



Consistent summer temperature signals in a latewood blue intensity network from the upper tree line in the Caucasus

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ABSTRACT

Climate variability in the Caucasus region significantly influences tree growth in alpine tree line ecotones. However, long-standing human land-use history disrupted the natural equilibrium between montane forests and alpine meadows. These complex vegetation dynamics may cause traditional proxies such as tree-ring width (TRW) to display a weak climate signal, limiting their utility for understanding growth-climate relationships. To address these challenges, we established a multispecies network of seven tree ring width index (TRWI) and seven latewood blue intensity (LWBI) chronologies from three coniferous species (*Picea orientalis*, *Abies nordmanniana* and *Pinus sylvestris*) at current tree line sites (1900–2300 masl) in the Greater and Lesser Caucasus. Our results show that almost all the LWBI site chronologies demonstrate consistent and stable correlation with summer temperature (June–August). In contrast, corresponding TRWI chronologies reveal much weaker correlations with temperature, mainly with previous winter and spring. TRWI moderately responds to precipitation during the summer (JJA) while LWBI does not show any significant response to precipitation. The weaker and less consistent temperature signals in TRWI chronologies suggest additional influence of precipitation, non-climatic factors and local disturbance events on TRWI. Principal component analysis reveals a robust common signal in the LWBI network. First principal components from both proxies correlate with summer temperatures, although correlation is much higher for LWBI than for TRWI. The stable and consistent relationship between LWBI and summer temperature in different frequency domains indicates high potential of this proxy for annually resolved climate reconstructions at a regional level, which would be new for the Lesser Caucasus region.

1. Introduction

The multiple alpine mountain ranges of the Greater and Lesser Caucasus feature extensive tree line ecotones characterized by diverse ecological and climatic conditions (Nakhutsrishvili et al., 2006; Nakhutsrishvili and Abdaladze, 2017). Tree line vegetation in the Caucasus has been significantly modified by human activities over the last few millennia which may overshadow the influence of climatic factors in shaping the ecological history (Connor and Kvavadze, 2009). In many places, the current upper tree lines are likely positioned lower than the thermal minimum for tree growth (Dolukhanov, 1978; Holobâcă et al.,

2016; Solomina et al., 2016). Natural regeneration processes at the tree line in the region are directly linked to reduced land-use activities since the collapse of the Soviet Union enabling forest tree species in some areas to advance spontaneously into currently treeless areas (Akobia et al., 2022; Buchner et al., 2020; Hansen et al., 2018; Theissen et al., 2022). At the same time, global warming is reshaping thermal limitations and distribution limits of trees in the Caucasus region (Akobia et al., 2022), resulting in notable changes in tree growth (Akotov, 2009) and vegetation phenology (Karnieli et al., 2019). Although reduced human activities and land use changes have contributed to forest expansion in the Caucasus, it is unclear to which extent tree growth in

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these sensitive tree line environments is controlled by climatic factors, especially temperature.

Studies on Tree-ring width (TRW) data from the Lesser and Greater Caucasus have highlighted that temperature is limiting, but not the only factor influencing radial growth at higher elevations (Doğan and Köse, 2019; Dolgova, 2016; Holobacă et al., 2016; Martin-Benito et al., 2018). Overall, spring and summer droughts appeared to be more important limiting factors for tree growth, particularly with decreasing elevation. At some tree line sites in the Caucasus, summer temperature correlates moderately with TRW chronologies (Martin-Benito et al., 2018). A potential reason for weak correlations with temperature even at high-elevation sites could be the lack of thermal controls on tree growth at potentially anthropogenically lowered tree lines. However, growth disturbances that strongly impact tree growth may additionally impede the detection of climate signals (Frank and Esper, 2005; Jiang et al., 2022; Rydval et al., 2018). For *Picea orientalis* and high-elevation *Pinus sylvestris* TRW chronologies a notable decrease in seasonal temperature response has been observed under global warming (Martin-Benito et al., 2018).

In undisturbed open-canopy tree line ecotones with limited competition TRW is expected to respond positively to the increasing temperature trend associated with global warming (Cook, 1995). This has been shown for sites in the White Mountains of California (Salzer et al., 2009), the Andes (Brand et al., 2022; Gibson-Carpintero et al., 2022), the Carpathian (Schurman et al., 2019), the Eastern Qinling Mountains (Yuan et al., 2024), the Himalaya (Ali et al., 2022) and the Tibetan plateau (Shi et al., 2015). In some cases, TRW at upper tree lines does not increase with global warming due to decreased temperature limitation and related competition (Martinez del Castillo et al., 2022; Salzer et al., 2014; Treml and Veblen, 2017), increased moisture limitation (Diego Galván et al., 2015; Fajardo et al., 2019; Lu et al., 2021; Millar et al., 2020; Sigdel et al., 2018) and other stressors such as bark beetles (Kharuk et al., 2021), fire as well as grazing (Johansson and Granström, 2020; Wang et al., 2019). These studies emphasize that growth responses at tree lines are highly diverse and increasing temperatures may not always result in positive effects on TRW. To address these limitations, researchers have increasingly turned to wood density-related proxies, such as Maximum Latewood Density (MXD) and Latewood Blue Intensity (LWBI) which are less affected by precipitation and help to minimize other, non-climatic influences on tree growth.

MXD offers a significant advantage over TRW due to a stronger summer temperature signal in tree line ecotones (Esper et al., 2015; Hartl et al., 2022; Schneider et al., 2015) and reduced sensitivity to ecological disturbances (Kunz et al., 2023). Latewood Blue Intensity (LWBI) is a cost-effective alternative to MXD which is based on inverted light reflectance of wood in the blue part of the visible spectrum (Björklund et al., 2024; Rydval et al., 2014). Light reflectance depends on wood density and, thus, MXD and LWBI values are highly correlated (Björklund et al., 2024). Like MXD, LWBI is mainly measured for coniferous species due to the empirical success of such measurements which may be related to their less complex wood anatomy compared to angiosperms (Björklund et al., 2024). Latewood density reflects the physiological processes of cell expansion, cell-wall thickening and lignification which are typically directly temperature driven, responds to growth conditions during the current growing season (Rydval et al., 2014). In contrast, TRW depends on cell production ratios (cell numbers) and cell-enlargement, which are influenced by multiple environmental factors like temperature, precipitation or competition, which are difficult to disentangle (Björklund et al., 2017; Rathgeber, 2017; Rathgeber et al., 2016). TRW and particularly earlywood, strongly depends on resources stored from the previous year (Rathgeber, 2017). LWBI has consistently shown its response to summer temperature in cold limited environments in the Northern Hemisphere making it a reliable proxy to understand past temperature changes (Björklund et al., 2015; Davi et al., 2021; Dolgova, 2016; Jiang et al., 2022; Kaczka and Wilson, 2021; Rydval et al., 2018).

