

Modulating Norway spruce growth and resilience through thinning intensity under climate change conditions

PETRA JABLONICKÁ¹ , PAVEL HORÁK¹ , JAKUB ČERNÝ^{1,2*} 

¹Department of Silviculture, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic

²Department of Silviculture, Forestry and Game Management Research Institute, Opouch, Czech Republic

*Corresponding author: cerny@vulhmop.cz

Citation: Jablonická P., Horák P., Černý J. (2025): Modulating Norway spruce growth and resilience through thinning intensity under climate change conditions. J. For. Sci., 71: 482–500.

Abstract: In recent decades, Norway spruce (*Picea abies*) stands have become increasingly vulnerable to frequent droughts and associated outbreaks of secondary biotic pests, resulting in significant degradation of forest ecosystems. To preserve their production and ecological functions, it is necessary to apply well-adapted silvicultural practices that mitigate the risk of stand decline. This study examines the effects of two thinning intensities (moderate and heavy) on stand productivity and resilience under varying site conditions. Three long-term research sites with paired differently thinned plots located within and outside the natural range of Norway spruce in the Czech Republic were analysed. Tree-ring width measurements were used to calculate radial growth trends and four resilience indices (resistance, resilience, recovery and average relative growth reduction). Across sites Blaník (BL), Tetřeví Boudy (TB) and Železná Ruda (ZR), basal area increment (*BAI*) differed significantly between thinning intensities (BL: $P = 0.044$; TB: $P = 0.0076$; ZR: $P < 0.001$), with moderate thinning showing higher *BAI* at BL and TB, whereas heavy thinning reduced growth at the waterlogged TB site. Site-specific differences in tree growth responses to negative pointer years were evaluated, particularly concerning drought events. Resilience metrics computed for five drought pointer years (1976, 2000, 2003, 2015, 2019) showed no consistent differences between thinning intensities; however, at ZR, heavy thinning yielded higher resilience (*R_s*) and resistance (*R_t*) in 2015 and 2019. During drought years, the average relative growth reduction (*ARGR*) ranged from 3% to 31%, with the lowest values under moderate thinning. Overall, moderate thinning enhanced stand productivity and resilience, whereas heavy thinning had adverse effects at the waterlogged site. These results highlight the need to adapt silvicultural practices to local ecological conditions to ensure long-term stability and productivity.

Keywords: climate-growth relationships; climatic stress; dendroecology; resilience indices; silvicultural treatments; tree-ring analysis

Nowadays, one of the most discussed topics in forestry is the influence of climate change on forest ecosystems (Vacek et al. 2023). Global climate change (GCC) is characterised by rising

air temperatures and altered precipitation patterns during the growing season (Cavin et al. 2013), both of which increase the risk of reduced tree growth and higher mortality (Adams et al. 2012). The re-

Supported by the Internal Grant Agency of the Faculty of Forestry and Wood Technology, Mendel University in Brno (Project No. IGA-LDF-23-IP-032), and by the Ministry of Agriculture of the Czech Republic through institutional support (MZE-RO0123).

© The authors. This work is licensed under a Creative Commons Attribution-NonCommercial 4.0 International (CC BY-NC 4.0).

<https://doi.org/10.17221/55/2025-JFS>

sistance of forest stands against the adverse effects of GCC can be positively influenced by suitable silvicultural treatments (Cosofret, Bouriaud 2019).

In Europe, Norway spruce remains the most economically important conifer (Skrøppa 2003; Jansson et al. 2013; Huber et al. 2023). Since the 1950s, it has been intensively planted on secondary non-native sites has been applied (Spiecker 2000). Over the past two decades, forest management in Central Europe has increasingly promoted the establishment of mixed stands (Brang et al. 2014). However, despite this, there are still extensive areas with pure spruce stands, even after the recent bark beetle outbreaks, for which it is necessary to consider their production efficiency, stability and resistance to the ongoing GCC (Hlásny et al. 2021; Jaime et al. 2024). When adapted to the local climatic conditions, Norway spruce is a highly frost-tolerant species. However, when regenerated artificially on clearings, it may be exposed to several stress factors simultaneously (Westin et al. 2013).

Forest stands in unsuitable habitats are severely affected by drought, resulting in large-scale outbreaks of secondary biotic pests (Hlásny et al. 2021). Dušek et al. (2014) consider that well-timed interventions with appropriate intensity are necessary in declining spruce stands to improve their resistance. Delayed or missed interventions in young spruce stands merely postpone the problem to later developmental stages, at which point abiotic stressors are highly likely to cause stand decline (Novák et al. 2017; Đodan, Perić 2019). For instance, Štefančík (2013) also recommends intervention based on individual positive selection in pole stands of Norway spruce to eliminate production losses. Based on the goals of regeneration and types of forest stands, applying the principles of close-to-nature forestry is recommended (e.g. Brang et al. 2014; Spathelf et al. 2015). This method uses the production potential of the stand during the regeneration period. Thus, it provides potential for successful natural regeneration. The fundamental silvicultural methods applied within these principles include small-gap fellings or selective cuttings (Poleno et al. 2009).

There are many ways to evaluate which interventions are appropriate and whether they are applied at the right time. Most studies assess the suitability of interventions based on productivity, health status, or competitive relationships. An-

other option is the use of dendroclimatic analysis. Recent advances in dendroecological and dendroclimatological methods allow for a more detailed analysis of tree response to disturbance events, providing insights into their sensitivity, resistance, and recovery capacity (Lloret et al. 2011). Through tree-ring data and the quantification of growth responses during and after extreme climatic events, it is possible to identify the resistance of individual trees and entire stands (Anderegg et al. 2015). This approach is especially useful in the context of GCC, as it provides a long-term perspective on tree growth dynamics and helps to evaluate the effectiveness of different silvicultural strategies in enhancing forest resistance and adaptability (Schuldt et al. 2020). Thus, dendroclimatological analyses have become an important tool for assessing the stability of forest stands (Fritts 1971), especially those situated at the edge of their ecological optimum.

In this context, resilience indices are increasingly used to evaluate tree responses to stress events such as droughts (Lloret et al. 2011). These indices are valuable tools for comparing the effects of various thinning regimes and for determining whether specific tending intensities can enhance the ecological stability of forest stands (Pretzsch et al. 2020).

To quantify long-term growth trends and detect potential growth suppression under stress, basal area increment (*BAI*) is frequently calculated from tree-ring width data. *BAI* provides a standardised growth metric that accounts for changes in tree size over time, thereby enabling more accurate comparisons across individuals and treatments. The metric is particularly useful for assessing the cumulative effects of climatic factors and silvicultural interventions on radial growth (Biondi, Qeadan 2008; Campelo et al. 2018).

In addition, climatic stress events are often identified and quantified using drought indices such as the standardised precipitation-evapotranspiration index (*SPEI*), which integrates both precipitation and potential evapotranspiration, thereby more accurately capturing the physiological relevance of drought (Vicente-Serrano et al. 2012). Combining *SPEI* data with tree growth responses enables the temporal synchrony of drought events with changes in growth patterns, thereby supporting the attribution of observed growth reductions to specific climatic drivers (Vicente-Serrano et al. 2010; Novák et al. 2017).

For Norway spruce, which is particularly susceptible to water deficits when growing beyond its native range – characterised by relatively cold and moist conditions, typically at elevations between 500 and 1 900 m a.s.l., with annual precipitation ranging from 1 000 mm to 2 000 mm, mean annual temperatures between 3 °C and 6 °C, and deep, well-drained, acidic to slightly acidic soils rich in organic matter (Caudullo et al. 2016) – such analyses provide essential guidance for adaptive forest management.

Silvicultural practices that optimise light and water availability – such as well-timed and moderate thinning – can enhance physiological resilience and improve stand structure in terms of mechanical and production stability. By linking site-specific climate data with growth responses using resilience metrics, forest managers can develop strategies that maintain productivity and reduce the risk of large-scale disturbances in spruce-dominated ecosystems (Klimo et al. 2006; Souček et al. 2008; Hlásný et al. 2021). Building on this, recent research has shown that not only timing but also the intensity of thinning is crucial, with heavy pre-commercial thinning improving production efficiency compared to moderate thinning or no intervention (Černý 2023).

This study aimed to assess the effects of different silvicultural treatments on the ecological stability of Norway spruce stands and to identify which treatment is most suitable for their tending. Based on this objective, we formulated the following hypotheses:

H_1 : In the observed pure Norway spruce stands, heavy thinning from below primarily promotes tree growth and enhances drought resistance by reducing competition in the crown canopy layer.

H_2 : The resilience of Norway spruce depends on stand structure and site-specific conditions, particularly annual precipitation and mean annual air temperature.

MATERIAL AND METHODS

Study sites. For this study, three sets of permanent research plots consisting of pure Norway spruce stands subjected to different silvicultural treatments were selected: Blaník (BL; 49°39'04.0"N, 14°51'54.0"E), Tetřeví Boudy (TB; 50°50'40.0"N, 15°12'30.0"E) and Železná Ruda (ZR; 49°12'47.0"N, 13°20'49.0"E), as shown in Figure 1.

