric humidity to fully open stomata and maximize net carbon uptake (Zweifel et al. 2009). By contrast, *P. sylvestris* exhibits an isohydric response, rapidly closing stomata under drought to maintain stable leaf water potentials. This strategy reduces transpirational water loss and prevents hydraulic failure, yet it also leads to prolonged suppression of gas exchange and photosynthesis (Irvine et al. 1998).

Study site

The study site (~ 3 ha) is situated on the south-facing, submontane slopes of the Mieming Range near Mieming, Tyrol, Austria (N47°18.9981', E10°58.2108'; 959 m a.s.l., Imst District), with a moderate inclination of 5–10%. The vegetation corresponds to a montane *Erico-Pinetum sylvestris* Br.-Bl. forest community, dominated by *Pinus sylvestris* L. in the canopy, *Erica carnea* L. in the herbaceous layer, and *Juniperus communis* L. in the shrub layer, where it frequently exhibits a tree-like growth form. Soils are shallow (10–20 cm), poorly developed, and classified as skeletal rendzic leptosols (WRB 2022), with an L–Ah–C profile overlying carbonate-rich, unconsolidated substrates. These soils exhibit high permeability but low water-holding capacity, making the site particularly prone to drought.

Climatically, the area lies within an inner-Alpine transitional zone influenced by both humid oceanic and dry continental air masses. This setting is marked by strong seasonal variability and a pronounced continental character. Compared to the wetter northern Alpine flanks, the region receives considerably less precipitation. Long-term climate data from the Obsteig meteorological station (991 m a.s.l., 5.1 km from the site) indicate a mean annual temperature of 7.9 °C and an average annual precipitation of 937 mm, of which ~ 371 mm fall during June–August (BML, <https://ehyd.gv.at>, 1998–2022; Fig. 2a).

Microclimatic records

Microclimatic conditions at the study site were continuously monitored using permanently installed sensor systems. From 1 January to 4 October 2024 (the date of the final microcore extraction), environmental variables—including precipitation, air and soil temperatures, and soil water potential—were logged at 30-minute intervals. Precipitation was measured with a tipping-bucket rain gauge

(Model 52202/52203, Campbell Scientific Ltd., UK); air temperature was tracked using HC2A-S3 sensors (Rotronic AG, Switzerland); and soil temperature via ThetaProbe ML3 (Delta-T Devices Ltd., UK) and TCAV sensors (Campbell Scientific Inc., USA). Soil water potential was assessed using Watermark sensors (Models 253/257, Campbell Scientific Inc., USA). Air temperature was measured at 10 m above ground level, approximating the canopy height of *P. sylvestris* at the study site. Soil parameters were recorded at a depth of 10 cm at three representative locations within the plot. For all variables, daily means were derived from 48 measurements per day. To contextualize short-term field measurements within long-term climate variability, historical data on air temperature (1998–2022) and precipitation (1971–2022) were retrieved from the nearby Obsteig meteorological station (~ 5 km from the study site in linear distance).

Field sampling and sample preparation

Xylem phenology—referring to xylogenesis in 2024 based on quantitative wood anatomy—and dendrochronological analyses, including age determination and assessment of vitality-related growth patterns of *P. sylvestris* and *J. communis*, were assessed in situ over the 2024 growing season (March–October). Prior to sampling in March 2024, CT of 20 randomly selected co-occurring individuals per species was visually evaluated in 5% classes, with all trees/shrubs being of comparable species-specific height and stem diameter (Dobbertin et al. 2004; Dobbertin 2005; Eilmann et al. 2013; Camarero et al. 2015). Only individuals without mistletoe infestation or visible pathogens, showing intact canopies and green foliage, were chosen using binocular inspection. CT ranged from 0% (fully foliated) to 95% (nearly completely defoliated), assessed by comparison with an optimally foliated reference tree or shrub. Three CT classes were defined: low (CT < 35%), medium (CT 35–70%), and high (CT > 70%) (Fig. 1). The number of individuals assigned to each CT class ranged from 5 to 8 in *P. sylvestris* and 4–9 in *J. communis* (Table 1).

All sampled trees were measured for total height and stem diameter (at 1.30 m for *Pinus*, 0.30 m for *Juniperus*), and soil depth was recorded at four compass points within a 1 m radius around each individual. Means per species and vitality class were computed (Table 1).

To track intra-annual xylem cell development, microcores (2 mm dia., 15 mm long) were extracted with a Trephor Tool (Rossi et al. 2006a) at 1- to 3-week intervals from designated heights, with sampling points ascending spirally and spaced at least 5 cm vertically to avoid reaction wood in subsequent samples (Forster et al. 2000; Deslauriers et al.

Fig. 1 Crown transparency (CT) classes in *P. sylvestris*, illustrating the three categories: low (CT < 35%), medium (CT 35–70%), and high (CT > 70%)

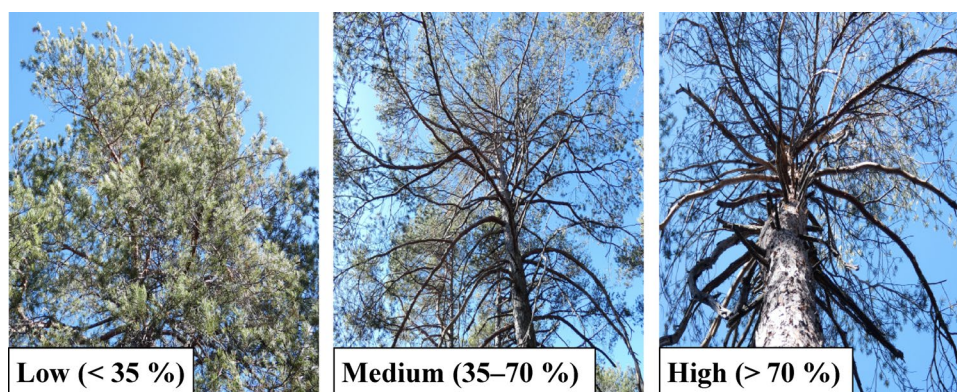


Table 1 Structural and site characteristics of sampled trees and shrubs grouped by CT, including sample size (n). Stem diameter was measured at 0.3 m for shrubs and at 1.3 m for trees. Values are represented as means $\pm$ standard deviations (SD) for age, tree/shrub height, stem diameter, and soil depth

	CT (%)	n	Age (years)	Height (m)	Stem diameter (cm)	Soil depth (cm)
<i>P. sylvestris</i>	< 35	7	130.9 $\pm$ 21.4	10.9 $\pm$ 0.5	24.2 $\pm$ 1.5	12.8 $\pm$ 2.2
	35–70	8	141.6 $\pm$ 14.8	10.6 $\pm$ 0.9	24.4 $\pm$ 3.4	10.8 $\pm$ 2.9
	> 70	5	144.0 $\pm$ 10.2	9.0 $\pm$ 1.2	20.3 $\pm$ 2.8	8.3 $\pm$ 2.7
<i>J. communis</i>	< 35	7	60.0 $\pm$ 20.1	4.1 $\pm$ 0.5	7.9 $\pm$ 1.2	9.9 $\pm$ 2.0
	35–70	9	67.1 $\pm$ 20.8	4.9 $\pm$ 0.3	8.5 $\pm$ 1.5	9.0 $\pm$ 1.7
	> 70	4	65.0 $\pm$ 5.2	4.4 $\pm$ 0.8	6.4 $\pm$ 0.9	10.8 $\pm$ 4.6

2003; Rossi et al. 2008; Prislán et al. 2022; Balzano et al. 2022). Beginning with budburst, two microcores per individual were extracted across nineteen dates for *Pinus* (DOY 86–278, $n=20$) and thirteen for *Juniperus* (DOY 95–275, $n=20$), this yielded 1,280 microcores in total.