For the Caucasus region, two local temperature reconstructions based on LWBI have been developed (Bakhtiyorov et al., 2025; Dolgova, 2016). Extending the LWBI network to additional tree line sites across the Caucasus, encompassing diverse microclimates and tree species (Alexander et al., 2019), will enhance our understanding of historical climate change contextualizing projected future climates.

Here we present a multispecies network of two tree ring proxies (TRWI and LWBI) comprised of samples from seven tree line sites across the Caucasus region. The network focuses on mature stands of conifers in open and semi-open canopy, high-elevation forests to enhance the strength of the recorded climate signals. We analyze the relationship between different growth chronologies, evaluate their shared variability and test the correlation with different climate parameters, seasons, frequencies and time periods between 1902 and 2014. The results will elucidate to which degree tree growth at upper tree lines is limited by temperature despite human impacts on tree line ecotones and evaluate the potential of this multi-species and multiproxy network to develop multi centennial temperature reconstruction.

2. Material and methods

2.1. Study area

The Caucasus region, located between the Black Sea and the Caspian Sea, covers diverse climatic conditions due to its complex topography including the Lesser and Greater Caucasus Mountain ranges (Fig. 1a). Particularly the Lesser Caucasus, which stretches from southwestern Georgia and northeastern Turkey to southwestern Azerbaijan, is dominated by a steep precipitation gradient from the northwest to the southeast: the very western regions experience a humid subtropical climate dominated by temperate rainforests, while the eastern regions are characterized by a dry subtropical climate and steppe vegetation (Shahgedanova, 2003). The Greater Caucasus features a predominantly continental climate. In these areas, the highlands are cool and humid, sometimes reaching alpine conditions, while the mid-elevations are warm and humid, and the plains are hot and dry (Shahgedanova, 2003).

2.2. Climate data

To describe local climate, we utilized the CRU TS 4.08 dataset with gridded monthly mean temperature and precipitation (Harris et al., 2020). We extracted grid cells nearest to each sampling site from the 0.5° x 0.5° grid. Differences in the seasonal temperature and precipitation course are related to average grid elevation (Fig. S1), which has a wider spread than the elevation of sampling sites. The northern part of the Lesser Caucasus appears to receive more rainfall in winter months (Fig. S1). All other sites report a precipitation maximum during late spring/early summer. The southern-most site (Grid 2) receives less rainfall than the others. In the Greater Caucasus higher precipitation sums result from the high altitudes of the mountain ranges. Despite these differences in absolute values and the seasonal course, we found high agreement of year-to-year variability (Fig. S2) of climate anomalies from the different grid cells and therefore averaged the climate data for growth climate relationship over the entire study region (N 41–43°, E 42–43°) for the period 1902–2014.

We used linear regression analyses to estimate trends in temperature and precipitation data for the first and second half of the observational period (1902–1957 and 1958–2014). Summer temperature shows a significant positive trend for pre-1957 (+0.10°C/decade, $p < 0.05$) and post-1957 (+0.27°C/decade, $p < 0.001$) (Fig. 1b). Winter temperature increases too, but this trend is not statistically significant for pre- and post-1957. Regarding precipitation, only the winter season shows a significant trend during the pre-1957 period (+0.34 mm/year, $p < 0.05$).

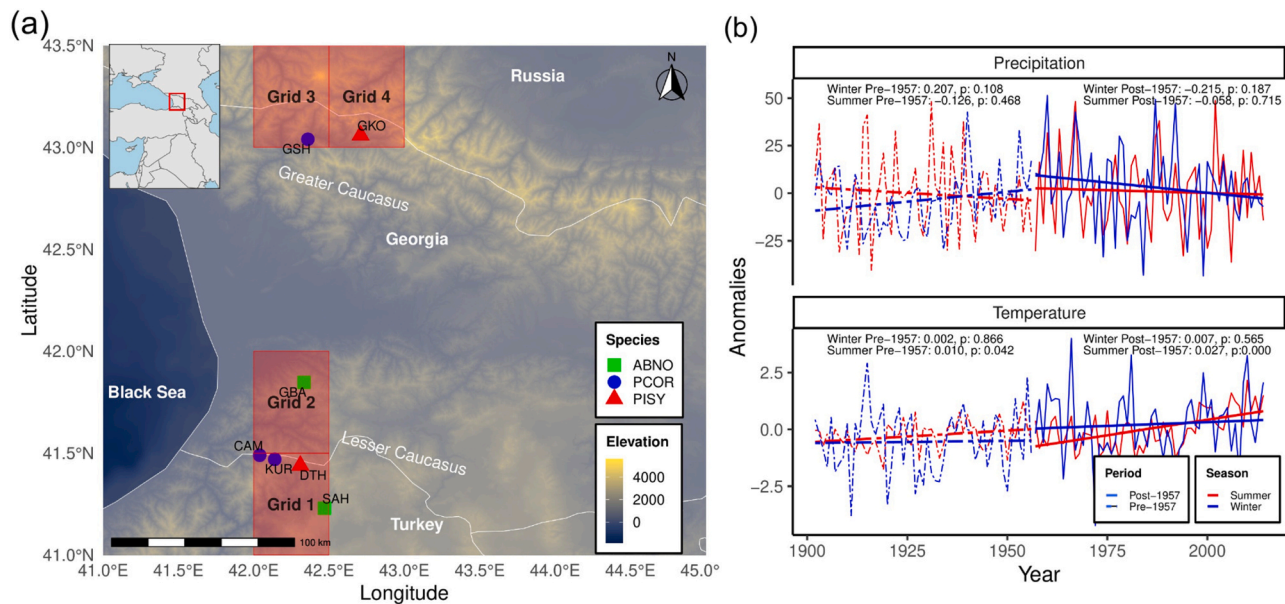


Fig. 1. Study area and regional climate change (a) Map of the study region. Reference tree-ring sites are marked with different shapes and colour to represent species; *Abies nordmanniana* (ABNO), *Picea orientalis* (PCOR), and *Pinus sylvestris* (PISY). Nearest CRU grid points used in the study are represented by red shaded polygons. (b) Time-series of precipitation and temperature anomalies for pre-1957 and post-1957 period. Anomalies are calculated with respect to the 1902–2014 period and averaged for all the CRU grids. The trend analysis results, represented by the slope followed by the p-values are displayed in their respective panels. Units are mm/year and °C/year, respectively.