All three sites are part of the long-term silvicultural monitoring programme operated by the Forestry and Game Management Research Institute (FGMRI, Department of Silviculture) and have been monitored since the 1960s through regular five-year forest inventories. Each plot covers an area of 50 × 50 m, with a buffer zone 10–15 m wide separating the individual silvicultural variants and minimising the edge effects. Research plots were established in artificially regenerated stands using planting stock of autochthonous origin.

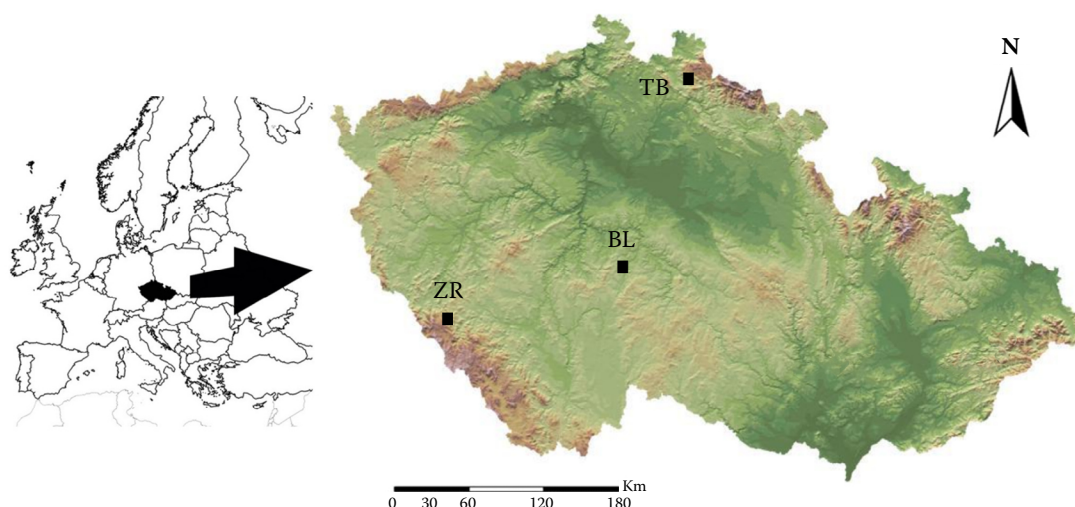


Figure 1. Localisation of the studied sites

BL – Blaník; TB – Tetřeví Boudy; ZR – Železná Ruda

<https://doi.org/10.17221/55/2025-JFS>

At the beginning of the experiment, each site comprised three plots: a control with no intervention and two thinning treatments (moderate, heavy). During the regional bark beetle outbreak, the control plots (and all comparable unmanaged stands of the same age and site conditions in the surrounding area) collapsed due to bark beetle-related mortality. Accordingly, the present analysis focuses on the two thinning treatments (moderate *vs* heavy).

Specifically, silvicultural treatments of varying cumulative intensities were applied: moderate thinning from below (hereinafter referred to as treatment 1) and heavy thinning from below (treatment 2). In the case of moderate thinning, the basal area was reduced by 7% during each intervention (cumulatively by 35%; $5 \times 7\%$), while heavy thinning involved a 10% reduction in basal area per intervention (cumulatively by 50%; $5 \times 10\%$). Interventions were conducted periodically every 10 years. The first intervention was carried out at the age of 31 years at the BL site (in 1965), 29 years at the TB site (1983), and 40 years at the ZR site (1969). Site characteristics are summarised in Table 1.

Sampling and descriptive statistics. At each plot, 20 trees were sampled using a Pressler increment borer (Haglöf, Sweden). Increment cores were extracted at the breast height (1.3 m) in two opposite directions (east-west). Trees were selected randomly at the plot, while focusing on including individuals from each tree class (dominant, co-dominant, intermediate) to avoid potential bias in the climate signal (Nehrbass-Ahles et al. 2014). On sloping terrain, cores were taken along the contour line to minimise the influence of reaction wood. In total, 120 cores were obtained, stabilised in wooden holders, and progressively sanded with sandpaper of increasing grit size (from 80 to 800) following the standard procedures (Stokes 1996).

All sanded cores were scanned using an Epson Perfection V600 Photo scanner (Epson, Japan) and saved in .jpg format. Ring widths were then measured using the CooRecorder software (Version 9.8.1, 2022) (Maxwell, Larsson 2021). Cross-dating was performed visually and statistically in CDendro (Version 9.8.1, 2022) using the Baillie-Pilcher *t*-value (Baillie, Pilcher 1973) and the Gleichlaufigkeit coefficient (Eckstein, Bauch 1969; Buras, Wilmking 2015).

The cross-dated dataset was exported in .rwl format and analysed using R (R Core Team 2024). To remove non-climatic effects, individual series were first detrended using a cubic smoothing

Table 1. Characteristics of the study sites in 2024

Site	Altitude (m a.s.l.)	PT (mm)	MAT (°C)	Soil type*	Typology**	Stand age (years)	YEE	Slope (%)	Aspect	Site index	Stand density (trees·ha ⁻¹)	Growing season (days)	K-G classifica- tion***
Blaník (BL)	410	625	7.9	Modal Cambisol	Fageto oligo- mesotrophicum	93	1966	2–4	N-W	32	485	200–205	Cfb
Tetřeví Boudy (TB)	935	861	7.2	Gleysol	Piceetum acidophilum	72	1979	2	N-W	28	419	190–200	Dfb
Železná Ruda (ZR)	930	1 106	6.2	Skeletal Cambisol	Abieto-Fagetum acidophilum	110	1969	5	S-W	26	540	170–180	Dfb

*Soil types according to WRB (2022); **site classification according to Viewegh et al. (2003); ***Köppen-Geiger classification according to Peel et al. (2007); PT – annual precipitation; MAT – mean annual air temperatures for 1960–2024; YEE – year of experiment establishment; K-G classification – Köppen-Geiger classification

spline with a 50% frequency cut-off at 30 years (Klesse et al. 2016). For analyses of long-term growth trends, the raw data were also detrended using a 100-year cubic smoothing spline (Cook, Peters 1981). The detrended chronologies were pre-whitened and combined into site chronologies using a robust biweight mean (Razavi, Vogel 2018).

Descriptive statistics were calculated to assess the quality of the tree-ring chronology. For raw measurements, the first-order autocorrelation ($Ar1$) was computed to evaluate the influence of previous growth on the current year's growth (Fritts 1976; Speer 2010). For the detrended series, we calculated the expressed population signal (EPS), the signal-to-noise ratio (SNR), and the mean inter-series correlation ($rbar$). EPS quantifies how well the samples represent a theoretical infinite chronology, while $rbar$ reflects the strength of the common growth signal. All dendrochronological statistics were computed using the 'dplR' package (Bunn 2008).

Climate. For the analysis of climate growth relationships, we obtained climate data from the nearest grid point of the E-OBS version 25.e dataset (Cornes et al. 2018). The dataset provides daily values of mean, minimum and maximum air temperatures, and daily precipitation sums. Based on these

variables, the $SPEI$ was calculated for each study site using the $SPEI$ R package (Beguería et al. 2014).

$SPEI$ values were computed on a daily basis for the period 1960–2023 and aggregated across multiple time scales (1–12 months) to capture short- and long-term drought effects.

Figures 2–4 show the trends in mean annual temperature and seasonal precipitation for each study site.

Data analysis of climate-growth relationships.

To assess site productivity, BAI was calculated from the raw tree-ring data (Bunn 2008). To evaluate the statistical difference between thinning intensities at individual sites, t -tests were performed. Long-term growth trends were evaluated using chronologies detrended with a cubic spline, which has a 50% frequency response at 100 years (Cook, Peters 1981).

