

Climate sensitivity of Norway spruce inferred from blue intensity and tree-ring width

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Abstract

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In high-mountain Norway spruce stands, contrasting tree health and strong within site growth divergence may alter climate sensitivity and obscure climate reconstructions when trees are analysed together. We tested whether blue intensity (BI) chronologies, developed for all trees or separately by health status, provide stronger climatic signals than tree-ring width (TRW) chronologies. We established 12 plots and sampled neighbouring canopy trees of similar size and social position but contrasting health status (healthy vs. declining or dead). High resolution tree-ring images were used to develop indexed TRW and BI chronologies and assess their temperature sensitivity. During 1961–1990, BI showed stronger correlations with temperature than TRW, whereas in recent period 1991–2022 TRW became more strongly related to temperature in healthy trees. In declining or dead trees, BI retained a stronger temperature signal than TRW. These findings indicate that tree health and recent warming may alter the climate-growth relationships and that BI and TRW provide complementary information for climate reconstruction.

Keywords

dendroclimatology, growth trend, *Picea abies*, temperature signal, tree-ring, Western Carpathians

Introduction

Tree-ring-based reconstructions of interannual weather variability are essential for understanding past and predicting future climate dynamics because they capture the full range of climate fluctuations beyond mean conditions, including extremes (SAKALIS and KASTRIDIS, 2025; ALAM et al., 2025). These reconstructions also help to assess the magnitude of anthropogenic impacts by providing a long-term baseline against which recent warming trends can be compared (BJÖRKLUND et al., 2023). High mountain and treeline sites are commonly selected for temperature reconstructions because tree growth there is strongly limited by growing-season temperature (FRITTS, 1976).

Tree-ring width (TRW) is a broadly applied param-

eter representing overall growth conditions but in temperate high-mountain spruce forests its climate signal can be relatively weak. In the Carpathians, including Slovakia, high-elevation spruce TRW commonly explains up to 20%, and rarely up to 40%, of seasonal temperature variance (BURAS et al., 2018; POPA et al., 2022). Non-climatic factors, such as disturbance, biologically inherited individual growth divergence, health status, or methods used, can further affect the climate signal extraction and the reconstruction accuracy (ČERMÁK et al., 2019; BÜNTGEN et al., 2021; SEDMÁKOVÁ et al., 2022; JIANG et al., 2022). Maximum latewood density (MXD) represents a superior parameter for reconstructing summer temperatures, but its applicability is limited by the high costs and technical challenges involved in sample processing (SCHWEINGRUBER et

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al., 1978; BJÖRKLUND et al., 2014; RYDVAL et al., 2014).

The technique of measuring reflected blue light intensity (BI) offers a more accessible alternative to X-ray densitometry for obtaining tree-ring predictors sensitive to climate (WILSON et al., 2019). Its application can nevertheless be constrained by colour biases and image resolution. High resolution tree-ring imaging combined with appropriate measurement software (e.g. CooRecorder, LARSSON, 2013) can help reduce these uncertainties (BABST et al., 2009; RYDVAL et al., 2014; FRANK and NICOLUSSI, 2020).

The primary objective of this study is to determine whether high resolution tree-ring imaging combined with BI measurement enables more precise extraction of temperature signals from Norway spruce chronologies.

We hypothesise that:

- i) Blue intensity, in comparison to tree-ring width, allows the extraction of a stronger climatic temperature signal.
- ii) Health-specific groups (healthy and declining or dead) of spruce trees show higher growth synchronicity and stronger climatic signals within groups compared with all spruce trees analysed together.
- iii) Correlations with climate differ among identified health-specific groups, thus reflecting the influence of tree health conditions on growth divergence.
- iv) Recent warming has a stronger effect on tree-ring width chronologies than on blue intensity chronologies.

Materials and methods

Study area

The mountain range “Poľana” and the National Nature Reserve (NNR) “Zadná Poľana” are characterized by relatively high air humidity, which contributes to higher stand volumes and larger tree sizes compared with other spruce-dominated mountain forests in Slovakia. Enhanced mortality events in spruce-dominated stands were recorded in 1996 and 2004 following windstorms and subsequent bark beetle outbreaks (KONÔPKA and KONÔPKA, 2005). However, spruce forests at high elevations have retained the character of natural forests and are relatively well-preserved.

For this study, we selected a high-mountain forest vegetation zone dominated by spruce, mixed with mountain ash, maples, and beech trees. Norway spruce accounted for an average of 93% of the stand basal area. The study area was located at an elevation of 1,250–1,449 m asl, with a slope gradient of 5–25° and an E–S–SW aspect. Spruce trees reached an average height of 19 m at 100 years of age. The average stand basal area was 47 m² ha⁻¹. For the period 1950–2022, the mean annual temperature (T_{mean}) was 3.4 °C and precipitation sum (P_{sum}) is 1,172 mm (*EasyClimate* – an R package; CRUZ-ALONSO et al., 2023).

Climate data

High-resolution mean daily precipitation and temperature data for Europe, covering the period 1950–2022, were obtained at spatial resolution of 0.0083° (approximately 1 × 1 km) and used for the dendroclimatic analyses (*EasyClimate* – an R package; CRUZ-ALONSO et al., 2023). Standardized annual deviations from mean temperature (T_{mean}) and precipitation sum (P_{sum}) values (1950–2022) for the sampling location (NNR “Zadná Poľana”) were calculated and graphically presented as annual Z-scores. Long-term trends were illustrated using *Lowess* smoothing with a stiffness of 0.5 to provide a clearer overall representation of past and recent climate conditions.