2.3. Tree-ring sites

We collected tree core samples from two sites in the Greater Caucasus (GSH and GKO) and two sites in the Lesser Caucasus (DTH and GBA) to produce a high-elevation tree-ring network with 4 TRW and 4

LWBI chronologies. At each site we sampled 12–56 trees with one to two cores per tree oriented perpendicular to the slope. In addition, 3 new LWBI chronologies were established for three sites in the Lesser Caucasus that had been sampled previously (Martin-Benito et al., 2018). In total, the collection included 154 trees (224 cores) sampled from 7 sites.

Table 1
Chronology statistics for the studied sites and species.

Site name	Species	Coordinates		Elevation (m a. s.l.)	Chronology period	Number of samples (Cores/trees)		R	AC1	EPS (from 1875)	Data source
		Latitude	Longitude								
SAH	ABNO	41.23	42.47	2000–2100	1739–2014	24 (17)	SAH _{TRWI}	0.437	0.79	0.86	(Martin-Benito et al., 2018)
						23 (16)	SAH _{LWBI}	0.418	0.687	0.80	present study
DTH	PISY	41.44	42.31	2300	1613–2022	68 (56)	DTH _{TRWI}	0.519	0.8	0.95	(Martin-Benito et al., 2018)+
						51 (33)	DTH _{LWBI}	0.48	0.65	0.91	present study
KUR	PCOR	41.47	42.14	2075	1696–2014	20 (17)	KUR _{TRWI}	0.65	0.82	0.92	(Martin-Benito et al., 2018)
						20 (17)	KUR _{LWBI}	0.42	0.62	0.94	present study
CAM	PCOR	41.49	42.04	1930	1588–2014	31 (24)	CAM _{TRWI}	0.49	0.84	0.92	(Martin-Benito et al., 2018)
						28 (22)	CAM _{LWBI}	0.43	0.41	0.87	present study
GBA	ABNO	41.84	42.33	1980	1594–2022	30 (26)	GBA _{TRWI}	0.56	0.83	0.91	present study
						26 (23)	GBA _{LWBI}	0.37	0.68	0.76	
GSH	PCOR	43.04	42.36	2200	1716–2022	19 (12)	GSH _{TRWI}	0.54	0.88	0.83	present study
						19 (12)	GSH _{LWBI}	0.42	0.68	0.82	
GKO	PISY	43.06	42.71	2100	1873–2022	32 (19)	GKO _{TRWI}	0.52	0.89	0.93	present study
						31 (19)	GKO _{LWBI}	0.39	0.65	0.79	

Abbreviations: TRWI-Tree Ring width index, LWBI- Latewood Blue intensity, PCOR- *Picea orientalis*, ABNO- *Abies nordmanniana*, PISY- *Pinus sylvestris*, NS-Number of series, $\bar{R}$ - Mean interseries correlation, AC1-First order autocorrelation, EPS- Expressed population signal

The network is comprised of the most common coniferous tree species in the region: *Abies nordmanniana*, *Pinus sylvestris* and *Picea orientalis* (Fig. 1a, Table 1). *Pinus sylvestris* sites are characterized by open canopy stands on drier, south facing slopes. *Pinus orientalis* and *Abies nordmanniana* were growing in open forests with groups of individuals or closed-canopy forests with gaps (Martin-Benito et al., 2018). All the samples were collected from tree line sites located at elevations ranging from 1930 to 2300 masl. The site selection was focused on old-grown forests and resulting chronologies covered 149–429 years. Except for the GKO site, all chronologies in the network exceed 250 years, with the longest spanning 428 years at the GBA site (*Abies nordmanniana*, 1594–2022) followed by the CAM site (*Picea orientalis*, 1588–2014) and the DTH site (*Pinus sylvestris*, 1613–2022; Table 1).

2.4. Development of TRWI and LWBI chronologies

The collected tree cores were immersed in a 99.5 % acetone solution for 72 hours in order to remove resin and to reduce potential color transitions associated with the heartwood-sapwood boundary (Rydval et al., 2014). Once removed from the acetone, the cores were air-dried, sanded and scanned using an Epson Expression 12000XL scanner with the Silverfast software at a resolution of 2400 dpi. The scanned images of each core were imported into the image analysis software Coorecorder 8.1 (Maxwell and Larsson, 2021) for ring-width measurements and cross dating. TRW was measured with a precision of 0.01 mm and the measured cores were visually cross-dated and verified using CDendro (Maxwell and Larsson, 2021) and COFECHA (Holmes, 1983). LWBI was derived from the 30 % darkest pixels in the latewood section of each ring. For each ring, a box was selected over the latewood area, with different frame settings depending on the width of the latewood avoiding damaged wood or cracks in the samples. We detrended individual TRW and LWBI series by subtraction of an age-dependent smoothing spline (ADP) with variance stabilization using the ARSTAN program (Cook and Holmes, 1999). Power transformation was applied to the TRW data (Cook and Peters, 1997). All chronologies were calculated with the bi-weight robust mean of detrended measurement series to reduce the effects of outliers (Cook and Kairiukstis, 1990). In addition, raw measurements of TRW and LWBI were age-aligned and averaged to construct the regional growth curves (Helama et al., 2017). To quantify the quality of tree ring proxies over time, we calculated the following statistics: averaged pairwise inter-series correlation ($\bar{R}$), Expressed Population Signal (EPS) and first order auto-correlation (AC_1) (Wigley et al., 1984).