The relationships between climate and growth were analysed using Pearson correlation at both monthly and daily resolutions, employing the 'dendroTools' R package (Jevšenak 2020), specifically the 'monthly_response' and 'daily_response' functions. Climate-growth responses were calculated for overlapping periods spanning the previous and current calendar years, using time windows rang-

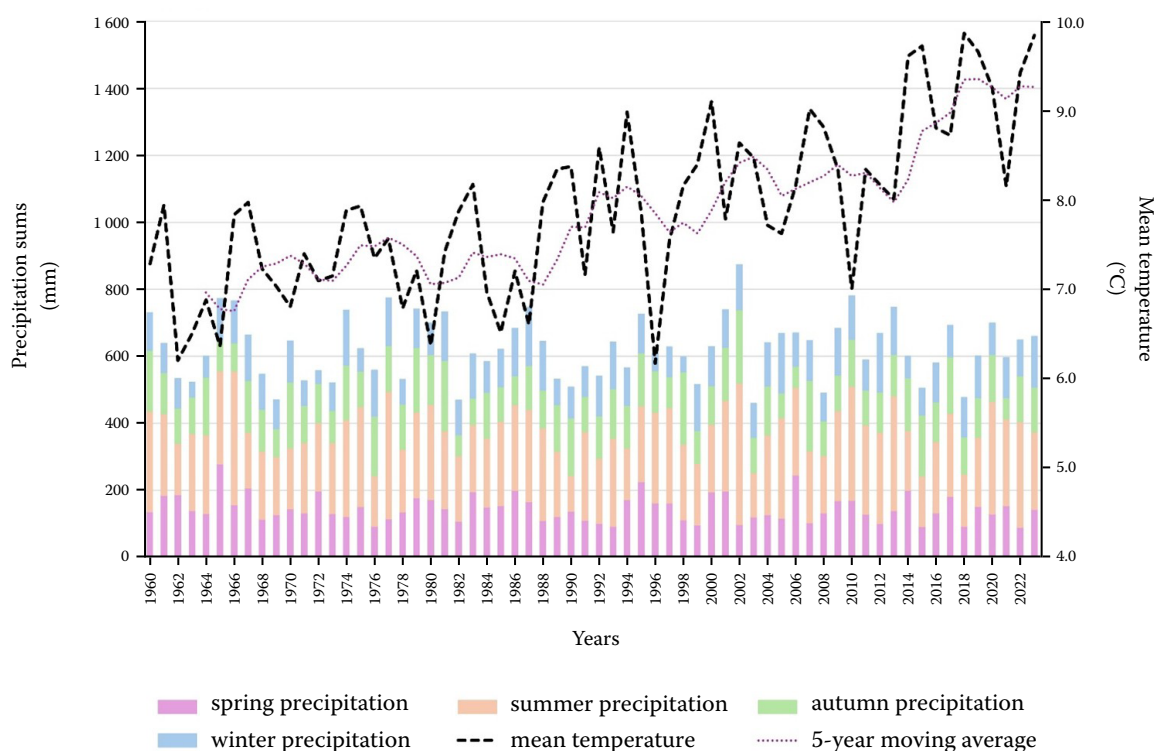


Figure 2. Course of mean annual temperature and seasonal precipitation at the Blaník (BL) study site

<https://doi.org/10.17221/55/2025-JFS>

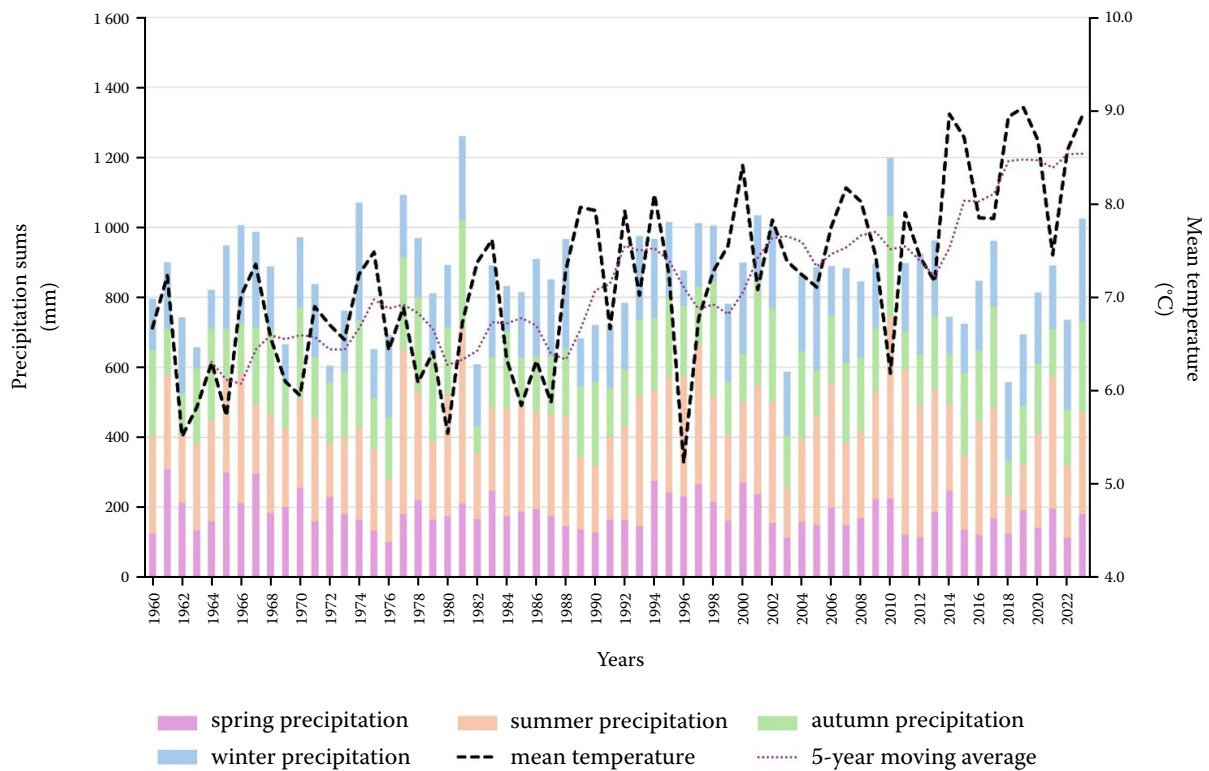


Figure 3. Course of mean annual temperature and seasonal precipitation at the Tetřeví Boudy (TB) study site

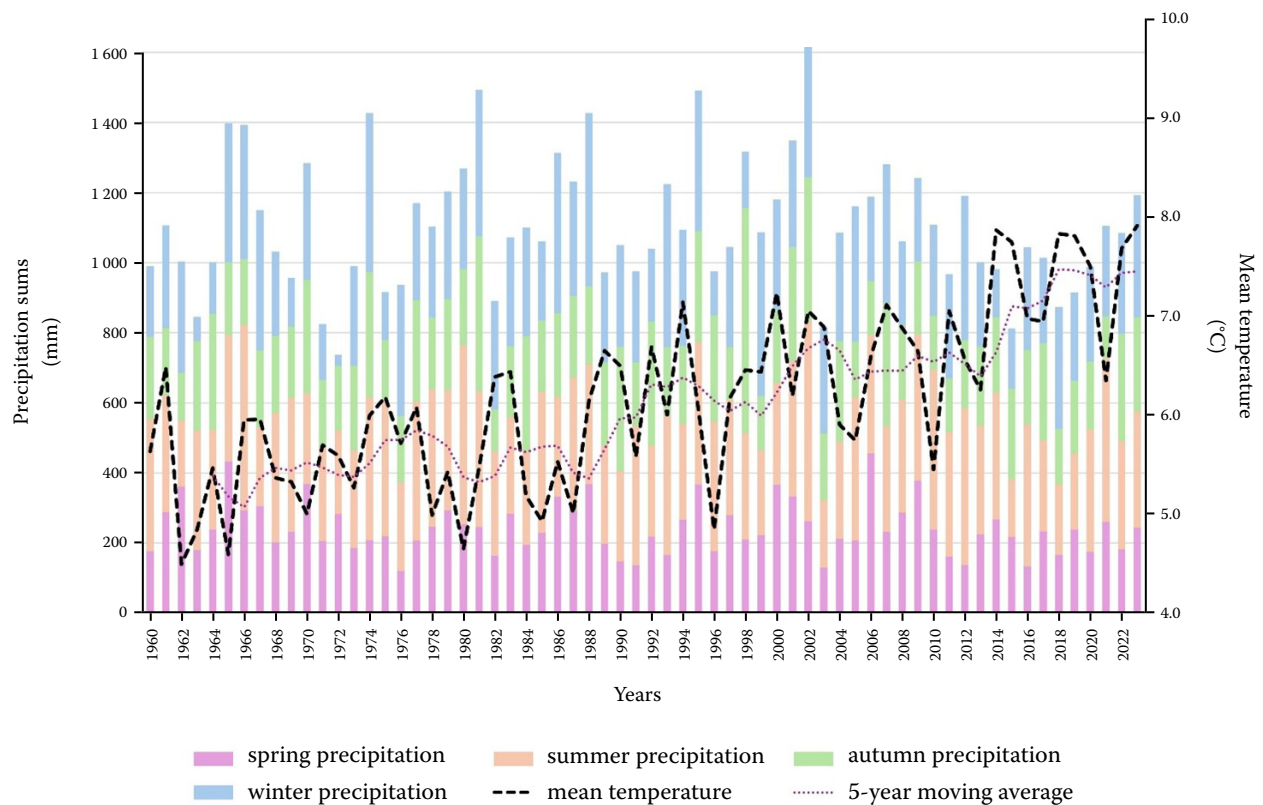


Figure 4. Course of mean annual temperature and seasonal precipitation at the Železná Ruda (ZR) study site

ing from 1 to 12 months (from January of the previous year to December of the current year).