Immediately after extraction, samples were preserved in 70% aqueous ethanol at 5 °C. In the laboratory, wood cores were dehydrated through an ethanol series (70–100%), cleared in RotiHistol, embedded in paraffin, sectioned at 9 μ m thickness using a rotary microtome (CUT 5062, SLEE, Mainz) and stained with Safranin and Astra Blue to distinguish lignified from non-lignified cell walls (Gärtner and Schweingruber 2013). Thin sections were finally mounted in Euparal. Detailed protocols follow Prislán et al. (2022) and Gärtner and Schweingruber (2013).

To assess age structure and radial growth trends, two opposite increment cores per individual (5 mm borer) were taken in late October 2024 (at 1.20 m for *Pinus*, 0.20 m for *Juniperus*) following standard dendrochronological methods (Schweingruber 1988; Pilcher 1990). Cores were air-dried, mounted, and surfaces smoothed; ring boundaries were enhanced with chalk dust (Gärtner and Schweingruber 2013).

Xylogenesis

Cell counts for cambium and developing xylem during the 2023 and 2024 growing seasons were conducted along three continuous radial files per individual using a transmitted

light microscope (Olympus BX50, Olympus Corporation, Tokyo, Japan) (Skene 1969; Antonova et al. 1995; Deslauriers et al. 2003; Rossi et al. 2006b). Images were acquired using a high-definition microscope camera (ProgRes Gryphax, Jenoptik, Jena, Germany) at 40 $\times$ magnification for *Pinus* and 100 $\times$ for *Juniperus*. At the cell level, cambial and xylem cells were classified according to their differentiation stage as (i) cambial cells, (ii) enlarging cells, (iii) secondary wall thickening cells, and (iv) mature xylem cells. In cross-sectional view, cambial cells were identified by their flattened appearance, small radial diameter, and narrow lumen. The onset of xylogenesis was defined as the first appearance of a tangential row of enlarging tracheids considering all individuals. Enlarging xylem cells were distinguished from cambial cells by the onset of radial expansion and increased lumen diameter (Camarero et al. 2010). Cells undergoing secondary wall thickening were identified by rounded cell corners and the appearance of birefringence and a glistening layer under polarized light, indicating the deposition of crystalline cellulose microfibrils. The onset of lignification was further indicated by initial red staining with safranin. Mature tracheids were characterized by fully lignified secondary walls, complete red staining, birefringence under polarized light, and empty lumina without visible cytoplasmic remnants, indicating completed programmed cell death (Rathgeber et al. 2022). Xylem formation was considered complete once the last-formed tracheids had fully differentiated and lignified. For each sampling date and individual, the number of cells in each differentiation phase was

averaged across the three radial files to obtain individual-level estimates of cambial activity and xylem development. Total xylem cell production was calculated as the sum of enlarging, wall thickening, and mature cells. Based on these observations, key phenological phases of xylem formation were determined at the individual-tree level, including (i) onset of cell enlargement, (ii) onset of secondary wall formation, (iii) appearance of the first mature tracheids, (iv) cessation of cell enlargement, and (v) cessation of secondary wall formation and lignification in the last-formed cells. For each sampling date, individual-level cell counts for each phenological phase were averaged within CT classes and subsequently compared among classes. Ring widths for 2023 and 2024 were measured using ImageJ software (version 1.53k) (Rasband 1997).

Normalisation of cell number

In *P. sylvestris*, both the number of tracheids formed during the growing season and the width of the annual ring exhibit circumferential variation within individual trees, leading to differences between samples taken from the same stem. Therefore, normalisation of cell number is required (Rossi et al. 2003). Tracheid counts from the previous year's ring were used for each sample to normalize cell number and account for radial variation (Swidrak et al. 2014). Accordingly, cell number in each j sample (i.e., microcores taken throughout the 2024 growing season) and by each i phase (i.e., enlarging, wall thickening and mature tracheids) was corrected as follows:

$$nc_{ij} = n_{ij} * \frac{n_m}{n_s}$$

where:

nc_{ij} = corrected cell number,

n_{ij} = counted cell number,

n_m = mean cell number of previous ring of all j samples,

n_s = cell number of previous ring for each j sample.

The examined *J. communis* individuals exhibited a helical growth pattern along the stem axis, which is characteristic of the Cupressaceae family (i.e., growth strain). This spiral growth frequently occurred in a highly heterogeneous manner, leading to asymmetric mechanical stress within the wood body. As a consequence, localized formation of reaction wood and partial cambial dieback were observed. Because of these peculiar growth patterns, normalising xylem cell counts led to an increase in between-shrub variability in the number of developed xylem cells, rather than a decrease, and was therefore not performed.

Dendrochronological data

Tree-ring widths were measured at a resolution of 10 μm using a light microscope (Olympus SZ61) coupled with a LINTAB (Rinntech, Heidelberg, Germany) measurement system. For each individual, the mean ring width was calculated from two opposing increment cores. Ring-width chronology was developed for every tree. To ensure dating accuracy and minimize potential measurement errors, each chronology was verified using the program COFECHA (Holmes 1994). Synchronization of the series was statistically evaluated in TSAP-WIN scientific software package (version 4.89; Rinntech, Heidelberg, Germany) based on overlap length, Gleichläufigkeit (GLK), and the t-value (Baillie and Pilcher 1973).

Tree-ring widths were converted into basal area increment (BAI) to account for the influence of increasing stem circumference on radial growth (Biondi and Qeadan 2008; Peters et al. 2015). Accordingly, BAI was calculated as:

$$\text{BAI} = \pi \times (R_n^2 - R_{n-1}^2),$$

where R is the tree radius inside the bark and n denotes the year of ring formation. Bark thickness and diameter at breast height (DBH) was recorded at the time of core sampling to calculate the radius inside the bark. To examine species-specific growth patterns, annual BAI values were averaged across all trees of the same species. BAI data were left unstandardised to preserve long-term growth rate throughout the study period.