2.5. Statistical analysis

To analyze common variability over time and space among proxy time series from different sites and species in both TRWI and LWBI, a Principal Component Analysis (PCA) was performed for the common period 1873–2014. The relationship between both proxies and climate data (monthly mean temperature and precipitation) was tested for the period 1902–2014 using Pearson correlation analysis. To check the stability of correlation over time, we performed 31-year moving correlations between PC scores and climate data. To examine the tree growth/climate relationships at both long and short time-scales, we applied a 10-year moving average as a low-pass filter to smooth both tree ring proxies and climate data and to isolate long-term trends. The high-pass filtered component was derived by subtracting the low-pass filtered data from the original signal emphasizing the short-term fluctuations.

3. Results

3.1. Chronology strength

All the TRWI and LWBI chronologies retained variability at decadal

to multidecadal scales using the ADP detrending method (Fig. 2). The values of average inter-series correlation ($\bar{R}$) ranged from 0.43 to 0.65 for TRWI and from 0.37 to 0.48 for LWBI (Table 1). A higher $\bar{R}$ in TRWI data indicates a stronger common signal than in LWBI. The lower $\bar{R}$ resulted in lower EPS values for LWBI chronologies, because replication was identical (Table 1). However, the threshold of $EPS > 0.85$ was reached in both proxies, with typically a more recent cut-off for LWBI. Although EPS drops below 0.85 for 3 out of 14 chronologies already in the first half of the 20th century (Table 1), we used the overlapping period from 1873 to 2014 for comparison and subsequent analyses to avoid an extremely early truncation for some of the multi-centennial chronologies. The inter-site cross-correlation analysis revealed that all TRWI chronologies were positively correlated with each other, with correlation coefficients ranging from $r = 0.20$ ($p < 0.05$) to 0.58 ($p < 0.01$) (Fig. 3). In contrast, the cross-correlation among LWBI chronologies were notably high, with correlation coefficients ranging from $r = 0.20$ ($p < 0.05$) to 0.77 ($p < 0.01$) (Fig. 3). Sites in the Lesser Caucasus exhibit stronger correlations among TRWI chronologies than in the Greater Caucasus. The mean inter-site correlations were $r = 0.40$ for TRWI and $r = 0.52$ for LWBI demonstrating that LWBI shows higher consistency between sites compared to TRWI. Similarly, mean inter species correlation was lower for TRWI ($r = 0.38$, $p < 0.01$) compared to LWBI ($r = 0.51$, $p < 0.01$). Within species, fir LWBI chronologies from the sites SAH and GBA had the strongest correlation ($r = 0.67$, $p < 0.01$) with each other (Fig. 3). Only the LWBI chronologies from the KUR and GKO sites had low correlation with each other ($r = 0.20$, $p < 0.05$). TRWI chronologies had moderate to low, but significant positive correlations ($r = 0.19$ – 0.46) with LWBI chronologies (Fig. 3). Highest inter-proxy correlations (TRWI vs LWBI) were observed for DTH ($r = 0.46$, $p < 0.01$), GBA ($r = 0.42$, $p < 0.01$) and SAH ($r = 0.39$, $p < 0.01$), which were also the sites with highest inter-site correlations.

3.2. Variability in TRWI and LWBI chronologies over time and space

Regional curves showed stronger age effects on TRWI compared to LWBI indicating less age-related noise and lower impact of detrending on LWBI data (Fig. S3). The detrended site chronologies show similar amounts of low-frequency variability in TRWI and LWBI chronologies (Fig. 2). The PCA, performed separately for TRWI and LWBI chronologies for the common period (1873–2014), revealed very strong loadings on the first principal components (PCs). For TRWI, the first three PCs together captured a substantial portion of variance (74 %), with PC1 (hereafter PC1_{TRWI}) explaining 49 %, PC2 13 %, and PC3 11 % (Fig. 4a). For LWBI, a total of 79 % of variance was represented by PC1, PC2 and PC3 (hereafter PC1_{LWBI}) with 60 %, 11 % and 7 % variance explained, respectively (Fig. 4b). All the sites showed positive loadings on both proxies. Neither PC1, PC2 nor PC3 showed a clear loading pattern that could be attributed to the spatial proximity of sites or to certain species characteristics. We found a moderate, but significant, positive correlation ($r = 0.36$, $p < 0.01$, $n = 141$) between PC1s calculated from TRWI and LWBI for the common period 1873–2014 indicating some overlap in the environmental signal they capture but far from being identical in their responses over time (Fig.S3).

3.3. TRWI/LWBI-climate relationship

Correlations between TRWI and climate data showed the strongest responses to mean temperature during previous winter and spring season (Fig. 5a). The well replicated TRWI chronology from the site DTH revealed a moderate summer temperature signal in July and August (Fig. 5a). Six out of seven LWBI chronologies (all except KUR) showed strong relationships with JJA temperature for the period 1902–2014 with correlation values ranging from 0.40 to 0.69 ($p < 0.01$) (Fig. 6a). Correlations were also significant for September ($r = 0.35$ – 0.44 , $p < 0.01$). Only the LWBI chronology from KUR showed a low