We focused on mean temperatures for May–August (T_{mija}) and May–October (T_{mjjaso}), representing the presumed main climatic windows with the strongest influence on tree-ring formation. The May–October window was included because late-season controls on Norway spruce growth can extend into autumn. Photo-period and precipitation can influence the duration of cell production and growth cessation, while latewood maturation and lignification may continue into October at some high-elevation Central European sites (JEŽÍK et al., 2021; POPA et al., 2022). Daily data were aggregated into monthly means to calculate these seasonal averages. The seasonal climate series were smoothed using a 5-year moving average to illustrate temporal trends and divided into two periods: the climatically stable period (1961–1990) and recent warming period (1991–2022). The region experienced a temperature increase of approximately 0.86 °C since 1990, together with increased climate variability (BALÁŽ and PECHO, 2012). In particular, changes in precipitation amount and seasonality, as well as an increase in extreme rainfall, have also been reported (GDINA et al., 2017).

Radial increment parameter extraction from dendrometers

Changes in stem circumference were monitored continuously during the 2007–2019 seasons. We used high-resolution band DRL26 dendrometers with embedded data loggers (resolution 1 µm; EMS Brno, Czech Republic), which were attached to the sample trees at a height of 2.5 m. Hourly mean values were derived from measurements taken at 30-min intervals.

Seasonal daily increment (SCI) chronologies were calculated as differences between consecutive daily measurements. Monthly SCI values for analyses of seasonal growth dynamics were calculated as the sum of daily SCI values for each month. Relative monthly values were used to characterize intra-seasonal growth dynamics. Three younger spruce trees were selected for monitoring in 2007, and four additional large, dominant spruce trees were added in 2018. Mean monthly current and cumulative growth curves were calculated from 3–7 spruce trees and fitted using a distance-weighted least squares smoothing procedure.

Tree-ring sampling

In the NNR "Zadná Poľana", Norway spruce trees were sampled in autumn 2023. Selected forest stands were surveyed following the contour lines (isohypses), with sampling plots established approximately every 200–300 m. At each plot, a healthy spruce tree with a dominant position (defined as having the largest diameter among the 10 nearest trees) was selected together with a nearby conspecific dead or declining canopy tree. For dead trees, standing trees in the first decay class were sampled. Selection was based on the presence of needles, fine twigs, and branches, intact sapwood with minimal decay, the presence of the top of the crown, and intact bark. A tree was considered dead when it had 100% needle loss. Declining trees were defined as having >75% needle loss, whereas healthy trees had <35% needle loss.

Diameter at breast height (DBH) of the trees was measured using a calliper in the direction of core sampling. Twelve sampling plots were established at the site. Two dead trees were sampled on two of the plots, resulting in a total of 26 sampled trees: 12 healthy (H) and 14 declining or dead (D) spruce trees with dominant or co-dominant social positions within the stands. The H and D tree groups were comparable in pith age (125 ± 19 yrs), DBH size (48.0 ± 9.8 cm), mean annual increment (0.385 ± 0.060 cm yr⁻¹) and social status. The mean basic specific gravity per stem was 0.369 ± 0.041 g cm⁻³ for living trees and 0.380 ± 0.061 g cm⁻³ for standing dead trees, with no significant difference between the groups (SEDMÁKOVÁ et al., 2024).

Tree-ring width and blue intensity measurements

Increment cores were transported to the laboratory in plastic straws, placed into 5 mm wooden bars, air-dried, mounted, and progressively sanded to a minimum grit size 600 until the wood cells were clearly visible under the microscope. Emphasis was placed on obtaining a perfectly flat sample surface to minimize potential measurement artefacts during digital image analysis. Digital images were obtained using the advanced Tree-Ring Image Capturing System (ATRICS; LEVANIČ, 2007). This system provides greater detail and higher resolution than images from conventional scanners because optical magnification under a microscope has many advantages over digital magnification, particularly for samples containing extremely narrow growth rings. Each core was scanned sequentially under dark conditions at a resolution of 3,800–4,500 dpi.

Tree-ring widths (TRW) were measured to an accuracy of 0.01 mm and graphically cross-dated using Co-Recorder software (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden, MAXWELL and LARSSON, 2021). The dating, i.e., the correct assignment of calendar years to individual rings, was subsequently checked against the compiled reference chronology in TSAP software (Rinntech; RINN, 2003) and confirmed using COFECHA software (HOLMES, 1983).

Blue intensity (BI) values, representing the amount of blue light reflected from the wood surface, were obtained

from images of the measured and cross-dated tree-ring width series. As denser wood reflects less light, BI values were inverted so that higher BI values corresponded to higher wood density. For each tree-ring, latewood BI was calculated as the mean value of the darkest 30% of pixels in the latewood section. This measure, referred to as “30% inverted Blue Intensity”, was used in subsequent analyses as a proxy for maximum latewood density (MXD; RYDVAL et al., 2014; HEETER et al., 2022). Following the semi-automatic measurements, each ring was manually checked. Colour distortions caused by damaged wood, cracks, or other image artefacts were corrected to ensure that they did not affect the BI measurements.