To assess synchronous growth patterns, the development of basal area increment (BAI) was compared among vitality classes, based on class-specific mean values. Standard and residual chronologies were generated using the ARSTAN program (Cook and Holmes 1984; Cook 1985). A two-step detrending procedure was applied to account for low-frequency, non-climatic variability in the ring-width series, primarily associated with age- and size-related growth patterns and stand structural changes. In the first step, a negative exponential function (or linear function where appropriate) was fitted to each individual series to remove long-term growth trends related to tree aging. In the second step, a cubic smoothing spline with a 50% frequency cutoff equal to two-thirds of the series length was applied to remove medium-frequency variability while preserving inter-annual and decadal climate signals (Cook 1987). Residual chronologies were then generated by applying autoregressive modeling to the standardised indices, which are suited for dendroclimatic applications (Cook 1987).

Data analyses

Intra-annual wood increment dynamics—defined as the temporal progression of tracheid formation (i.e., the total

number of enlarging, wall thickening, and mature cells) over the course of the growing season—were modeled using the Gompertz growth function (Rossi et al. 2003). Model parameters were estimated via nonlinear regression implemented in OriginPro (version 2024b; OriginLab Corporation, Northampton, MA, USA). The Gompertz equation provides a mathematical framework for describing sigmoidal cell growth dynamics and facilitates the identification of the inflection point, corresponding to the maximum growth rate (Rossi et al. 2003, 2006b; c). Cumulative growth y at time t was modeled using the Gompertz function:

$$y(t) = a \cdot \exp(-\exp(-k \cdot (x - xc)))$$

where a is the upper asymptote (i.e., the theoretical upper limit of growth), k is the rate of growth (i.e., determines how quickly the system approaches the asymptote), x is the independent variable ‘time’ and xc is the inflection point (i.e., the value of x at which the maximum growth rate occurs). Climate-growth relationships 2024 were analysed for the main period of growth (Deslauriers et al. 2007). Accordingly, at 19 sampling dates from April to August, Pearson correlation coefficients were calculated to assess the relationships between cell growth rates and climatic variables (i.e., precipitation, air temperature, and soil temperature). The climatic dataset comprised 7-day mean soil and air temperatures and 7-day cumulative precipitation for the period preceding each sampling date (Camarero et al. 2010). Statistical differences among vitality classes were determined using one-way ANOVA ($\alpha=0.05$), followed by Bonferroni-adjusted pairwise comparisons (t-tests, $\alpha=0.0167$). Prior to analysis, the assumptions of normality of residuals and homogeneity of variances were assessed using the Shapiro–Wilk and Levene’s tests, respectively. When these assumptions were violated, differences among groups were evaluated using the non-parametric Kruskal–Wallis test. Long-term relationships (1998–2022) between tree-ring growth and climatic variables were examined using Pearson correlation analyses. To assess climate sensitivity, monthly mean air temperatures (1998–2022) and cumulative monthly precipitation sums (1971–2022) were used as explanatory variables in correlation analyses with mean indexed ring-width chronologies, stratified by species and vitality class. Chronologies were standardised and detrended (second order) using the ARSTAN program.

Statistical analyses were conducted using Statistica version 13.5.0.17 (TIBCO Software Inc., Tulsa, OK, USA). Statistical significance was defined at three levels $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***)

Microclimate 2024

The period from January to September 2024 was markedly warmer and wetter than the long-term average (1998–2022), with a positive temperature anomaly of $+1.7^\circ\text{C}$ and a cumulative precipitation surplus of 120 mm. Above-average rainfall was particularly pronounced in April ($+10$ mm), May ($+30$ mm), June ($+70$ mm), and September ($+83$ mm), whereas July (-10 mm) and August (-53 mm) were comparatively dry. The mean daily air temperatures for January ($0.1 \pm 3.9^\circ\text{C}$) and February ($5.4 \pm 3.2^\circ\text{C}$) exceeded the long-term means by 1.4°C and 5.6°C , respectively. This warming trend continued into March, with a mean daily air temperature of $6.3 \pm 2.7^\circ\text{C}$, representing an increase of 2.8°C relative to the 1998–2022 average (Fig. 2a). A cold spell between 17 and 25 April 2024 caused mean daily air temperatures to drop sharply from $17.68 \pm 5.91^\circ\text{C}$ on 14 April to $1.59 \pm 2.11^\circ\text{C}$. During this period, mean daily soil temperatures remained relatively stable at $6.64 \pm 0.57^\circ\text{C}$. The highest monthly mean air temperatures were recorded in July ($18.2 \pm 2.5^\circ\text{C}$) and August ($19.2 \pm 2.2^\circ\text{C}$), which also represented the driest months within the May–August period, with total precipitation of 103 mm and 88 mm, respectively (Fig. 2b). The lowest daily mean values of soil water potential were recorded on 7 May (DOY 128; -0.031 ± 0.001 MPa), 24 May (DOY 145; -0.056 ± 0.001 MPa), and 9 September (DOY 253; -0.108 ± 0.005 MPa) (Fig. 2c). During mid-May (DOY 140–146), mean weekly conditions included a soil water potential of -0.043 ± 0.008 MPa, air temperatures of $12.21 \pm 1.68^\circ\text{C}$, and soil temperatures of $12.8 \pm 0.34^\circ\text{C}$.

Results

Intra-annual wood formation

Cambial activity and tracheid development in both *P. sylvestris* and *J. communis* were closely linked to CT (Fig. 3). Increasing CT generally delayed the onset of cell differentiation phases (enlargement, wall thickening, and maturation) and shortened their duration (Table 2).

In *P. sylvestris*, cambial cell counts on 26 March (DOY 86) differed among CT classes, being highest in trees with low CT and progressively lower in the medium and high CT classes (Fig. 3a). In *P. sylvestris*, peak cambial cell numbers occurred earlier in trees with low CT (DOY 137, 4.3 ± 1.4 cells) than in those with medium (DOY 145, 3.4 ± 0.8 cells) and high CT (DOY 173, 2.5 ± 0.6 cells). Cambial cell number differed significantly among CT classes (ANOVA: $F(2, 54) = 36.82$, $p < 0.001$), and Bonferroni-adjusted pairwise comparisons indicated significant differences between all classes ($p \leq 0.001$). In *J. communis*, cambial cell counts on