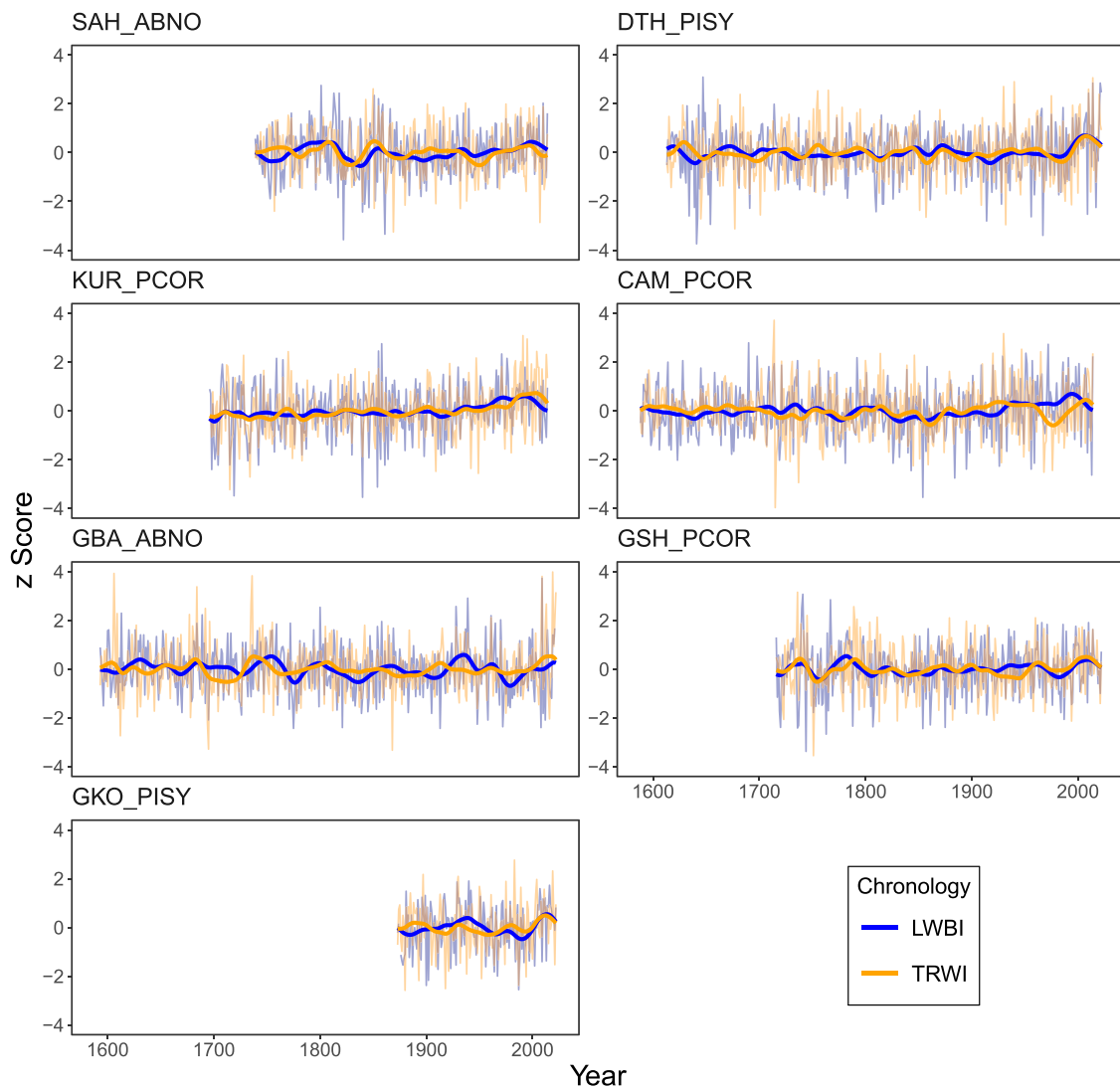


Fig. 2. Plot of TRWI and LWBI chronologies from the Caucasus region. A 30-low pass filter was applied to all the series. Chronologies are displayed from Lesser Caucasus (beginning from the left) to Greater Caucasus.

correlation ($r = 0.21$, $p < 0.05$) with summer temperature. At the DTH site, LWBI revealed again strongest positive correlations during an extended summer (June–August) season ($r = 0.69$, $p < 0.01$) (Fig. 6a).

Moderate correlations of TRWI with precipitation were observed in May, June, and July (Fig. 6a). Significant positive correlations were identified between June–August (JJA) precipitation and TRWI at spruce sites, GSH and KUR (Fig. 6b). Conversely, precipitation showed either negative (-0.23 to -0.36) or non-significant correlations with LWBI (Fig. 6b). Despite differences in signal strength, there is very high consistency regarding the seasonality of the climate signal among the sites. In the high-frequency domain, the winter temperature signal in TRWI chronologies faded slightly (Fig. S5a), whereas the summer temperature signal in LWBI is similarly strong at high frequencies than for the full signal (Fig. S6a). In the low-frequency domain, a strong correlation pattern emerges for LWBI during summer (Fig. S6b), while no consistent pattern was observed for TRWI (Fig. S5b). Over time, the correlation between TRWI and DJF temperature was unstable with even negative correlations observed at multiple instances during the early 20th century (Fig. S7a). The correlations were temporally consistent for the six LWBI chronologies (Fig. S7b).

PCA shows that $PC1_{TRWI}$ responded strongest to spring ($r = 0.41$, $p < 0.01$) and winter ($r = 0.36$, $p < 0.01$) temperature (Fig. 5a) while, $PC1_{LWBI}$ displayed a strong correlation ($r = 0.63$, $p < 0.01$) with

summer temperature (Fig. 6a). The running correlation of $PC1_{LWBI}$ with summer temperature was consistent and strong throughout the period with climatic observations (Fig. S7b). We did not find any consistent correlation other PCs and climate.

4. Discussions

4.1. TRWI/LWBI network

We present here a new TRWI and LWBI network of 14 tree ring chronologies from the Caucasus region and its sensitivity to climate variability. Our results indicate that TRWI generally exhibits a stronger common growth signal (i.e., $\bar{R}$) at the site level. Several studies noted that the common signal of LWBI is weaker in comparison to TRWI which increases the required sample replication to reach reliable thresholds compared to TRWI (Wilson et al., 2021, 2019; Zheng et al., 2021). Low mean inter-series correlation values in LWBI data may result from resolution deficits in the scanned images, wood discolorations or the presence of resin channels that influence light reflectance, collectively reducing signal coherence and diminishing inter-tree correlations (Rydval et al., 2018, 2014; Wilson et al., 2021, 2019).