To determine the temporal stability of climate-growth correlations, we applied a moving window correlation analysis. The dataset was systematically subdivided into 10-year intervals, starting with 1961–1970 and ending with 2014–2023. Within each subperiod, climate-growth relationships were computed between the tree-ring indices and monthly values of precipitation, air temperature, and *SPEI*.

To assess tree responses to extreme climatic events (e.g. extreme drought or air temperatures) in negative pointer years, we calculated four resil-

ience indices following Lloret et al. (2011): (i) resistance (*Rt*), (ii) recovery (*Rc*), (iii) resilience (*Rs*), and (iv) average relative growth reduction (*ARGR*). All resilience metrics were computed using the 'pointRes 2.0.' R package (Van der Maaten-Theunissen et al. 2021). To test for statistical differences in resilience indices between sites, we applied the Kruskal-Wallis test, and for statistical differences in resilience indices between different thinning intensities, we used the Wilcoxon signed-rank test, as the data did not follow a normal distribution (Jevšenak, Saražin 2023). Values of resilience indices and *P*-values are given in Table 2. Pointer years were defined as those with *SPEI* ≤ −1.5 during the

Table 2. Comparison of resilience indices between different thinning intensities on the studied sites and among-site comparison for specific treatment (Treatment 1 – moderate; Treatment 2 – heavy)

Year	BL1	BL2	<i>P</i> -value	TB1	TB2	<i>P</i> -value	ZR1	ZR2	<i>P</i> -value	<i>P</i> -value var. 1	<i>P</i> -value var. 2
<i>Rs</i>											
1976	1.20	1.11	0.36	1.68	1.67	0.49	1.17	1.42	0.01	0.61	0.00
2000	1.27	1.31	0.41	1.19	1.31	0.08	0.90	0.89	0.41	0.00	0.00
2003	1.20	1.37	0.16	1.22	1.21	0.45	0.83	0.87	0.22	0.00	0.00
2015	0.88	0.92	0.34	0.71	0.74	0.34	0.56	0.70	0.02	0.00	0.02
2019	1.01	1.20	0.07	0.93	0.81	0.14	1.40	1.79	0.02	0.00	0.00
<i>Rc</i>											
1976	1.44	1.60	0.12	1.43	1.59	0.11	1.54	1.60	0.28	0.25	0.82
2000	1.67	2.09	0.07	1.22	1.33	0.04	1.10	1.16	0.19	0.00	0.00
2003	1.13	1.30	0.09	1.24	1.27	0.38	1.27	1.19	0.14	0.18	0.42
2015	1.34	1.28	0.29	0.97	0.88	0.05	0.89	0.98	0.17	0.00	0.00
2019	1.47	1.83	0.02	1.14	1.02	0.11	1.32	1.56	0.03	0.82	0.00
<i>Rt</i>											
1976	0.79	0.73	0.24	1.14	1.07	0.30	0.77	0.88	0.01	0.16	0.00
2000	0.77	0.68	0.09	0.98	0.99	0.44	0.84	0.78	0.15	0.01	0.00
2003	1.18	1.06	0.24	0.99	0.96	0.29	0.69	0.74	0.15	0.02	0.00
2015	0.69	0.77	0.23	0.74	0.85	0.07	0.64	0.73	0.04	0.52	0.43
2019	0.77	0.69	0.17	0.81	0.81	0.49	1.09	1.19	0.24	0.05	0.00
<i>ARGR</i>											
1976	22.81	21.03	0.35	5.58	5.29	0.46	19.33	11.34	0.02	0.03	0.01
2000	18.57	29.24	0.02	6.54	4.99	0.32	16.79	18.07	0.37	0.04	0.00
2003	10.56	9.26	0.39	4.70	8.03	0.17	22.36	22.21	0.48	0.01	0.02
2015	28.39	25.69	0.33	13.10	11.24	0.41	30.88	28.79	0.37	0.02	0.04
2019	20.57	23.19	0.32	13.80	14.12	0.48	3.36	6.20	0.14	0.00	0.03

Rs – resilience; *Rc* – recovery; *Rt* – resistance; *ARGR* – average relative growth reduction; BL – Blaník; TB – Tetřeví Boudy; ZR – Železná Ruda; suffixes in plot names indicate the thinning intensity: 1 – moderate thinning, 2 – heavy thinning; *P*-value (var. 1) – the among-site comparison within Treatment 1 (moderate); *P*-value (var. 2) – the among-site comparison within Treatment 2 (heavy); bold – statistically significant values ($P < 0.05$)

<https://doi.org/10.17221/55/2025-JFS>

vegetation period (April–August) and a concurrent decrease in ring-width indices (computed using a 30-year spline). For the study, negative pointer years common to all three sites were considered.

RESULTS

Tree-ring chronology characteristics. The fundamental statistical parameters of the analysed tree-ring series are summarised in Table 3. All chronologies are suitable for further analysis. Pronounced first-order autocorrelation was observed, particularly at BL and ZR, indicating a significant effect of the previous year's conditions

on radial growth. *EPS* values (common threshold of 0.85; e.g. Cook et al. 1990; Bunn et al. 2020; Fuchs et al. 2025) and *SNR* (> 10 indicates a strong common signal in the chronology) show that the chronologies are representative and appropriate for subsequent analyses.

Growth trends. Among the studied sites, BL showed the most positive growth trends, with higher *BAI* under moderate thinning. Within sites, *BAI* differed significantly between thinning intensities at each site: $P = 0.044$ (BL), $P = 0.0076$ (TB), and $P < 0.001$ (ZR), indicating a clear effect of the thinning regime on radial growth across all locations (Figures 5–7).

Table 3. Summary statistics of tree-ring chronologies and climate-growth parameters for Norway spruce stands

Plot	No. Series	Avg. Ser. Lng.	Timespan	Mean <i>Ar1</i>	<i>rbar</i>	<i>EPS</i>	<i>SNR</i>
BL1	19	75.78	1939–2023	0.57	0.46	0.94	16.33
BL2	20	71.50	1939–2023	0.60	0.40	0.93	12.86
TB1	16	56.13	1961–2023	0.75	0.47	0.88	7.07
TB2	18	56.72	1964–2023	0.70	0.49	0.95	17.19
ZR1	19	73.68	1943–2023	0.78	0.49	0.95	18.50
ZR2	18	66.88	1946–2023	0.71	0.49	0.95	17.05

No. Series – number of measured trees; Avg. Ser. Lng. – length of the average tree ring series; Mean *Ar1* – mean first-order autocorrelation of raw data; *rbar* – mean inter-series correlation; *EPS* – expressed population signal; *SNR* – signal-to-noise ratio; BL1 – Blaník moderately thinned from below; BL2 – Blaník heavily thinned from below; TB1 – Tetřeví Boudy moderately thinned from below; TB2 – Tetřeví Boudy heavily thinned from below; ZR1 – Železná Ruda moderately thinned from below; ZR2 – Železná Ruda heavily thinned from below

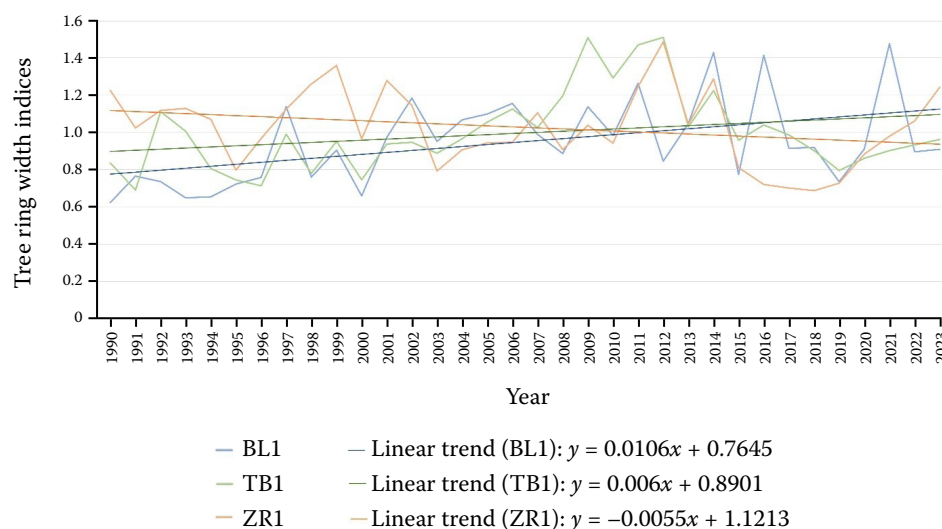


Figure 5. Growth trend of Norway spruce stands thinned from below with moderate intensity at all sites (1990–2023)

BL1 – Blaník moderately thinned from below; TB1 – Tetřeví Boudy moderately thinned from below; ZR1 – Železná Ruda moderately thinned from below