Chronology development

TRW and BI series were individually detrended by age-dependent spline smoothing, a method that more naturally fits tree-ring growth (MELVIN et al., 2007). The initial spline value was set to 50 years, and a positive slope was allowed at the end of the fitted curve. Indexed series values were derived as ratios between the observed and fitted values. We selected this detrending approach and constructed standardized chronologies without autoregressive (AR) modelling to retain non-age-related mid-term positive trends observed in the absolute TRW series of healthy (H) old spruce trees during the recent period. Mean chronologies were established using Tukey's bi-weight robust mean and truncated to ensure a minimum replication of five trees since 1901, thereby reducing the effects of outliers (COOK and KAIRIUKSTIS, 1990).

Indexed ring-width (RWI) and blue intensity (BI) chronologies were developed for all spruce trees (All) and separately for health-specific groups of healthy (H) and declining or dead (D) trees. For each group of trees and tree-ring parameter, standard dendrochronological statistics were calculated from the raw tree-ring series. The mean between tree correlation (RBT), expressed population signal (EPS) and signal to noise ratio (SNR) were calculated from the established chronologies (WIGLEY et al., 1984) using the “dplR” R package (BUNN, 2008).

Climate–growth relationships

Assuming temperature control over radial growth and that warmer growing seasons promote wider tree rings and greater lignification and cell-wall density, resulting in higher inverted BI values, we used mean temperature as the primary climatic variable.

Climate–growth relationships were assessed separately for each tree group using Pearson correlation coefficients between annual standardized RWI and BI indices and mean monthly temperatures from April of the previous year to October of the current year. Seasonal means for May–August (T_{mija}) and May–October (T_{mijaso}) were evaluated together with other combinations of temperature months, and the strongest seasonal relationships were identified for these time windows. Correlations were then calculated separately for the 1961–1990 and 1991–2022.

Finally, running correlations were calculated and graphically presented between standardized RWI and May–August mean temperature (T_{mija}), as well as between standardized RWI and seasonal May–August precipitation sum (P_{mija}). The analyses were performed separately for the health-specific tree groups using a 20-year moving window over the period 1950–2022 in the “TreeClim” R package (ZANG and BIONDI, 2015).

Results

Two mid-term periods of approximately equal length, 1961–1990 and 1991–2022, with distinct climatic conditions, were selected to compare tree-ring width (RWI) and blue intensity (BI) parameters. The colder period (1961–1990) showed no significant temperature trend and was characterized by temperatures below the long-term

average, together with a drier climate in the last decade. In contrast, the 1991–2022 period exhibited a mid-term increasing temperature trend, while precipitation fluctuated around normal levels (Fig. 1a).

In NNR “Zadná Poľana”, trees initiated xylem production in early May and completed xylogenesis in October with mature wood formation (Fig. 1b). By early August, approximately 90% of tree-ring formation was accomplished (Fig. 1c). Within the 2007–2019, two growing seasons showed an early cessation of cambial activity in early August, which may have reduced secondary-wall formation, lignification and mature-wood formation.

The D tree group showed lower mean TRW and higher variability and sensitivity (Table 1). For both TRW and BI, D chronologies had lower between-tree correlations and expressed population signal values than H chronologies (Table 1–2). However, the tested differences were not statistically significant.

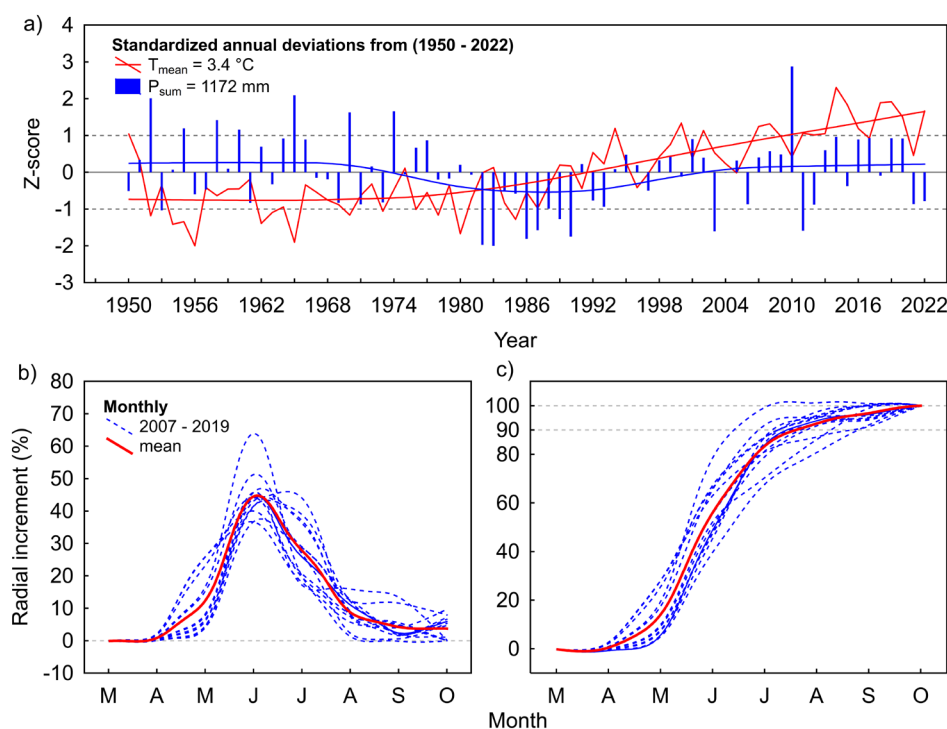


Fig. 1. a) Standardized mean annual temperature (T_{mean}) and precipitation sum (P_{sum}) values at study area (NNR “Zadná Poľana”) showing the above/below normal or extreme deviations; smoothed values illustrate the long-term (1950–2022) trends; b) Relative current and c) cumulative monthly radial increments showing the main season window of spruce tree-ring formation, red solid line refers to mean growth trajectory of 2007–2019 intra-seasonal growth.