Cross correlation analysis among TRWI chronologies, particularly in the Lesser Caucasus, indicates that the tree line sites share common

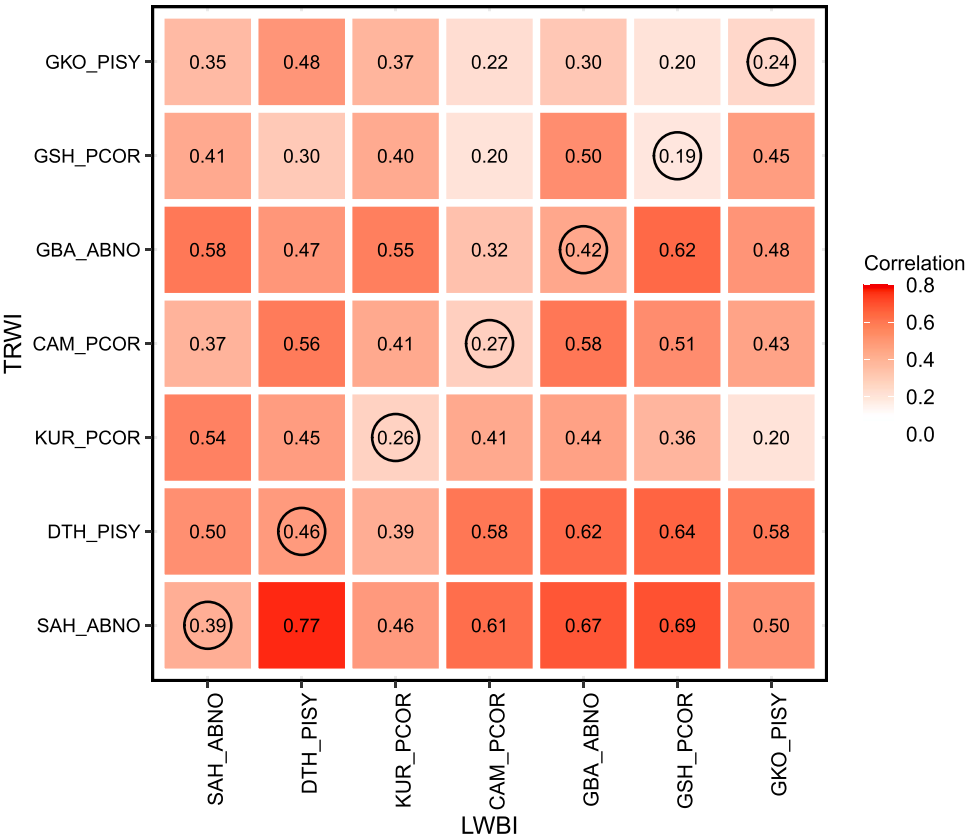


Fig. 3. Cross correlation among site chronologies for TRWI (upper left half), LWBI (lower right half) and TRWI vs LWBI (main diagonal filled with circles) calculated over the period 1873–2014. All the correlation values represent significant correlations ($p < 0.05$).

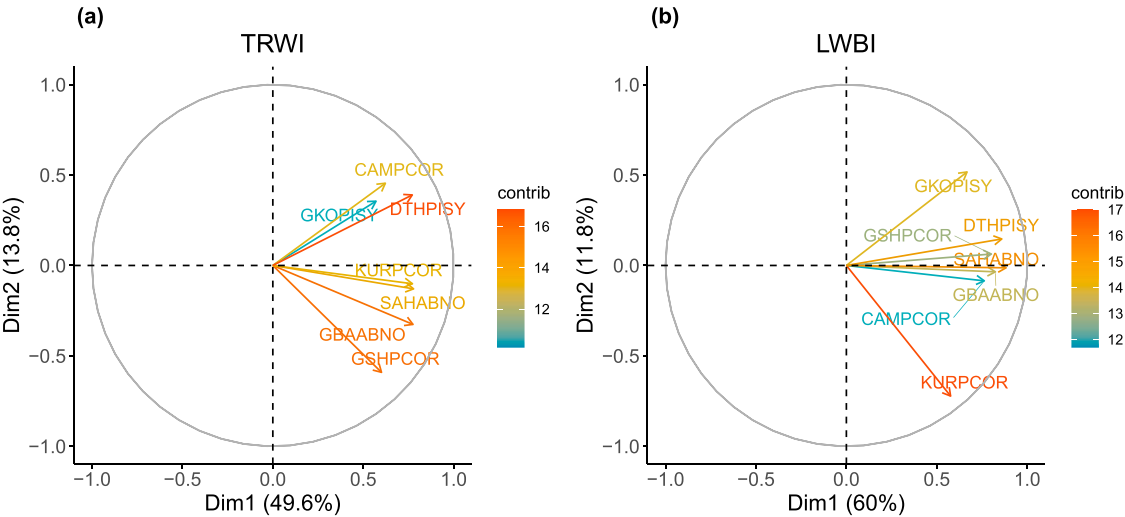


Fig. 4. PCA loading plots of first two principal components (PC1 and PC2) for (a) TRWI and (b) LWBI over the common period 1873–2014.

environmental signals, likely driven by regional climate factors. However, the weak mean inter-site correlation of $r = 0.40$ suggests that local site conditions, like competition or anthropogenic impacts limit the consistency among sites. The high degree of site heterogeneity prevented us from identifying growth characteristics that can be assigned to spatial proximity within the network or species-specific behavior in TRWI. Previous findings revealed that growth at tree line elevations cannot be assumed to exhibit a pure climate signal because the current upper tree line in the Caucasus region is likely lowered by several hundred meters due to anthropogenic activity (Dolukhanov, 1978;

Elumeeva et al., 2013). The higher inter-site cross correlation in LWBI compared to TRWI is in line with its stronger link to temperature variability, particularly during latewood formation in late summer, making it more effective at recording temperature signals across different sites (Babst et al., 2016; Rydval et al., 2014). The stronger pairwise inter-species correlations observed in LWBI, particularly for pine and fir trees reflects uniform environmental controls across species especially during latewood formation (Björklund et al., 2017; McCarroll et al., 2002). Correlations between the two proxies were positive, but low or moderate suggesting different physiological and environmental controls