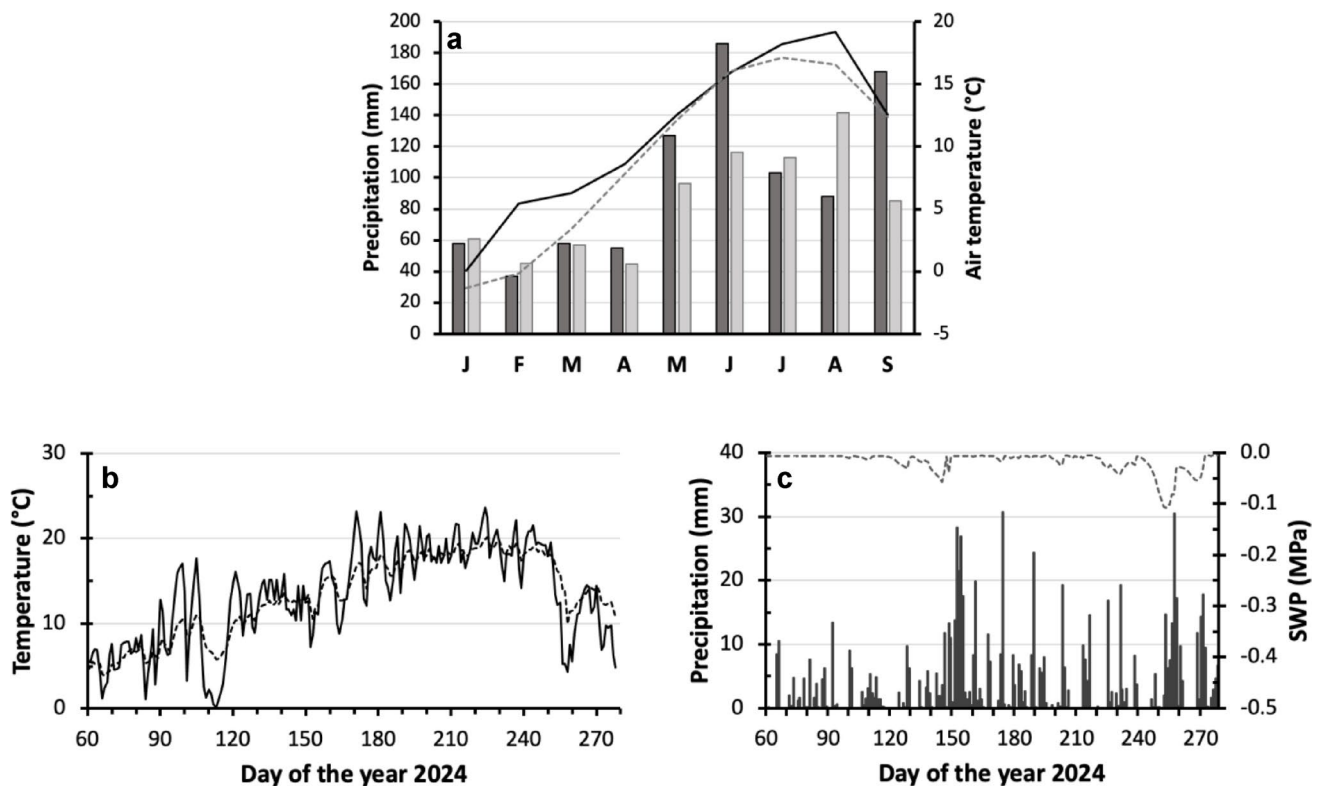


Fig. 2 Temporal patterns of climate variables recorded in the study area in 2024. **a** Comparison of monthly means in 2024 for precipitation (dark bars) and air temperature (solid line) with those of the reference period 1998–2022 (precipitation: light bars; air temperature: dashed

line). **b** Daily mean values of air temperature (solid line; measured at 10 m height) and soil temperature (dashed line; measured at 10 cm depth) in 2024. **c** Precipitation pattern in 2024 (dark bars) and corresponding dynamics of soil water potential (SWP; dashed line)

4 April (DOY 95) were generally lower, and differences among CT classes were less pronounced (Fig. 3b). In *J. communis*, peak cambial cell numbers occurred on DOY 158 in shrubs with low CT (2.8 ± 1.1 cells), DOY 128 in those with medium CT (2.2 ± 1.1 cells), and DOY 206 in shrubs with high CT (2.2 ± 1.1 cells). Nevertheless, a significant effect of CT on cambial cell production was detected (ANOVA: $F(2, 36) = 6.12$, $p < 0.01$). Post hoc comparisons revealed a significant difference between the low and high CT classes ($p < 0.01$), whereas differences involving the medium CT class were not statistically significant.

Radial enlargement in both *P. sylvestris* and *J. communis* started earlier in individuals with low and medium CT, whereas trees and shrubs in the high CT class showed a delay of 3–4 weeks (Table 2). The onset of cell enlargement in individuals with low and medium CT occurred between 6 April (DOY 97) in *P. sylvestris* and 19 April (DOY 110) in *J. communis*.

The duration of the enlargement phase decreased with increasing CT, by 42 days in *P. sylvestris* and 43 days in *J. communis* (low vs. high CT; $p < 0.05$). In addition, across corresponding CT classes, the enlargement phase lasted 9–38 days longer in *P. sylvestris* than in *J. communis*. A one-way ANOVA revealed a significant effect of CT on the dynamics

of cell production during the enlargement phase, as reflected by the number of enlarging cells recorded throughout the season (*P. sylvestris*: $F(2, 54) = 5.94$, $p < 0.001$; *J. communis*: $F(2, 36) = 3.92$, $p < 0.05$). Bonferroni-corrected post hoc tests showed significant differences between low and high CT classes (*P. sylvestris*: $p = 0.003$; *J. communis*: $p = 0.014$).

A similar pattern was observed for the wall thickening phase. In *P. sylvestris*, trees with low CT began wall thickening at the end of April (DOY 116), about five weeks earlier than trees with high CT (DOY 148), and the phase lasted with roughly six weeks significantly longer in trees with low CT (ANOVA: $F(2, 54) = 8.39$, $p < 0.001$). For *J. communis*, the wall thickening phase showed a similar trend, with statistically significant differences among low and high CT classes (ANOVA: $F(2, 36) = 3.71$, $p < 0.05$). Moreover, in *P. sylvestris* with low CT, wall thickening started c. two weeks earlier and lasted c. one month longer than in *J. communis* of the same CT class (Table 2).