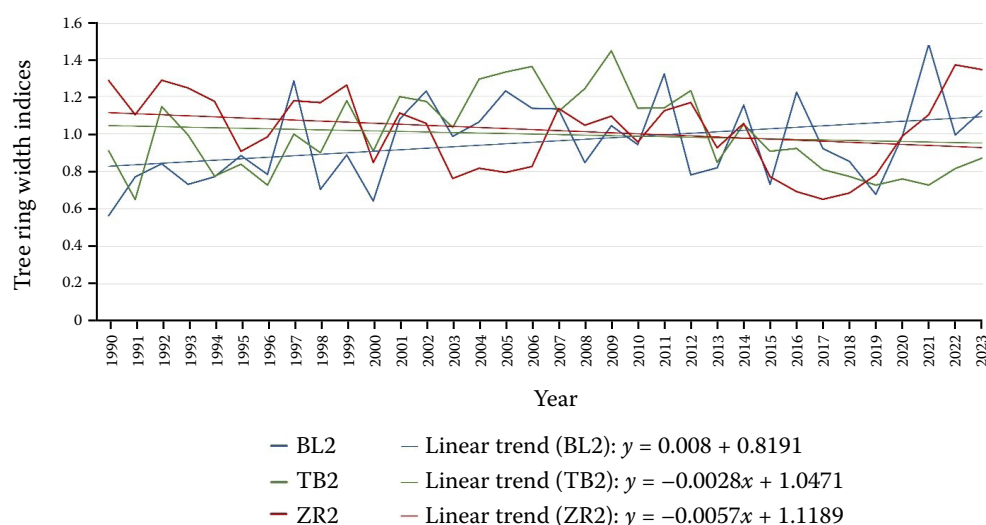


Figure 6. Growth trend of Norway spruce stands thinned from below with heavy intensity at all sites (1990–2023)

BL2 – Blaník heavily thinned from below; TB2 – Tetřeví Boudy heavily thinned from below; ZR2 – Železná Ruda heavily thinned from below

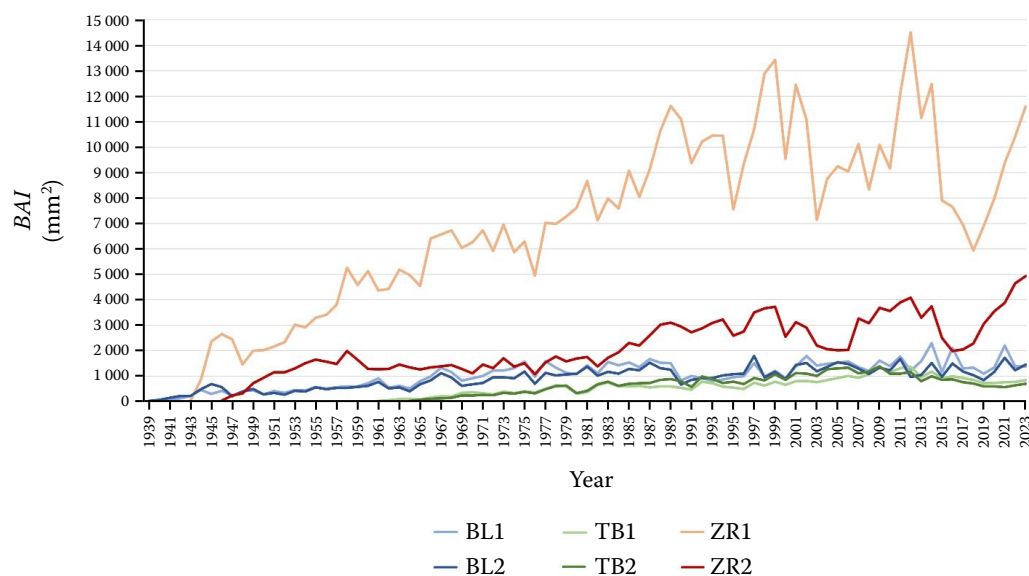


Figure 7. Basal area increment (BAI) of Norway spruce at all studied sites

BL1 – Blaník moderately thinned from below; BL2 – Blaník heavily thinned from below; TB1 – Tetřeví Boudy moderately thinned from below; TB2 – Tetřeví Boudy heavily thinned from below; ZR1 – Železná Ruda moderately thinned from below; ZR2 – Železná Ruda heavily thinned from below

The effects of climate on growth. The results of climate-growth analysis are presented as heat-maps for daily climate variables (Figures 8 and 9). At the BL site, tree growth was positively influenced by precipitation and the *SPEI* during both the year of tree-ring formation and the preceding year, regardless of thinning intensity. In shorter time windows, positive correlations emerged

around day of year (DOY) 170 (June) and 250 (early September). The positive influence extended from DOY 250 to DOY 365 when longer time windows were used. The effect of mean daily air temperature on radial growth was generally negative, with peaks around DOY 100 and 300 in the previous year and DOY 270 in the current year. Heavy thinning showed stronger correlations with the pre-

<https://doi.org/10.17221/55/2025-JFS>

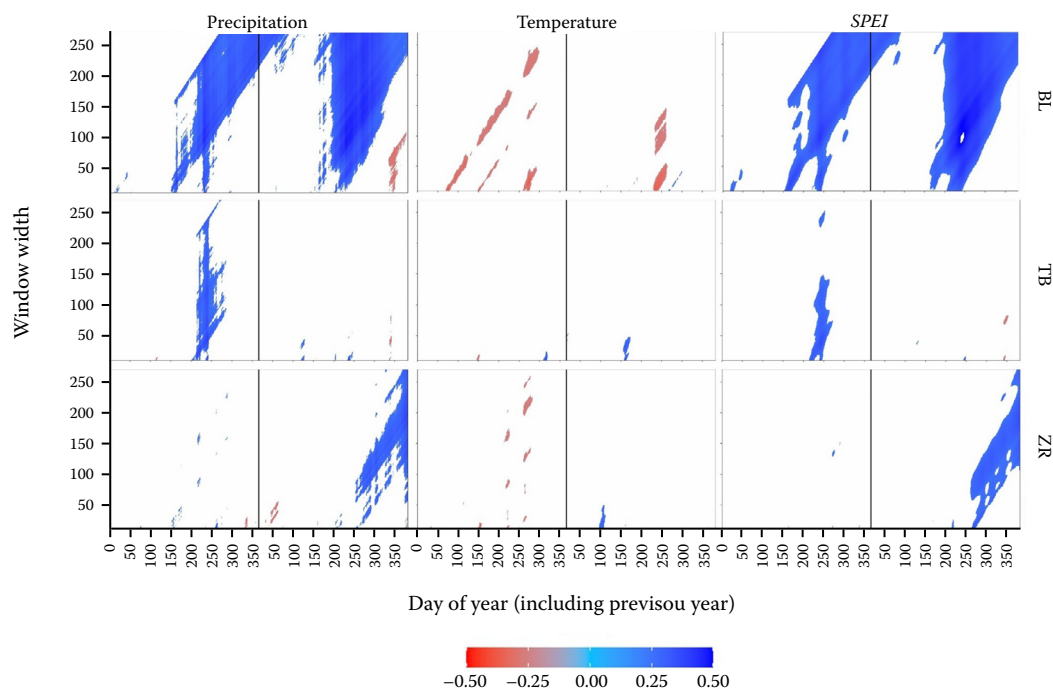


Figure 8. Heatmap of daily Pearson correlation coefficients between tree-ring indices and climate variables for moderately thinned Norway spruce stands

SPEI – standardised precipitation-evapotranspiration index; BL – Blaník; TB – Tetřeví Boudy; ZR – Železná Ruda; vertical lines separate the previous and current years; only statistically significant correlations ($P < 0.05$) are shown

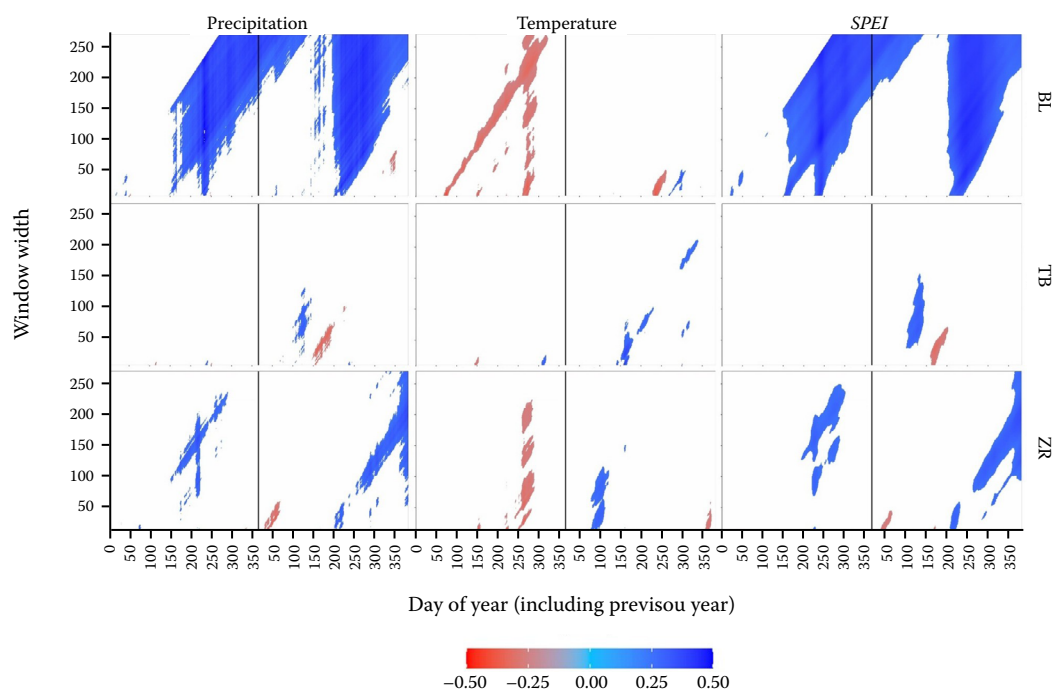


Figure 9. Heatmap of daily Pearson correlation coefficients between tree-ring indices and climate variables for heavily thinned Norway spruce stands