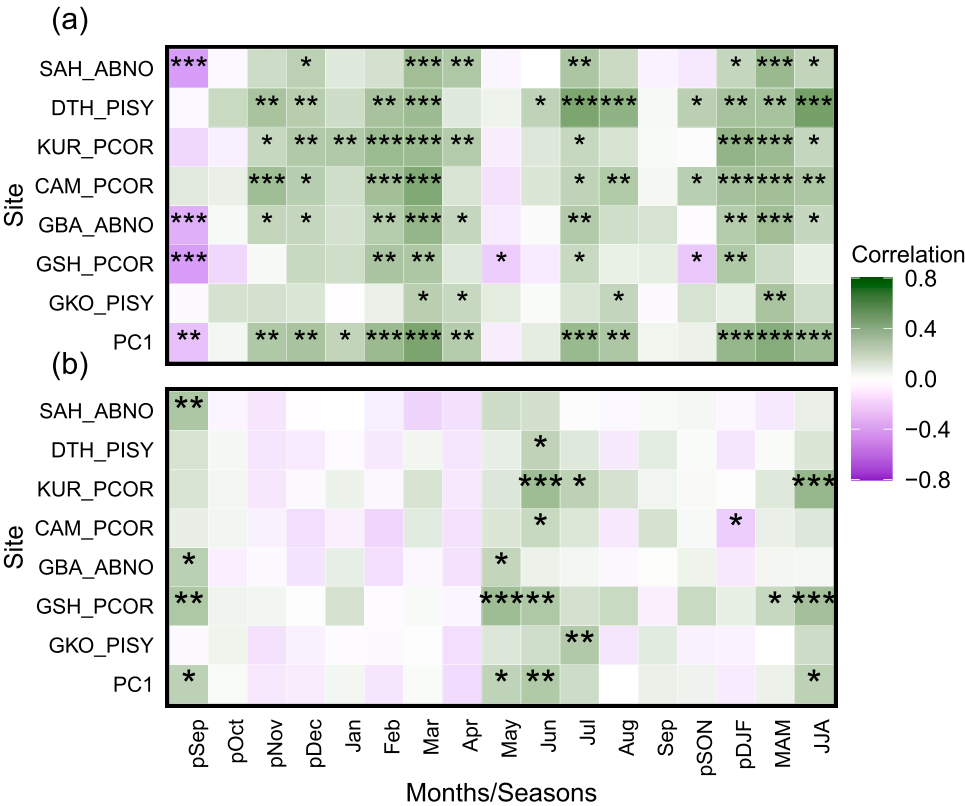


Fig. 5. Results of the Pearson correlation analysis of TRWI chronologies and a) monthly mean air temperature and (b) precipitation for the period 1902–2014.

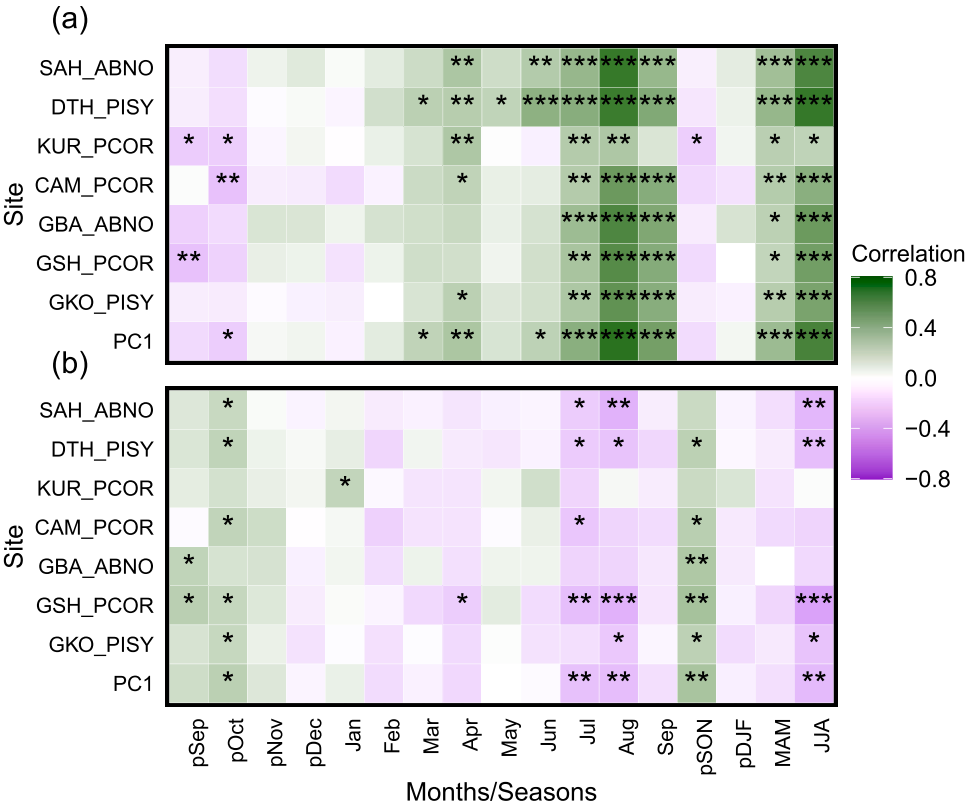


Fig. 6. Results of the Pearson correlation analysis of LWBI chronologies and monthly mean (a) air temperatures and (b) precipitation for the period 1902–2014.

on radial growth and latewood density (Björklund et al., 2017).

4.2. Sensitivity of TRW and LWBI to climate

Our results do not contradict that TRWI is largely a result of radial expansion at the beginning of the growing season which is significantly affected by memory effects from the previous year (Fritts, 2012). This is supported by high AC_1 values in TRWI and its relatively low climate sensitivity during the summer months. The more pronounced winter and spring temperature signals in TRWI are almost consistent over the entire network and thus seem to have a physiological reason. While spring temperatures can directly impact the early growing season, a causal relationship with temperatures in winter is less straight forward. However, winter temperature signals in TRWI chronologies from high elevations have been reported multiple times from the Caucasus (Martin-Benito et al., 2018), the Tibetan Plateau (Gou et al., 2007; Huang et al., 2019; Shi et al., 2017) and other places from the temperate and boreal Northern Hemisphere extratropics (Babst et al., 2013; Harvey et al., 2020; Heinrich et al., 2013; Pritzkow et al., 2016). Even for deciduous tree species (Pederson et al., 2004) such signals were found. A temperature signal during dormancy can be caused indirectly via the deeper freezing of soils or damages of buds, leaves and roots in cold winters (Huang et al., 2022, 2019; Körner et al., 2016).