Table 1. Basic descriptive characteristics of the measured TRWs and the established standardized chronologies. Spruce All – all grouped trees, H – group of healthy trees, D – group of declining or dead trees, Range – time span in calendar years of the tree-ring series, Length – mean length of the tree-ring series in years, TRW – tree-ring width in mm, SD – standard deviation, GINI – coefficient of inequality, AR1 – first order autocorrelation, NT – number of trees included, RBT – between trees correlation, EPS – expressed population signal, SNR – signal-to-noise ratio.

Spruce	Range	Length	TRW	SD	GINI	AR1	NT	RBT	EPS	SNR
All	1838–2023	123	1.80	0.94	0.29	0.83	26	0.294	0.916	10.851
H	1855–2023	125	1.83	0.82	0.24	0.81	12	0.392	0.886	7.741
D	1838–2023	121	1.77	1.04	0.33	0.85	14	0.235	0.811	4.300

Table 2. Basic descriptive characteristics of the measured BIs and the established standardized chronologies. Spruce All – all grouped trees, H – group of healthy trees, D – group of declining or dead trees, Range – time span in calendar years of the tree-ring series, Length – mean length of the tree-ring series in years, BI - blue intensity, SD – standard deviation, GINI – coefficient of inequality, AR1 – first order autocorrelation, NT – number of trees included, RBT – between trees correlation, EPS – expressed population signal, SNR – signal-to-noise ratio.

Spruce	Range	Length	BI	SD	GINI	AR1	NT	RBT	EPS	SNR
All	1838–2023	123	1.57	0.20	0.07	0.44	26	0.258	0.900	9.044
H	1855–2023	125	1.57	0.20	0.07	0.43	12	0.371	0.876	7.081
D	1838–2023	121	1.57	0.19	0.07	0.45	14	0.186	0.762	3.209

Table 3. Climate-growth correlations between standardized tree-ring width (RWI) and latewood blue intensity (BI) chronologies and mean seasonal temperature during the stable (1961–1990) and warming (1991–2022) periods. Significant Pearson's correlation coefficients ($p < 0.05$) are marked with an asterisk; Spruce All – all grouped trees, H – group of healthy trees, D – group of declining or dead trees, T_{mija} – mean seasonal May–August temperature, T_{mjjaso} – mean seasonal May–October temperature.

Index	Spruce	T_{mija} (1961–1990)	T_{mjjaso} (1961–1990)	T_{mija} (1991–2022)	T_{mjjaso} (1991–2022)
RWI	All	0.37*	0.37*	0.48*	0.60*
BI	All	0.60*	0.59*	0.30	0.43*
RWI	H	0.41*	0.32	0.53*	0.63*
BI	H	0.60*	0.57*	0.23	0.36*
RWI	D	0.32	0.37*	0.31	0.47*
BI	D	0.57*	0.57*	0.41*	0.47*

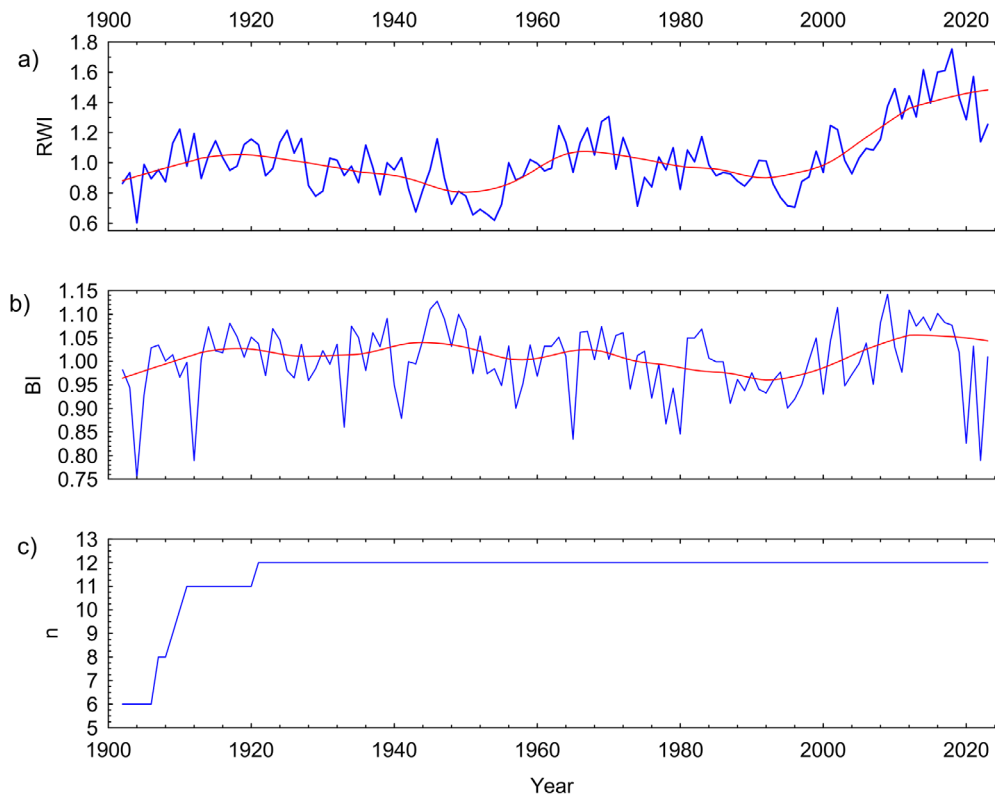


Fig. 2. Healthy (H) spruce trees – established standardized a) RWI and b) BI chronologies, red line denotes fitted spline to illustrate the medium-term trend; RWI – ring width index, BI – blue intensity index, c) n – sample depth of chronologies.