SPEI – standardised precipitation-evapotranspiration index; BL – Blaník; TB – Tetřeví Boudy; ZR – Železná Ruda; vertical lines separate the previous and current years; only statistically significant correlations ($P < 0.05$) are shown

vious year's climate, whereas moderate thinning was more strongly affected by the current year's conditions. In stands outside the natural range of Norway spruce (BL), heavy thinning appeared to reduce heat stress during the current year but increased sensitivity to heat stress in the preceding year. No evident differences were observed between thinning intensities in terms of precipitation and *SPEI* effects.

At the TB site, tree growth under moderate thinning was positively correlated with precipitation after DOY 200 (late June) in the preceding year. In contrast, under heavy thinning, precipitation during the current year was more important. Positive correlations began after DOY 120 (early May) when using a ≥ 50 -day window, while negative correlations appeared after DOY 150. The mean air temperature in the previous year has a negligible effect, but in the current year, temperatures after DOY 150 (June) positively influenced radial growth under both thinning regimes. Additionally,

growth responded positively to summer air temperatures when longer window sizes were used.

At the ZR site, all three climate variables (precipitation, temperature, *SPEI*) revealed differences between thinning treatments. Both regimes showed positive correlations with autumn precipitation, particularly using windows longer than 50 days. In the current year, heavy thinning was positively correlated with summer precipitation (DOY 200) but negatively with early February precipitation. In the preceding year, moderate thinning showed negligible correlations, whereas heavy thinning displayed a positive effect between DOY 150 and 200, with windows > 50 days. *BAI* in both studied treatments (moderate vs heavy) were positively influenced by spring air temperatures (DOY 100), although heavy thinning was more affected by autumn temperatures of the previous year.

The results of the moving-window correlation analysis (Figures 10 and 11) showed the temporal evolution of climate-growth relationships. At the BL site,

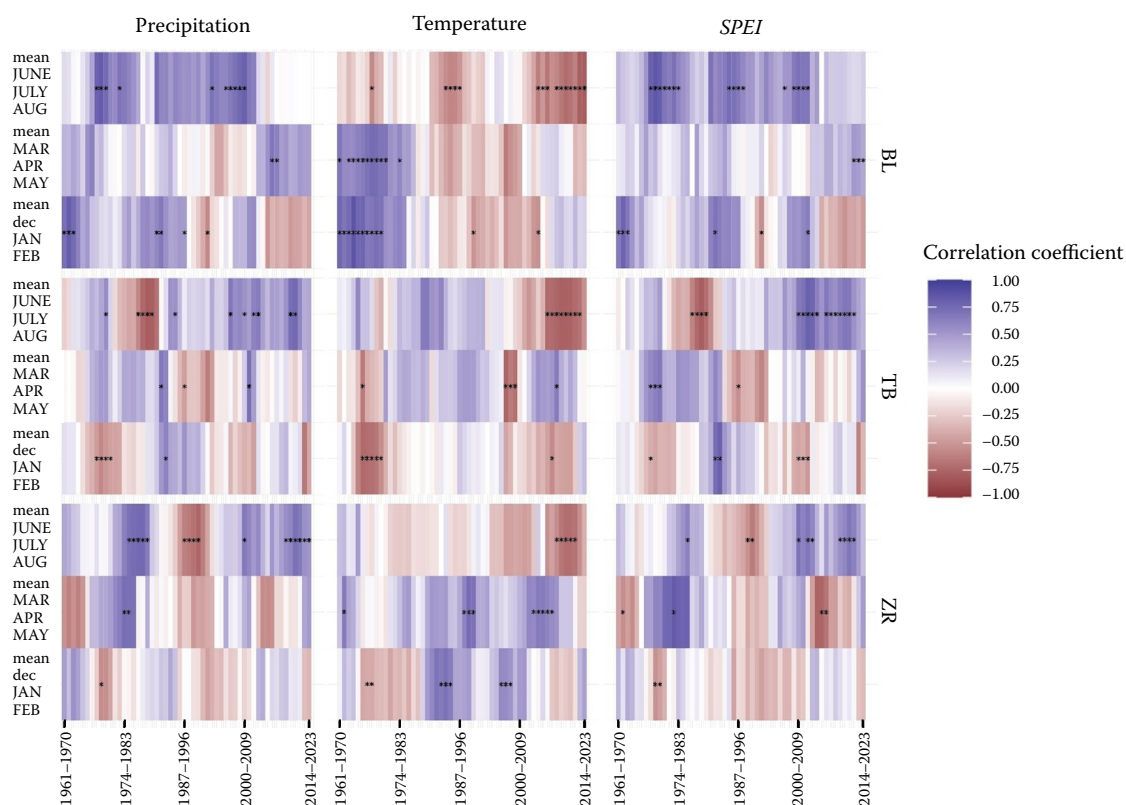


Figure 10. Moving-window (10-year) Pearson correlation coefficients between tree-ring indices and climate variables for moderately thinned Norway spruce stands

*Statistically significant correlations ($P < 0.05$); lowercase letters – months of the year preceding tree ring formation; uppercase letters – months of tree ring formation; *SPEI* – standardised precipitation-evapotranspiration index; BL – Blaník; TB – Tetřeví Boudy; ZR – Železná Ruda

<https://doi.org/10.17221/55/2025-JFS>

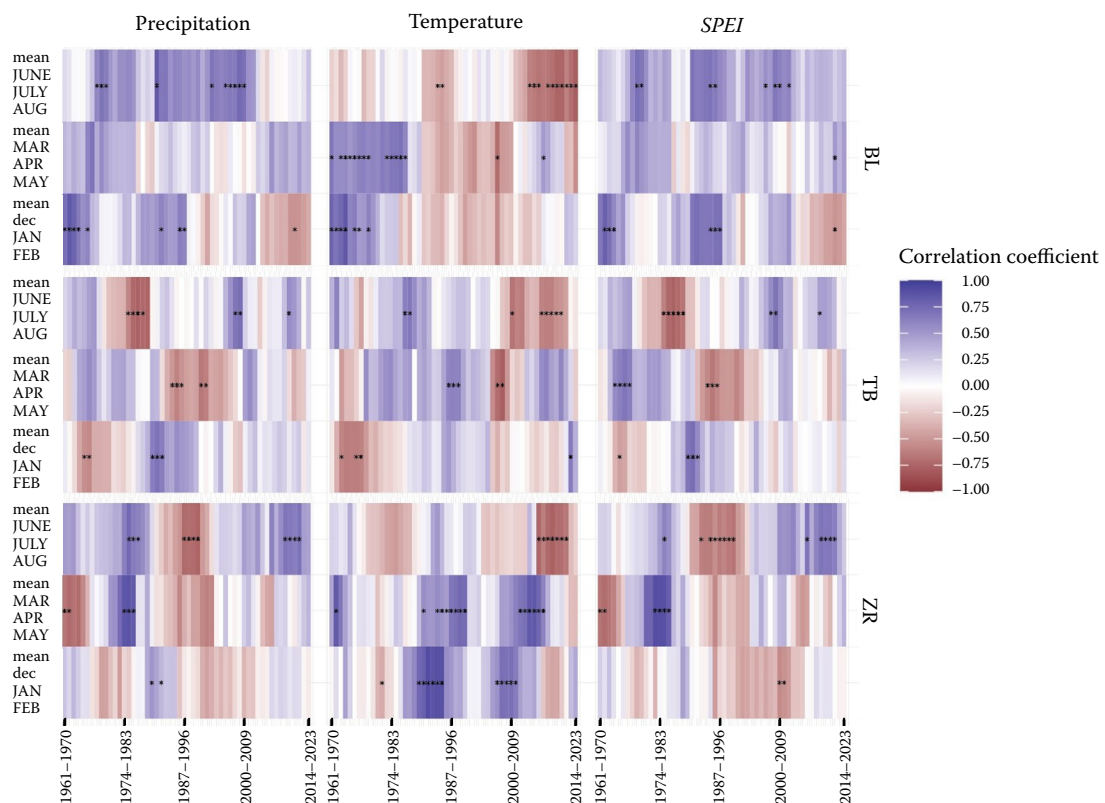


Figure 11. Moving window (10-year) Pearson correlation coefficients between tree-ring indices and climate variables for heavily thinned Norway spruce stands

*Statistically significant correlations ($P < 0.05$); lowercase letters – months of the year preceding tree ring formation; uppercase letters – months of tree ring formation; *SPEI* – standardised precipitation-evapotranspiration index; BL – Blaník; TB – Tetřeví Boudy; ZR – Železná Ruda

both thinning treatments displayed a shift in positive correlations with precipitation from summer to spring months in recent decades. Notably, moderate thinning consistently showed higher correlation values. In contrast, the previously positive influence of winter precipitation turned negative in recent decades. In recent decades, radial increment (*BAI*) in both thinning treatments has become increasingly negatively correlated with summer temperatures.