Besides the strong temperature signal during high summer, we found a weak positive correlation between LWBI and spring temperature in most of the sites (Fig. 6). Warmer spring temperatures may lead to an earlier onset of cambium activity and growing seasons might start already in April with the initiation of early physiological processes. In the southernmost grid cell, which reflects an elevation comparable to the sampling sites, temperatures exceed 5°C as early as April, a threshold commonly used to determine the onset of the growing season. Consequently, throughout an extended growing season more carbon may become available for cell wall thickening and the lignification of latewood cells (Rathgeber, 2017; Rossi et al., 2016, 2008). Björklund et al. (2017) found that resources used for cell wall thickening in the latewood can be accumulated well before the onset of latewood formation. Additionally, the early spring signal might also be influenced by the location of the study sites, probably located below what would be the natural tree line at these locations. Regarding the much stronger summer temperature signal in LWBI chronologies, there is empirical evidence suggesting that summer temperature directly influences tree growth by enhancing latewood development, a component particularly sensitive to thermal conditions during the late growing season (Björklund et al., 2017; Rossi et al., 2008). Among the LWBI chronologies, only the KUR site displayed little sensitivity to summer temperatures which might result from stand level responses to ecological disturbances.

Temperature sensitivity of the studied trees at tree line altitudes is stronger than precipitation sensitivity. Only the spruce sites KUR and GSH reveal a considerable precipitation signal during summer in TRWI chronologies. This is in contrast to previous findings, in which pine sites in the Caucasus revealed on average a stronger precipitation limitation than spruce (Martin-Benito et al., 2018) and underpins the relevance of local site conditions for climate/growth relationships. The LWBI chronologies reveal a weak and inverse relationship with summer precipitation, indicating that wood density is not negatively impacted by drought for the studied sites.

The correlations between LWBI and JJA temperature are more stable over time compared to TRWI. Although correlations are overall high and almost always positive for LWBI and JJA temperature, a small decrease in correlation was observed in the early 20th century, potentially indicating weaknesses in the early observational data, which are interpolated from a sparse network of instrumental recordings (Jones, 2016; Schneider et al., 2023). Furthermore, the analysis of both proxies in the high-frequency domain revealed more robust correlations in LWBI compared to TRWI likely due to reduced AC_1 in LWBI. At lower

frequencies, LWBI signals can still be affected by long-term, non-climatic processes, such as heart wood-sapwood transitions and other discolorations in the wood (Rydval et al., 2018, 2014). The LWBI network tends to retain its correlation with summer temperatures better in high-latitude environments even at low frequencies, due to the strong linkage between latewood density and temperature. For instance, the low inter-site LWBI correlations ($r = 0.19\text{--}0.21$) in pine and spruce sites in the Greater Caucasus suggest that while temperature-driven latewood formation is relatively consistent, localized disturbances, or other site- and species-specific factors can still influence growth variability.

The PCA analysis revealed a significantly higher explained variance for $PC1_{LWBI}$ than for $PC1_{TRWI}$ clearly reflecting a more uniform response of LWBI to regional climatic controls. In both proxies, the sites with strong positive loadings on PC1, including GBA, SAH and DTH, all show relatively strong correlation with seasonal temperature. The correlation between PC1 of the two proxies ($r = 0.36$, $p < 0.01$) supports the idea that both TRWI and LWBI networks are partly influenced by physiological processes, that are related to regional weather and climate during an overlapping season. The PC1s from both networks correlate with spring and summer temperatures. The correlation between $PC1_{TRWI}$ and winter temperature, which is not found for $PC1_{LWBI}$, suggests a differentiation of environmental controls between the two proxies.

The multiproxy and multispecies network described in this study has the potential to detect a climate signal in both proxies. Different species in both proxies responded to the same climate factors but are influenced by other factors in different ways allowing these effects to cancel out. It is important to test these findings on longer chronologies using multiple species to determine whether proxies respond to climate consistently over time and across regions and whether they can reliably capture and reconstruct low-frequency signals which are difficult to detect using TRW data alone.

Furthermore, the strong summer temperature signal captured in the LWBI network reflects the high potential for expanding tree ring density-based research in the Caucasus region. The high mountain region of the Caucasus holds a rich cultural and archaeological heritage (Matskovsky et al., 2019) but lacks tree ring density chronologies with sufficient length and replication that is necessary for proper dating of ancient wood; as such, most of the archaeological artefacts found within it remain undated (Solomina et al., 2022). The presence of historical buildings near some of the sampling sites presented here could provide an opportunity to extend temperature sensitive tree-ring chronologies from the region back in time.

5. Conclusion

This study presented a comprehensive assessment of multiproxy and multispecies tree-ring networks from the Caucasus mountains. For 7 high-elevation sites in the Lesser and Greater Caucasus, TRWI and LWBI chronologies were established and compared regarding their shared variability. High agreement in interspecies LWBI correlations and coherence between spatially distant LWBI chronologies from the Lesser and Greater Caucasus indicate a homogeneous climatic control throughout the network. The investigation of climate signals highlights the strength of LWBI as a reliable proxy for capturing temperature-driven growth at the upper tree line of the Caucasus, outperforming traditional TRWI in both climate signal strength and consistency. These results indicate that, while climate warming promotes wood formation at the upper tree line, this response can be influenced by seasonal temperature shifts and site-specific conditions in both proxies. The stronger temperature signal captured by LWBI compared to TRWI offers a promising approach for developing long summer temperature reconstructions for the region. This would be further enhanced through additional sampling and the dating of archaeological wood providing a stronger foundation for multi-species and multi-proxy temperature reconstructions in the Caucasus.

CRediT authorship contribution statement

Rupesh Dhyani: Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Dario Martin-Benito:** Writing – review & editing, Validation. **Mehmet Doğan:** Writing – review & editing. **Revaz Kvaratskhelia:** Writing – review & editing. **Nesibe Köse:** Writing – review & editing. **Hüseyin Tuncay Güner:** Writing – review & editing. **Lea Schneider:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare no conflict of interest.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.dendro.2025.126372](https://doi.org/10.1016/j.dendro.2025.126372).

Data availability

Data will be made available on request.

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