The appearance of the first mature tracheids also varied with CT. In low-CT *P. sylvestris*, the first mature tracheids developed in late May (DOY 145), c. three weeks earlier than in conspecific individuals with high CT (DOY 161). In *J. communis*, mature xylem cells appeared even later, between early June in shrubs with low CT (DOY 159) and

Fig. 3 Cambial activity and tracheid development dynamics in *P. sylvestris* and *J. communis*. Cell counts (mean $\pm$ SD) are shown for **a–b** cambial cells, **c–d** enlargement, **e–f** wall thickening, and **g–h** maturation phases across CT classes: < 35% (solid line), 35–70% (dashed line), and > 70% (dotted line)

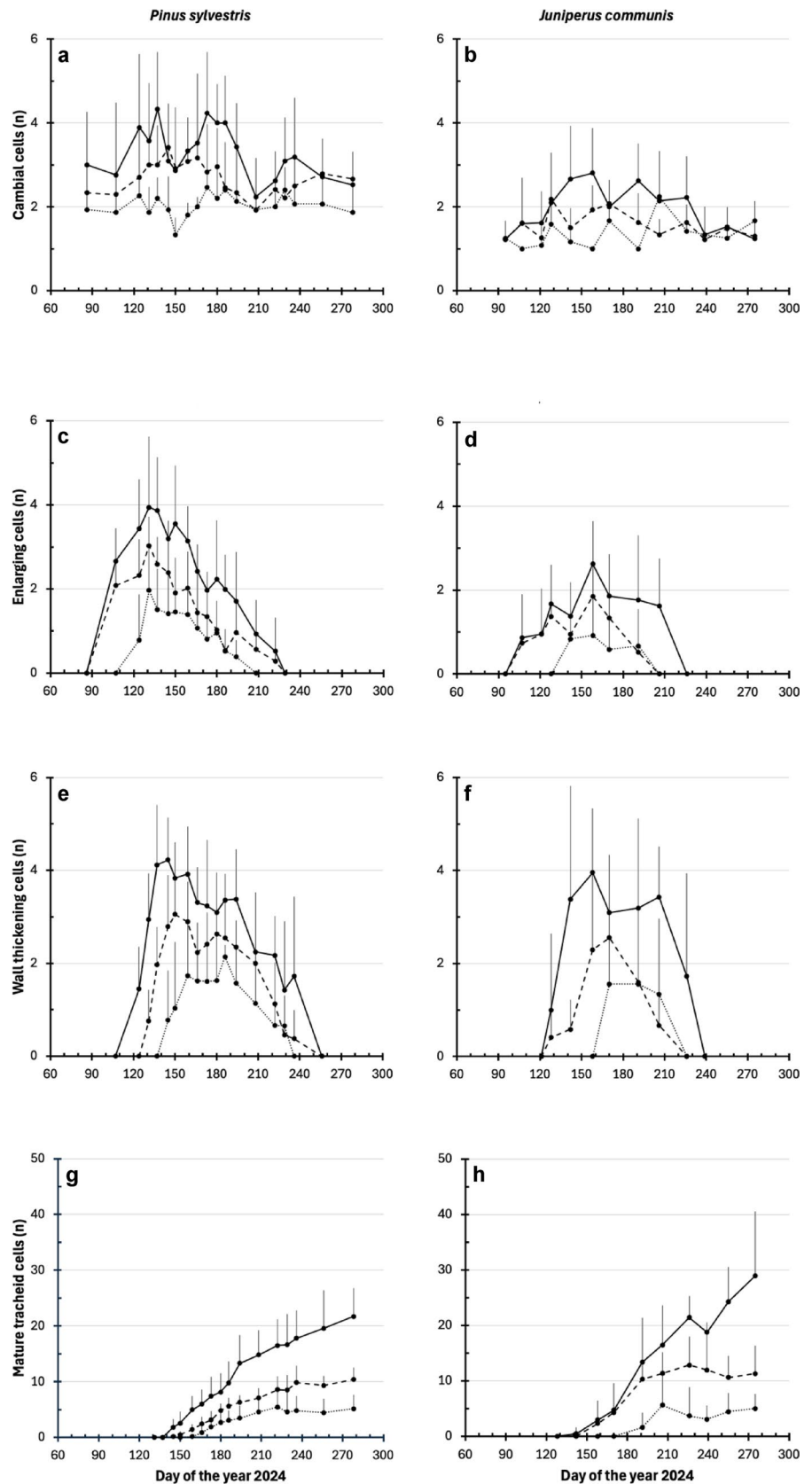
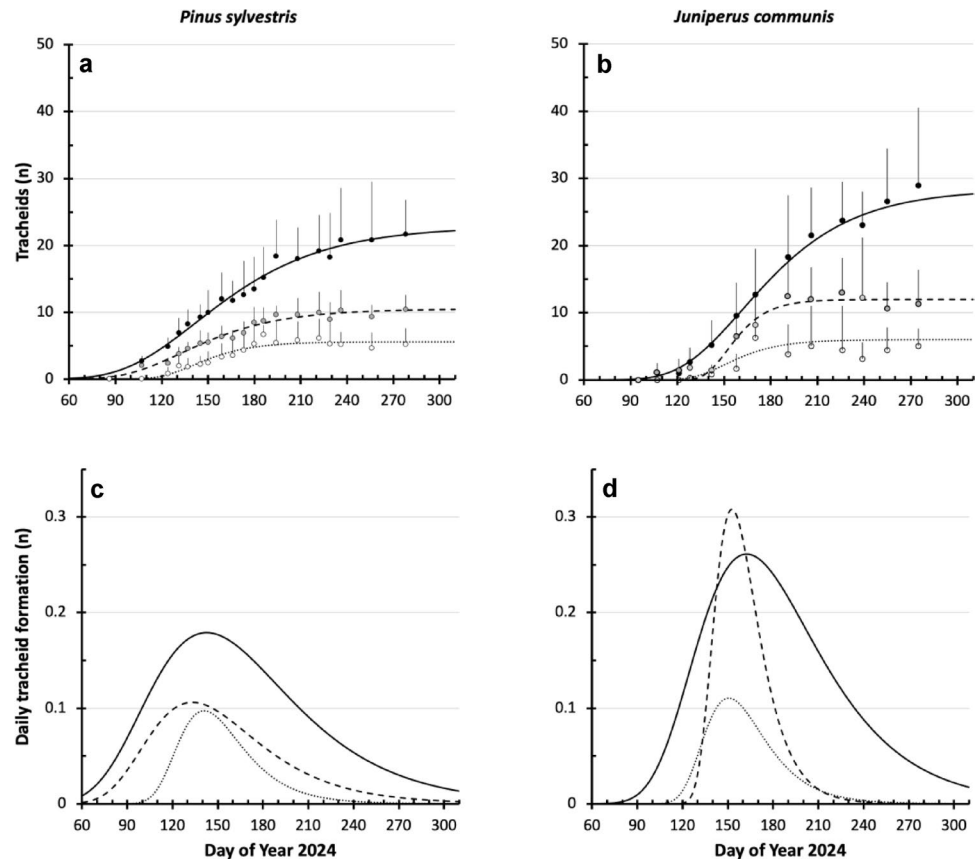


Table 2 Phenological timing of xylogenesis in 2024 for *P. sylvestris* and *J. communis* ($n=20$ per species) across three CT classes. The onset, end (DOY), and duration (days) of the main phases of tracheid development (cell enlargement, wall thickening, and maturation) are shown. Values represent means $\pm$ SD. Statistically significant intraspecific differences of mean values between CT classes are indicated by different letters ($p<0.05$; Bonferroni t-test)