The TB site followed a similar pattern. Correlation coefficients for both air temperature and precipitation increased over the last decade, with moderate thinning again showing stronger relationships. Temperature effects also shifted, becoming more negative in summer and more positive in spring in recent decades.

At the ZR site, a pattern similar to the TB site was observed. The correlation between radial growth and summer precipitation increased over time, while the negative effect of summer temperatures also became more pronounced. For both climate

variables, the moderate thinning treatment showed a greater climatic sensitivity.

Resistance, resilience, recovery and average relative growth reduction. We assessed differences in *Rt*, *Rc*, *Rs*, and *ARGR* both between thinning intensities within sites (Figure 12) and among sites within each intensity (Figures 13 and 14).

Within sites, differences were generally not significant. The ZR site was an exception: in 1976, all indices except *Rc* differed significantly; additional differences at ZR were observed for *Rs* and *Rt* in 2015, and for *Rs* and *Rc* in 2019 (Figure 12).

Among sites, contrasts were more pronounced (Figures 13 and 14). Under moderate thinning, most years showed significant among-site variation across indices, with all indices differing in 2000 (Figure 13). *ARGR* was consistently lower and differed significantly across years. Under heavy thinning, *Rs* and *ARGR* differed in all analysed years, *Rc* was not significant in 1976 and 2003, and *Rt* reached significance only in 2015 (Figure 14).

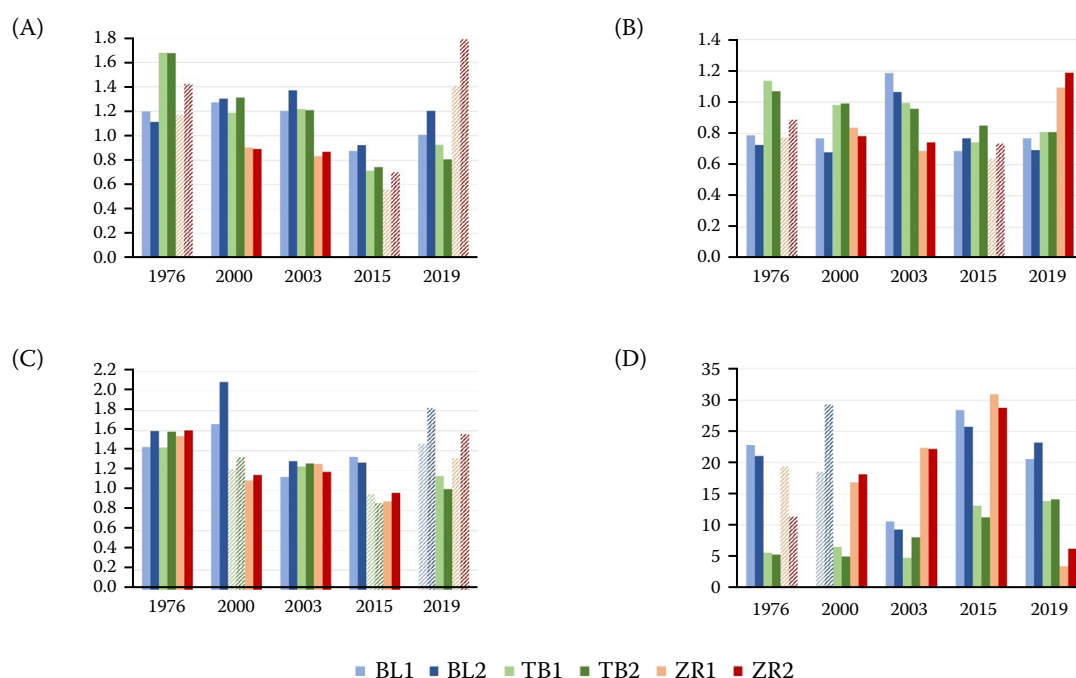


Figure 12. (A) Resilience, (B) resistance, (C) recovery, and (D) average relative growth reduction indices for the studied pure Norway spruce stands

Hatched bars – statistically significant values ($P < 0.05$); BL1 – Blaník moderately thinned from below; BL2 – Blaník heavily thinned from below; TB1 – Tetřeví Boudy moderately thinned from below; TB2 – Tetřeví Boudy heavily thinned from below; ZR1 – Železná Ruda moderately thinned from below; ZR2 – Železná Ruda heavily thinned from below

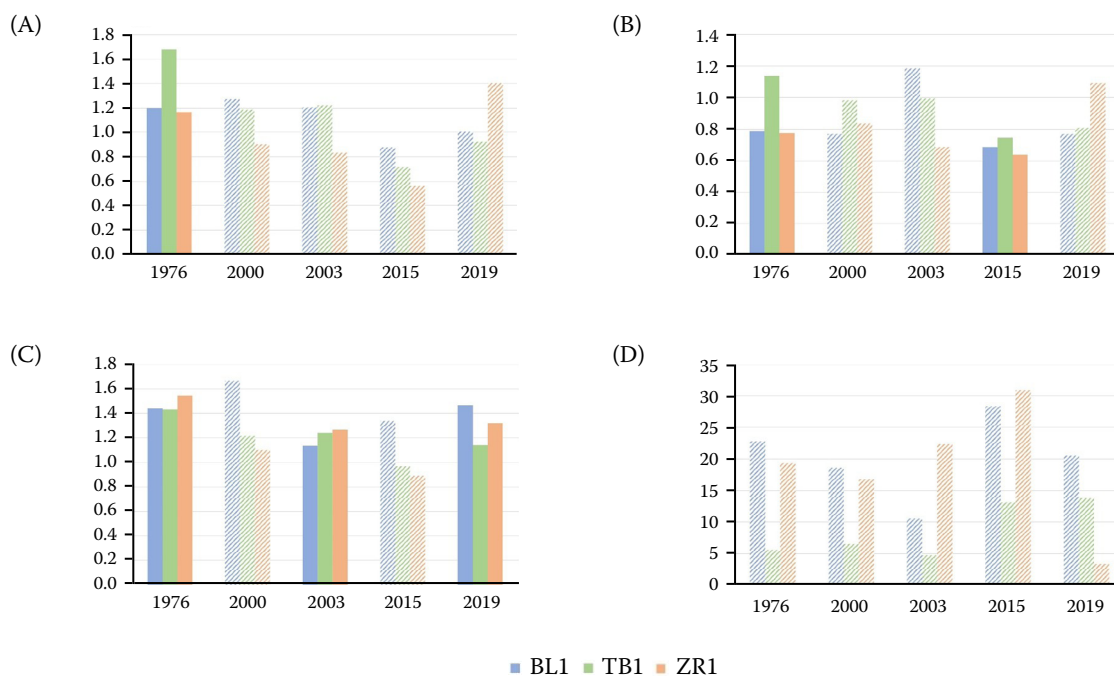


Figure 13. (A) Resilience, (B) resistance, (C) recovery, and (D) average relative growth reduction indices for moderate thinning from below at the studied sites

Hatched bars – statistically significant values ($P < 0.05$); BL1 – Blaník moderately thinned from below; TB1 – Tetřeví Boudy moderately thinned from below; ZR1 – Železná Ruda moderately thinned from below