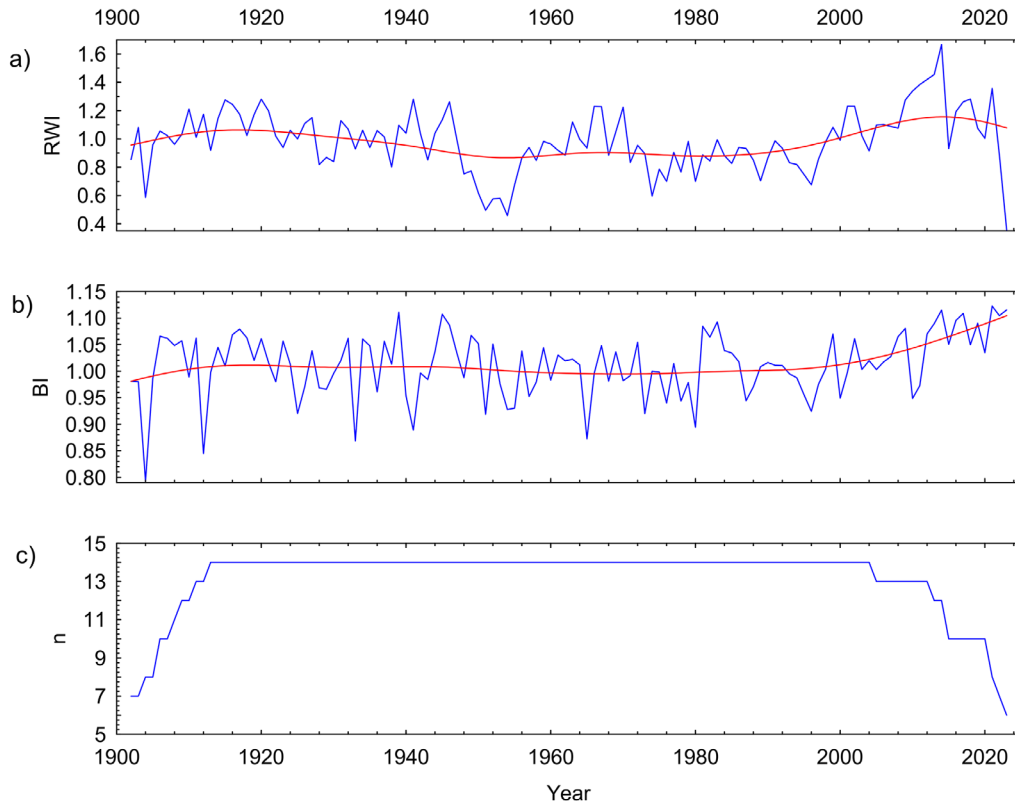


Fig. 3. Dead or declining (D) spruce trees – established standardized a) RWI and b) BI chronologies, red line denotes fitted spline to illustrate the medium-term trend; RWI – ring width index, BI – blue intensity index, c) n – sample depth of chronologies.

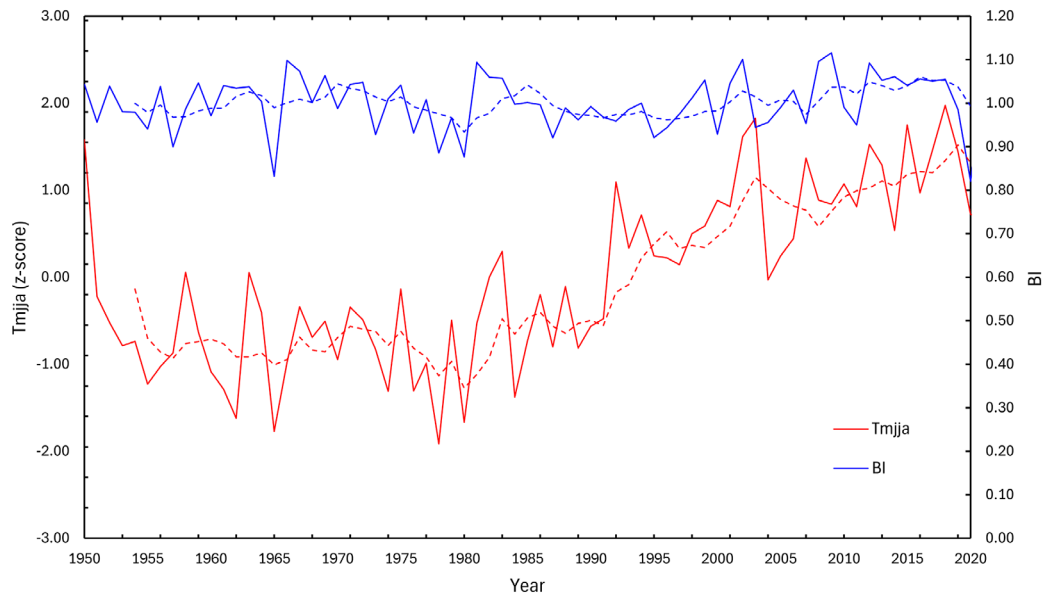


Fig. 4. Comparison of regional standardized blue intensity (BI) chronology with standardized seasonal May–August mean temperature deviations (T_{mjja}) over 1950–2022 period of healthy spruce trees. Dashed curves represent 5-year moving averages.