	CT (%)	Cell enlargement			Wall thickening			Maturation		
		Onset	End	Duration	Onset	End	Duration	Onset	End	Duration
<i>P. sylvestris</i>	<35	97 $\pm$ 0 ^a	216 $\pm$ 10 ^a	119 $\pm$ 10 ^a	116 $\pm$ 0 ^a	239 $\pm$ 8 ^a	124 $\pm$ 8 ^a	145 $\pm$ 6 ^a	267 $\pm$ 0 ^a	122 $\pm$ 6 ^a
	35–70	97 $\pm$ 0 ^a	209 $\pm$ 17 ^{ab}	113 $\pm$ 17 ^{ab}	131 $\pm$ 3 ^b	235 $\pm$ 10 ^a	104 $\pm$ 14 ^{ab}	155 $\pm$ 11 ^a	251 $\pm$ 9 ^{ab}	96 $\pm$ 20 ^{ab}
	>70	122 $\pm$ 6 ^b	198 $\pm$ 5 ^b	77 $\pm$ 11 ^b	148 $\pm$ 7 ^b	229 $\pm$ 4 ^a	81 $\pm$ 10 ^b	161 $\pm$ 3 ^b	233 $\pm$ 0 ^b	72 $\pm$ 3 ^b
<i>J. communis</i>	<35	106 $\pm$ 9 ^a	216 $\pm$ 0 ^a	110 $\pm$ 9 ^a	133 $\pm$ 9 ^a	225 $\pm$ 8 ^a	93 $\pm$ 17 ^a	159 $\pm$ 19 ^a	241 $\pm$ 7 ^a	82 $\pm$ 26 ^a
	35–70	110 $\pm$ 13 ^a	185 $\pm$ 11 ^b	75 $\pm$ 24 ^{ab}	138 $\pm$ 14 ^a	207 $\pm$ 17 ^b	69 $\pm$ 31 ^{ab}	160 $\pm$ 10 ^a	225 $\pm$ 17 ^b	65 $\pm$ 26 ^{ab}
	>70	132 $\pm$ 5 ^b	199 $\pm$ 0 ^b	67 $\pm$ 5 ^b	164 $\pm$ 0 ^b	204 $\pm$ 8 ^b	40 $\pm$ 8 ^b	192 $\pm$ 29 ^b	222 $\pm$ 8 ^b	29 $\pm$ 37 ^b

Fig. 4 Seasonal tracheid development modeled by Gompertz function. **a–b** Total cell number (enlarging, wall thickening, mature cells) shown as fitted curves: solid (CT<35%), dashed (CT 35–70%), dotted (CT>70%). Observed means $\pm$ SD as black, grey, and open circles. **c–d** Modeled daily tracheid production rates with matching line styles



early July (DOY 192) in individuals with high CT (Table 2). One-way ANOVA confirmed a significant effect of CT on the timing of maturation in *P. sylvestris* (ANOVA: $F(2, 54)=7.70$, $p<0.01$) and in *J. communis* ANOVA: $F(2, 36)=4.25$, $p<0.05$).

Consistent with these phenological patterns, both annual ring widths (Online Resource 1) and total tracheid production (Fig. 4a) differed significantly among CT classes in *P. sylvestris* (ring width: ANOVA, $F(2, 54)=25.93$, $p<0.001$; tracheid number: $F(2, 54)=22.19$, $p<0.001$). Bonferroni-corrected post hoc tests confirmed highly significant differences between all pairwise comparisons ($p<0.001$). In *J. communis*, significant differences for ring width (Online Resource 1) and xylem cell production (Fig. 4b) were

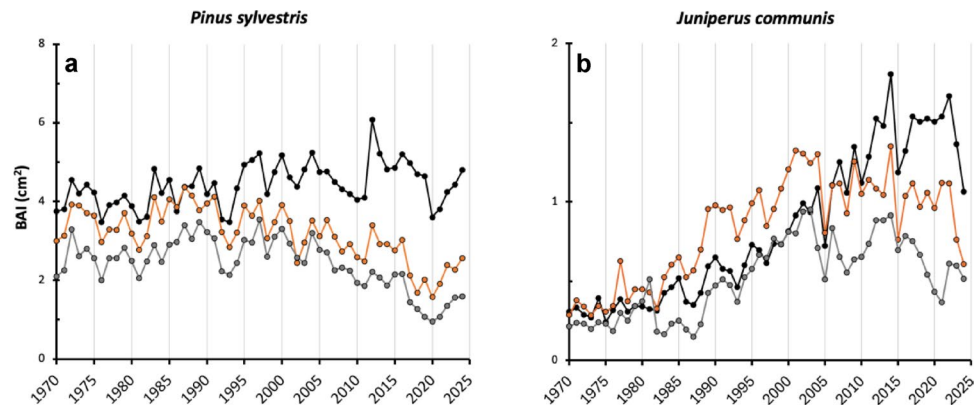
detected between shrubs with high CT and those in the low and medium CT classes (ring width: $F(2, 36)=8.26$, $p<0.01$; tracheid number: $F(2, 36)=7.21$, $p<0.01$). Both pairwise comparisons showed significance at $p<0.01$.

Gompertz modelling further revealed species-specific differences in intra-annual growth dynamics (Table 3; Fig. 4c–d). In *P. sylvestris*, the timing of maximum growth rate (inflection point) occurred between 12 and 21 May, c. two to three weeks earlier than in *J. communis*, where it was recorded between 29 May and 10 June. In both species, the inflection point occurred later in individuals with low CT compared to those with high CT (*P. sylvestris*: DOY 142 vs. DOY 140; *J. communis*: DOY 162 vs. DOY 150). During the two-week period surrounding the inflection point,

Table 3 Gompertz function parameters of tracheid development in *P. sylvestris* and *J. communis* ($n=20$ per species) across three CT classes. Displayed are the Gompertz parameters: the upper asymptote (a , cell number), the growth rate (k), the inflection point (lp , DOY), and cell production during the two-week period surrounding the inflection point (cells lp , n). Values represent means $\pm$ SD. The coefficient of determination (R^2) indicates model fit

	CT [%]	a	k	lp	cells lp	R^2
<i>P. sylvestris</i>	<35	23 $\pm$ 0.9	0.021 $\pm$ 0.002	142 $\pm$ 2.6	2.7	0.983
	35–70	10 $\pm$ 0.4	0.028 $\pm$ 0.003	133 $\pm$ 2.5	1.6	0.967
	>70	6 $\pm$ 0.3	0.047 $\pm$ 0.011	140 $\pm$ 3.2	1.4	0.909
<i>J. communis</i>	<35	28 $\pm$ 2.3	0.025 $\pm$ 0.005	162 $\pm$ 5.6	3.9	0.967
	35–70	12 $\pm$ 0.5	0.070 $\pm$ 0.019	152 $\pm$ 2.9	4.4	0.956
	>70	6 $\pm$ 0	0.050 $\pm$ 0.025	150 $\pm$ 12	1.6	0.679

Fig. 5 Basal area increments (BAI) of **a** *P. sylvestris* and **b** *J. communis* from 1970 to 2024, grouped by CT: low (black), medium (brown), and high (grey)



cell production decreased with increasing CT in both species (see Table 3 for values). By contrast, the Gompertz-derived growth rate (k), which describes how quickly the system approaches its maximum cell number, was higher in individuals with high CT than in those with low CT. This indicates that although high-CT individuals produce fewer tracheids overall, their cell production progresses more steeply toward the lower asymptote, whereas low-CT individuals accumulate more cells but approach a higher asymptote more gradually (Fig. 4c–d).