The standardized RWI chronologies showed positive correlations with mean seasonal temperatures, with correlation windows beginning in May and extending to August or October (Table 3). During the climatically stable period (1961–1990), the highest RWI–temperature correlation was observed in H trees for T_{mjja} ($r = 0.41$, p

< 0.05 , $n_{\text{year}} = 30$), compared with all trees ($r = 0.37$, $p < 0.05$, $n_{\text{year}} = 30$) and D trees ($r = 0.32$, $p > 0.05$, $n_{\text{year}} = 30$). BI showed consistently stronger temperature correlations across tree-health groups ($r = 0.57$ – 0.60 , $p < 0.05$, $n_{\text{year}} = 30$).

During the warming period (1991–2022), the relationships between RWI, BI and mean seasonal tempera-

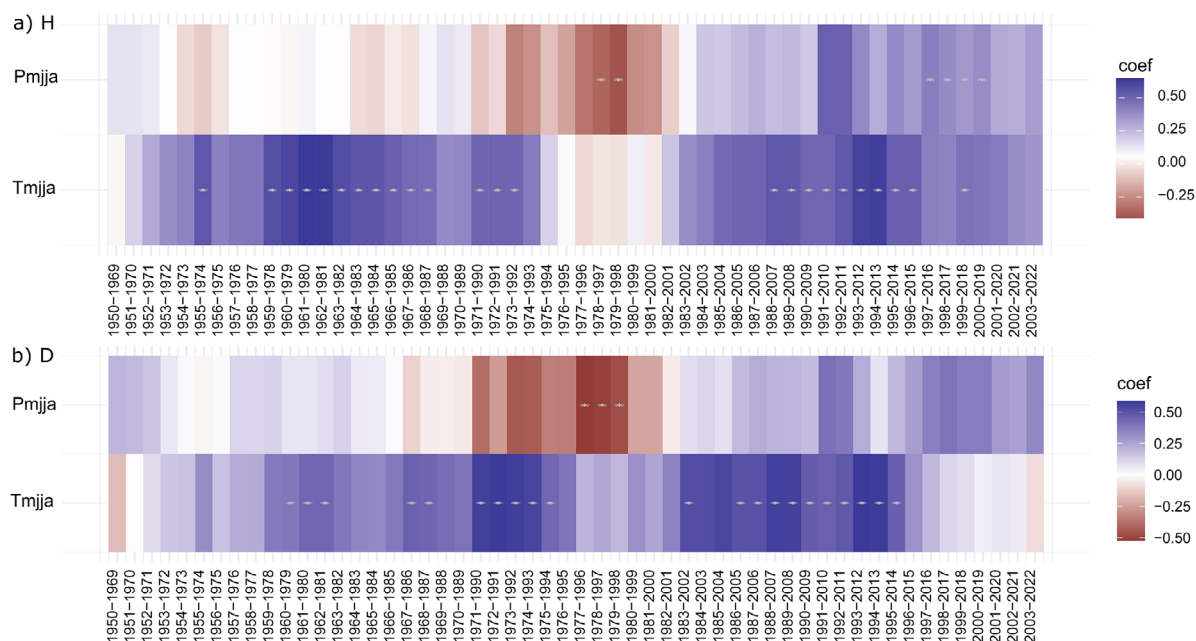


Fig. 5. Running correlation coefficients (coef) between standardized RWI chronology and seasonal temperature (T_{mjja}) and precipitation sum (P_{mjja}), calculated for a 20-year moving window over the period 1950–2022 for a) healthy (H) and b) declining or dead (D) spruce trees.

ture changed (Fig. 2, Table 3). RWI showed the strongest temperature correlation in H trees for T_{mjja} ($r = 0.63$, $p < 0.05$, $n_{year} = 32$), whereas the D-tree RWI correlation remained weak and statistically non-significant for T_{mjja} ($r = 0.32$, $p > 0.05$, $n_{year} = 32$). BI correlations were lower than RWI in H trees ($r = 0.23$ – 0.36 , $p < 0.05$) but remained comparatively stronger in D trees ($r = 0.41$ – 0.47 , $p > 0.05$).

The BI chronology of D trees retained increasing index values and showed higher correlations with temperature than the BI chronology of H trees. In contrast, the RWI chronology of D trees showed a decreasing growth trend and weaker climate relationships during the recent warming period than the H chronology (Fig. 3). The extreme weather course during the 2019–2020 and 2021–2022 seasons, which triggered minimum BI values, may have contributed to the declining trend in the BI chronology of H trees during the recent warming period (Fig. 2, 4).

The shift in temperature sensitivity of H and D trees was accompanied by a change in their sensitivity to precipitation during the main growing season, with the previously negative association changing to a weak positive relationship (Fig. 5).

Discussion

Blue intensity and tree-ring width as a temperature proxy

The results of our study contribute to a better understanding of current climate-growth relationships in high-mountain Norway spruce forests. One main finding is that blue intensity (BI) and tree-ring width (TRW) capture com-

plementary information on climate-growth relationships, and their relative sensitivity changes with tree health and climatic conditions. Our findings are consistent with previous studies demonstrating the potential of BI as a temperature proxy. Latewood BI in *Picea* species growing at high elevations captures a strong growing season temperature signal and can outperform ring width (BJÖRKLUND et al., 2014; WANG et al., 2020; POPA et al., 2022; ZHENG et al., 2025). FRANK and NICOLUSSI (2020), for example, utilized 30 cores from Norway spruce trees at a high-elevation site in the northern Alps and obtained strong correlations between temperature and latewood BI chronologies. In the eastern Canadian taiga, BI in black spruce showed stronger responses to May–August temperatures than TRW, and these were highly correlated with maximum latewood density (MXD), a conventional density metric (WANG et al., 2020). Similarly, in the Carpathians, spruce BI showed substantially stronger and more coherent growing season temperature signals than TRW (JIANG et al., 2022).