Climate–growth relationships across CT classes

To evaluate how CT modulates climate sensitivity of radial growth, we combined long-term records of basal area increments (BAI 1970–2024; Fig. 5) with intra-annual data (2024) on tracheid production in *P. sylvestris* and *J. communis*. In *P. sylvestris*, BAI followed similar interannual patterns across all CT classes, with pronounced declines observed in 1971, 1976, 1981, 1984, 1993, 1998, 2002, 2011, 2014, and 2020 (Fig. 5a). Trees in the high CT class consistently exhibited lower BAI than those in the low or medium CT classes. One-way ANOVA revealed significant differences among CT classes ($F(2, 162)=143.99$, $p<0.001$), with mean values ($\pm$ SE) of 4.41 ± 0.07 , 3.19 ± 0.09 , and 2.43 ± 0.09 cm² for the low, medium, and high CT classes, respectively. All pairwise comparisons were statistically significant ($p<0.001$). In *J. communis*, overall BAI was markedly lower than in *P.*

sylvestris. Synchronous growth reductions were observed in *J. communis* in 1993, 2005, 2015, and 2024 in all CT-classes (Fig. 5b). ANOVA confirmed significant effects among CT classes ($F(2, 162)=14.25$, $p<0.001$), with mean values ($\pm$ SE) of 0.83 ± 0.06 , 0.83 ± 0.04 , and 0.52 ± 0.03 cm² for the low, medium, and high CT classes, respectively. Pairwise comparisons showed no difference between low and medium CT shrubs ($p=0.926$), but significantly lower BAI in shrubs with high CT ($p<0.001$).

Climate–growth relationships were analysed at both long-term (ring width data 1971–2022) and intra-annual (cell production rates in 2024) scales. In *P. sylvestris*, long-term growth, i.e. ring width 1971–2022, was positively correlated with April–June precipitation (CT<35%: $r=0.29$, $p<0.05$; CT 35–70%: $r=0.42$; CT>70%: $r=0.35$; both: $p<0.01$) and negatively associated with June–August air temperatures in high CT trees ($r=-0.61$, $p<0.001$). Cell production rates in 2024 (April–August) also revealed temperature-driven responses (Fig. 6a): air temperature (CT<35%: $r=-0.59$, $p<0.01$; CT 35–70%: $r=-0.73$, $p<0.001$; CT>70%: $r=-0.45$, $p<0.05$) and soil temperature (CT<35%: $r=-0.73$; CT 35–70%: $r=-0.87$; both $p<0.001$; CT>70%: $r=-0.60$, $p<0.01$).

By contrast, in *J. communis* cell production rates 2024 were influenced by precipitation (CT<35%: $r=0.49$, $p<0.05$; CT 35–70%: $r=0.65$, $p<0.01$; CT>70%: $r=0.54$, $p<0.05$) (Fig. 6b). For long-term growth (tree ring width 1971–2022), no significant correlations were found between

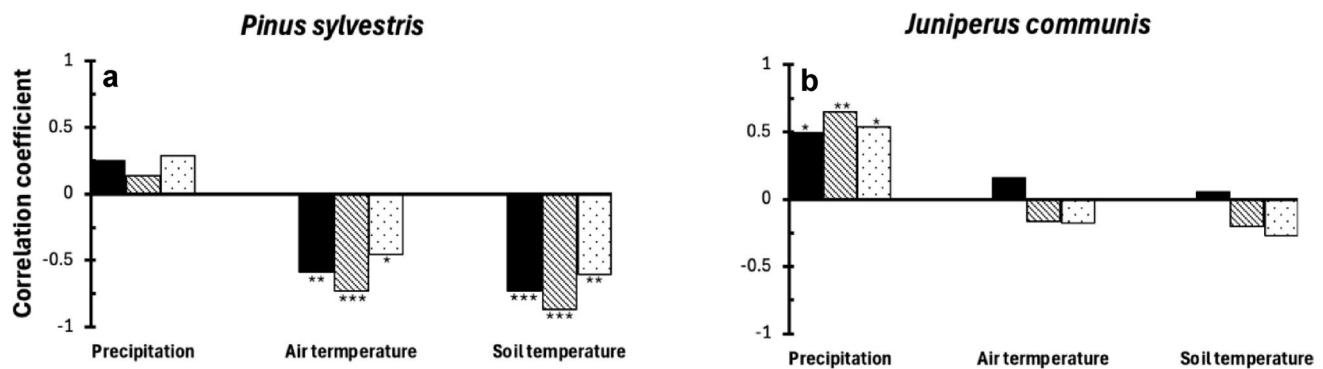


Fig. 6 Pearson correlation coefficients (April–August 2024) between environmental variables (i.e. precipitation [7-day sum] and air and soil temperatures [7-day means]) and tracheid growth rates [7-day sum] in *P. sylvestris* and *J. communis* across 19 sampling dates and three

CT classes: CT < 35% (black bars), CT 35–70% (hatched bars), and CT > 70% (dotted bars). Statistical significance is indicated by $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***)

ring width and the investigated climate variables (precipitation and air temperature).

Discussion

Using repeated microcoreg at high temporal resolution throughout the 2024 growing season, this study provides the first empirical evidence that CT exerts a significant influence on wood formation and the timing and duration of xylogenesis in *P. sylvestris* and *J. communis*. Our findings support the hypothesis that increasing CT is consistently associated with reduced wood production and a shortened duration of xylem development (Fig. 3; Table 2). Despite these clear differences in CT-dependent growth performance, *P. sylvestris* exhibited largely synchronized inter-annual growth patterns in BAI (1970–2024) across CT classes (Fig. 5a), suggesting a strong overriding control by climatic drivers (Gruber et al. 2010; Oberhuber et al. 2014; Oberhuber 2017). In contrast, long-term growth patterns in *J. communis* showed higher individual variability (Fig. 5b) and weaker climatic coupling, likely reflecting species-specific differences in hydraulic regulation. These contrasting responses align with known physiological strategies (West et al. 2008): *P. sylvestris* follows a predominantly isohydric strategy, characterized by early stomatal closure under water stress, minimizing xylem embolism and facilitating hydraulic recovery. *J. communis*, in contrast, exhibits a more anisohydric behavior, maintaining stomatal conductance longer during drought, thereby supporting short-term carbon assimilation but increasing the risk of hydraulic failure (Zweifel et al. 2009; West et al. 2008). These differing water-use strategies likely underpin the observed CT-dependent growth responses and may contribute to differences in growth resilience between *P. sylvestris* and *J. communis*.