In our study, we extracted and compared climate signals from high-resolution digital images of Norway spruce tree rings using BI and TRW. Under climatically stable conditions, BI chronologies generally exhibited stronger relationships with seasonal temperature than TRW chronologies. The strongest BI–temperature correlations (explaining approximately 36% of the seasonal temperature variance), indicate that BI may be particularly suitable for temperature reconstructions, especially for D trees, for which TRW temperature sensitivity was weaker (POPA et al., 2022; JIANG et al., 2022; JIANG et al., 2025). During the recent warming period, however, the relative strength of the two proxies changed. TRW showed a stronger relationship with temperature in H trees, whereas BI retained

a stronger relationship in D trees. This pattern indicates that the two proxies may respond differently to climate under changing environmental conditions (RYDVAL et al., 2018; POPA et al., 2022). The divergence between proxies also highlights the importance of considering tree health when interpreting climate signals derived from tree-ring parameters. Tree health may influence how different tree-ring properties respond to climatic variability, with BI potentially retaining a stronger temperature signal in stressed or declining trees, whereas TRW may more directly reflect changes in radial growth and associated reduction in climate sensitivity (RYDVAL et al., 2018; JIANG et al., 2022).

An extreme combination of seasonal temperature and precipitation anomalies in 1974 may have acted as a predisposing factor for long-term growth divergence in co-occurring Norway spruce trees, differentiating resilient individuals from those that became highly defoliated and chronically declining (SEDMÁKOVÁ et al., 2022). The year 1974 was also identified as a negative pointer year in Czech spruce chronologies (RYBNÍČEK et al., 2012). Such growth declines can persist for decades, indicating a long-term shift in growth trajectories rather than a transient reduction (CAMARERO et al., 2021; SEDMÁKOVÁ et al., 2022). The neighboring-pair sampling used in this study improves regional comparability by reducing differences in local site conditions. However, some differences between health classes may still reflect shared local environmental conditions rather than tree health alone (SHAW et al., 2025). Future studies could explicitly account for the hierarchical sampling design using paired statistical approaches or mixed-effects models to further disentangle the effects of tree health from local site variation (HARRISON et al., 2018).

BI is generally considered a surrogate for wood density, and wood density tends to decrease with increasing tree ring width (e.g. SEDMÁKOVÁ et al., 2024). Therefore, the recent increase in radial growth observed in H trees may be associated with lower wood density and consequently lower BI values. Conversely, decreasing mid-term growth trends in D trees may be associated with increasing BI values. In conifers, species-specific latewood width can remain relatively stable despite variability in TRW, consequently, wider rings with a smaller proportion of latewood tend to have lower wood density (WANG et al., 2002; MÄKINEN et al., 2002).

Growth diverging groups of spruce trees and climate sensitivity

Our results suggest that tree health, disturbance history, and growth divergence should be considered when developing conifer-based climate reconstructions. In the D tree group, trees had lower TRW, greater variability, lower between-tree synchronicity, weaker TRW climate signals, and different BI–temperature relationships. Grouping trees according to health status strengthened the common climate signal in the H tree group. This suggests that, in H trees, radial growth remains primarily temperature limited and may have benefited from recent warming, although

other environmental factors may also influence growth responses. In uneven-aged stands, climate–growth relationships may be distorted when trees are analysed jointly because neighbouring trees of different ages, sizes or health status can exhibit contrasting growth responses to the same climatic conditions. They may also show different or temporally unstable climate–growth relationships. Strong, site-specific growth divergence among neighbouring Norway spruce trees has been reported in the Western Carpathians since the 1970s and may be related to differences in their ability to recover from climatic stress (BURAS et al., 2018; SEDMÁKOVÁ et al., 2022). Small-scale gaps and differences in suppression and canopy accession may also contribute to divergent TRW trajectories (BJÖRKLUND et al., 2014; HOLEKSA et al., 2017; JIANG et al., 2022). Reduced coherence in TRW measurements can complicate the extraction of common climatic signals (RYDVAL et al., 2018; JIANG et al., 2022). Overall, our findings indicate that disturbance and tree decline may reduce the consistency of climate signals derived from TRW, whereas BI may retain a comparatively stronger temperature signal in declining trees. BI also showed relatively low synchronicity in the D group and the relatively small number of sampled trees in some groups may have reduced statistical power. The expected increase in the frequency and severity of wind and bark beetle disturbances under future climate conditions could further affect the resilience of Norway spruce forests (HONKANIEMI et al., 2020; DESAINE et al., 2022), but implications for future climate reconstructions remain uncertain. BI may therefore be less affected by some forms of disturbance than TRW and provide a comparatively more stable climatic signal.

High-resolution reconstructions of recent warming

Based on our results, climate sensitivity appears to change between the stable and warming periods, suggesting that the climatic window associated with tree growth may have changed during recent warming. Recently reconstructed past temperatures based on within-year BI records consistently indicate that recent decades have been warmer than previous periods spanning several centuries, with warming trends often exceeding the range of natural variability (DAVI et al., 2021; CHEN et al., 2023; BAKHTIYOROV et al., 2025). Unlike more stable BI temperature signals, TRW may be more sensitive and potentially less stable under recent warming (BURAS et al., 2018; JIANG et al., 2022). The reduced ability of TRW records to capture recent warming trends in *Picea* has been linked to growth divergence (D'ARRIGO et al., 2008; BURAS et al., 2018). Norway spruce growth responses to climate are heterogeneous and temporally variable, suggesting that TRW–climate relationships may be non-stationary (ČERMÁK et al., 2019; BURAS et al., 2018; SEDMÁKOVÁ et al., 2022). Several studies have also reported shifts in climate sensitivity under recent warming and increasing climatic extremes across the distribution range of Norway spruce (BOŠEĽA et al., 2020; POPA et al., 2023; OREŠKOVIĆ et al., 2024; POPA et al., 2024; PUTALOVÁ et al., 2019; BIČKOVSKIS et al., 2025).

Although these studies do not explicitly address individual-tree growth divergence, their findings are consistent with the possibility that climate sensitivity varies among trees and changes over time. TRW–climate correlations are also sensitive to chronology type, with some studies reporting a weakening of correlations during the early 1990s followed by subsequent strengthening (ČERMÁK et al., 2019).

In our study, the relationships between tree growth and seasonal climate variables also shifted between the recent warming period (1991–2022) and the climatically stable period (1961–1990). We found a shift from stronger relationships with temperature (T_{mija}) during 1961–1990 toward the extended period (T_{mijaso}) during 1991–2022. This may indicate an increasing influence of the late-season temperature on tree growth. The relationship between spruce growth and seasonal precipitation also appeared to change, with the previously negative association becoming weakly positive. Under warming, spruce growth at higher elevations may remain temperature-limited while increasingly reflecting a combination of temperature and precipitation effects (JEŽÍK et al., 2021). Environmental conditions may be shifting towards growth-optimum conditions, while strong and temporally stable temperature limitation associated with the extremely short growing season may become increasingly restricted to higher-elevation treeline ecotones. These interpretations remain tentative because mechanisms behind a possible weakening of the temperature signal were not directly tested.

In our study, recent extreme years provide an illustration of how BI can respond differently from TRW. Especially in 2020 and 2022, extreme weather may have contributed to the formation of "light" rings and pronounced reductions in BI values in the H tree group. This suggests that BI may respond to changes in latewood formation, lignification and wood density rather than simply recording radial growth. In high-mountain regions, historical "light" rings have more commonly been associated with cold and wet summers, potentially linked to volcanic eruptions (PIERMATTEI and CRIVELLARO, 2025). Recent extreme drought in 2022, or the transition from drought conditions to sudden cold rainy spells during lignification in 2020, may have reduced cell enlargement and secondary wall thickening, potentially resulting in formation of narrower tracheids with thinner walls and lower density (BALDUCCI et al., 2016; VIEIRA et al., 2020). Extreme weather conditions that cause early cessation of growth may therefore contribute to reduced latewood density and lower BI values (LARYSCH et al., 2021). In contrast, the D tree group showed an increase in BI values, which may reflect increased lignification or denser xylem formation per unit area as a possible adaptive response towards hydraulically safer xylem despite reduced radial growth (KERET et al., 2024). Early signs of wood degradation, damage to conductive tissues and bacterial activity, possibly associated with bark beetle infestation in healthy trees, have also been observed and may contribute to substantial changes in xylem properties and tree functioning (SEDMÁKOVÁ et al., 2024). Once conductive tissues and cambial activity are largely impaired, the growth of D trees may become

less responsive to interannual climatic variability. Tree-ring formation may then be increasingly influenced by internal damage, pathogens, and hydraulic failure than by interannual climate (VIEIRA et al., 2020; LI et al., 2023; DECUYPER et al., 2020). Although BI may provide a stronger temperature signal than TRW under some conditions, it is not free from potential biases caused by density fluctuations unrelated to climate (WANG et al., 2020; ZHENG et al., 2025). Overall, if temperature becomes a progressively weaker limiting factor for tree growth at high-elevation sites, the reliability of future temperature reconstructions based on spruce may decrease (RUTHERFORD et al., 2003). Combining multiple tree-ring parameters, such as TRW and BI, may therefore provide a more robust approach to capturing climate signals. Alternatively, the use of other temperature-sensitive tree species, such as beech, could complement spruce-based reconstructions where appropriate.

Conclusions

In the present dataset and under the climatic conditions studied, BI generally provided a stronger and more coherent temperature signal than TRW during the climatically stable period, whereas the relative strength of the two proxies changed during recent warming. Overall, the hypotheses were supported to varying degrees. Hypothesis I was supported, as BI generally provided stronger temperature signals than TRW under climatically stable conditions. Hypothesis II was partially supported: health-specific grouping revealed differences in climate–growth relationships and chronology coherence, but differences in synchronicity were not statistically significant. Hypothesis III was supported, as climate–growth relationships differed between healthy and declining or dead trees. Hypothesis IV was only partially supported: recent warming strengthened the temperature signal in TRW relative to BI in healthy trees, whereas BI remained comparatively stronger in declining or dead trees. These findings indicate that the relative performance of TRW and BI as climatic proxies depends on climatic conditions and tree health status. Combining both parameters may therefore provide complementary information when reconstructing climate–growth relationships in disturbed or declining Norway spruce stands.

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