In both species, individuals with high CT exhibited reduced cambial activity and fewer cambial cells, resulting in decreased wood increment (Fig. 3; Table 2). This observation corroborates earlier findings in *Picea abies* and *Abies alba* (Fink 1986) and highlights the functional coupling between CT, cambial dynamics, and xylem production. In individuals with low CT, tracheid formation extended from April to August in both species, aligning with previous findings on *P. sylvestris* (Gruber et al. 2010; Swidrak et al. 2014). In *J. communis*, however, the onset of radial enlargement was delayed by roughly one week (Fig. 3c–d; Table 2), potentially reflecting higher thermal thresholds for dormancy release in this shrub species under increasingly mild winters (Li et al. 2023). Climate records for the 2024 growing season show that air temperatures during January and February exceeded long-term means, while soil temperatures remained above freezing (Fig. 2a). Although soil moisture remained adequate for most of the season 2024, a transient decline in soil water potential occurred in mid-May (DOY 140–146) (Fig. 2c), coinciding with a temporary reduction in enlarging cells in both species (Fig. 3c–d), suggesting a direct influence of plant water status on radial cell expansion. This interpretation is consistent with the well-established dependence of cell enlargement on water availability and turgor maintenance (Cosgrove 2000; Koch 2004; Rathgeber et al. 2022).

In both species, individuals with low CT initiated radial enlargement 3–4 weeks earlier, maintained it for c. 40 days longer, and reached the growth inflection point about 10 days later in the season than those with high CT (Fig. 4c–d; Table 3). Consistently, in both *P. sylvestris* and *J. communis*, the duration of secondary wall development and tracheid maturation also differed significantly between low and high CT classes (Table 2), suggesting that CT influences multiple stages of xylem formation.

Tracheid production rates and total cell numbers differed significantly between CT classes (Fig. 4a–b; Table 3), mirroring patterns observed in annual ring width and basal area increment (Online Resource 1, Fig. 5). In both species, these metrics declined with increasing CT, consistent with the well-established relationship between CT, needle biomass, and stem growth reported for several conifers, including *P. sylvestris*, *P. halepensis*, and *A. alba* (Eilmann et al. 2013; Camarero et al. 2015). Accordingly, reduced foliar area likely limits both carbon assimilation and the carbohydrate supply available for cambial activity, thereby constraining wood formation.

Long-term climate-growth correlations (1971–2022) indicate that *P. sylvestris* is particularly sensitive to spring precipitation (April–June), highlighting the importance of precipitation at the start of the growing season. This pattern was consistent across all CT classes and aligns with previous studies emphasizing the role of early-season water supply for xylem formation in continental environments (Oberhuber et al. 2014; Oberhuber 2017). In contrast, high summer temperatures (June–August) disproportionately affected trees with high CT, likely reflecting increased vulnerability to water and carbon limitations (Eilmann et al. 2012; Camarero et al. 2015). During the unusually warm conditions of 2024 (Fig. 2a), growth responses in *P. sylvestris* were more closely associated with temperature, particularly soil temperature (Fig. 6). Such patterns are consistent with evidence that xylogenesis in conifers operates within relatively narrow thermal limits, with elevated soil temperatures potentially constraining root activity, water uptake, and radial cell expansion (Pregitzer et al. 2000; Rossi et al. 2007; Körner 2015).

In *J. communis*, tracheid production during the 2024 growing season was significantly correlated with weekly precipitation but not with air or soil temperature. This suggests that short-term fluctuations in water availability exerted a stronger control on intra-annual wood formation than thermal conditions. Even in generally moist years, precipitation events can temporarily enhance soil water availability and plant water status, thereby promoting radial cell expansion, which is known to be highly sensitive to turgor conditions (Cosgrove 2000; Rathgeber et al. 2022). Similar precipitation-driven responses have been reported for several *Juniperus* species, where growth and physiological activity are closely linked to changes in soil moisture following rainfall events (DeSoto et al. 2014; García-Fórner et al. 2016; Guo et al. 2024).

Overall, our findings highlight that CT is closely linked to the intra-annual dynamics of wood formation in both *P. sylvestris* and *J. communis*. The consistent reduction in cambial activity and tracheid production observed in individuals

with higher CT underscores the tight coupling between CT and xylogenesis.

Conclusion

This study provides empirical evidence that CT is associated with intra-annual wood formation dynamics in both *P. sylvestris* and *J. communis*, influencing cambial activity, the onset and duration of xylogenesis, tracheid production and radial increment. By combining intra-annual analyses of wood formation with long-term radial growth, our results underscore the importance of CT for growth performance.

The observed species-specific responses suggest that differences in hydraulic regulation and environmental sensitivity may modulate how increasing CT translates into reduced radial growth and altered temporal dynamics of wood formation. Future research that integrates longer observation periods and physiological measurements including determination of non-structural carbohydrate concentrations in needles and the stem could clarify how CT interacts with climatic stress to shape growth responses under ongoing climate change.

Acknowledgments Special thanks go to Tatjana Dietrich, Tamara Heinzle, Juliane Siebold, Tugba Dogan, Derya Ugur for support in field work and to Albin Hammerle for providing climate data. This research was funded in whole by the Austrian Science Fund (FWF), project “The Future of Mountain Forests”, grant-doi 10.55776/DOC171. For the purpose of Open Access, the author has applied a CC BY public copyright license to any Author Accepted Manuscript (AAM) version arising from this submission.

Author Contribution M.F. and W.O. conceived and designed the study. M.F. coordinated the project, collected the samples, implemented preparation methods, conducted data collection, processing and analysis. M.F. and W.O. jointly interpreted and discussed the data. M.F. wrote the manuscript, and W.O. provided editorial input. S.M. was responsible for funding acquisition and project administration. All authors read and approved the final version of the manuscript.

Funding Open access funding provided by University of Innsbruck and Medical University of Innsbruck. This research was funded in whole by the Austrian Science Fund (FWF), project “The Future of Mountain Forests”, grant-doi 10.55776/DOC171. For the purpose of Open Access, the author has applied a CC BY public copyright license to any Author Accepted Manuscript (AAM) version arising from this submission.

Data availability The data underlying this article are available in Zenodo at <https://doi.org/10.5281/zenodo.20200619>.

Declaration

Conflict of interest The authors declare no conflict of interest.

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