<https://doi.org/10.17221/55/2025-JFS>

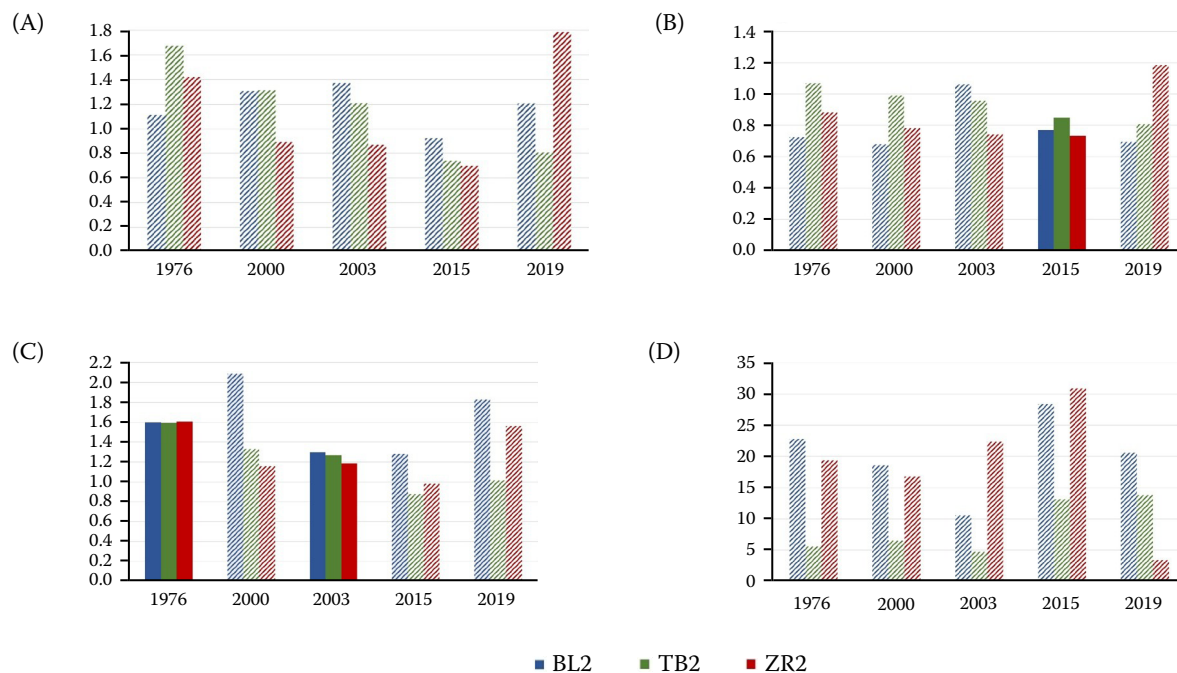


Figure 14. (A) Resilience, (B) resistance, (C) recovery, and (D) average relative growth reduction indices for heavy thinning from below at the studied sites

Hatched bars – statistically significant values ($P < 0.05$); BL2 – Blaník heavily thinned from below; TB2 – Tetřeví Boudy heavily thinned from below; ZR2 – Železná Ruda heavily thinned from below

DISCUSSION

Intensity and type of silvicultural management are widely discussed in forestry from both economic and ecological perspectives (Chen et al. 2017; Nolet et al. 2018; Toraño Caicoya et al. 2018; Vacek et al. 2020). As silvicultural treatments have long-term effects, we sampled permanent research plots established in the 1960s, where long-term effects are now observable. For this study, we selected three paired plots under heavy and moderate thinning, located inside and outside the natural range of Norway spruce in the CR (Figures 1–4; Table 1).

In terms of productivity (*BAI*), the highest values were observed at the ZR site, followed by the BL and TB sites. These results highlight the importance of evenly distributed and abundant precipitation (D'Andrea et al. 2023) and the negative effect of high water tables on Norway spruce productivity, even at sites within its natural range (Dymond et al. 2015). At lower elevation (BL), Norway spruce performed surprisingly well despite being outside its ecological optimum. Under such conditions, the use of local, lowland-adapted ecotypes can be beneficial (Šimůnek et al. 2023). However, since

the productivity of a stand does not necessarily reflect its ecological stability or sustainability (Vose et al. 2016), other metrics were evaluated, particularly linear growth trends since 1990.

At the BL and ZR sites, both thinning intensities showed similar growth trends, either positive or negative. Only at the TB site did radial growth trends differ between thinning intensities, with moderate thinning associated with a positive trend, while heavy thinning led to a negative one. This negative effect of heavy thinning at TB may be linked to elevated water table levels, as described by Leppä et al. (2020). Similar effects of thinning on the soil environment have also been documented with respect to organic horizon dynamics, where canopy opening reduced the accumulation of surface humus and modified its chemical properties (Podrázský 2006; Podrázský, Remeš 2007; Podrázský et al. 2005). In contrast, thinning intensity had less effect at sites without high soil water influence (BL, ZR), whereas on waterlogged sites (TB), higher thinning intensity led to a marked decline in radial growth. A similar phenomenon was reported by Mäkinen and Isomäki (2004) in Finland. This declining growth trend may be attributed to the disruption of the water

pump effect, where the removal of a critical number of trees results in a rising water table and subsequent hypoxia stress on the remaining trees (Wang et al. 2013; Tulik et al. 2020).

These observations allow us to critically evaluate our original hypotheses. While H_1 assumed that heavy thinning would promote growth and drought resistance through reduced crown competition, our findings show that this effect is not consistent. In fact, heavy thinning had adverse effects, especially at the waterlogged TB site. Conversely, H_2 was supported, as the observed differences in growth and resilience were largely driven by site-specific conditions such as precipitation, air temperature, and soil water regime.

Regarding climate-growth relationships, the effects of thinning intensity were highly site-specific. At BL and ZR sites, heavy thinning increased correlations between radial growth and previous-year variables (mean monthly precipitation, mean monthly temperature, and *SPEI*). It suggests that heavy thinning reduces competition for soil moisture, improving water availability and making tree growth more responsive to previous-year precipitation (Zavadilová et al. 2023). However, heavy thinning also increases exposure to air temperature extremes due to altered stand microclimate (Vejpustková, Čihák 2019).

At the waterlogged TB site, the opposite pattern was observed – correlations with climate were stronger in the current year. It can be explained by changes in root system architecture under high water table conditions. In such environments, Norway spruce typically develops a shallow root system concentrated in the better-aerated upper soil layers (Coutts, Philipson 1978). This shallow rooting makes the stand more susceptible to current climatic conditions, particularly when heavy thinning increases soil temperature and moisture variability (Parmenter, Losleben 2023). The most detrimental effects of heavy thinning occur during spring precipitation events, when rising water tables induce hypoxia and suppress growth (Wang et al. 2013). Nevertheless, no significant differences between thinning intensities were detected when assessing long-term trends in climate-growth relationships.

When evaluating resilience indices (R_s , R_c , R_t , and $ARGR$) across five pointer years, no significant differences were found between thinning intensities at most sites. The exception was the ZR site, where significant differences were observed in about one-

third of the evaluated indices. It suggests that under favourable site conditions for Norway spruce, heavy thinning may strengthen tree performance during years with pronounced growth reductions. Similar conclusions have been drawn by studies showing that, in nutrient-rich conditions, heavy thinning can reduce competition and improve access to water and light (D'Amato et al. 2013; Sohn et al. 2016).

On the other hand, multiple studies have shown that the effects of thinning on resistance to climate stress are highly variable, often being overridden by local site conditions, and in some cases, negligible (Zang et al. 2014). Our results support this: resilience indices varied significantly among sites under the same thinning intensity, which highlights that site-specific factors primarily shape stand response to non-favourable growing conditions. These findings are consistent with previous research that emphasised the importance of ecological context in determining forest resistance and resilience (Lloret et al. 2011; Gazol et al. 2017). However, our results on resilience indices must be interpreted with caution, as the age of the studied stands differed by up to 38 years. According to the findings of other authors, the response of spruce to non-favourable years differs with age due to physiological reasons (Schuster, Oberhuber 2013; Mikulénka et al. 2020).

CONCLUSION

This study evaluated the effects of thinning treatments of differing intensities on stand productivity and climate-growth relationships in pure Norway spruce stands established across contrasting site conditions. The results demonstrate that, under normal hydrological regimes, moderate thinning contributes positively to stand productivity and ecological stability. In extreme sites, such as those susceptible to strong winds, heavy thinning can be beneficial, but only if it is applied early, ideally during the initial developmental phases (thickets, small-pole stands), to secure long crowns and mechanical stability. When introduced too late, however, heavy thinning may induce adverse effects, including increased susceptibility to windthrow and alterations of nutrients and water cycles. At the waterlogged site, heavy thinning suppresses tree growth, likely due to disrupted soil water dynamics and reduced physiological tolerance resulting from the loss of the water pump effect.

<https://doi.org/10.17221/55/2025-JFS>

This phenomenon was also observed at the site presented in our study. Although thinning intensity can influence tree growth responses to adverse growing conditions, the results suggest that local site conditions have a more substantial effect on forest resilience. Based on our findings, at waterlogged sites, it is advisable to perform only moderate interventions up to the point of mechanical stabilisation of the stand, whereas at sites with a normal water regime, heavy thinning can be employed to enhance volume production. Moreover, to improve stand adaptability while maintaining production, management strategies must be tailored specifically to each site type. Nevertheless, this study is limited by the small number of sites and relatively basic climatic characterisation, which constrains the generalisation of our conclusions. Therefore, future research should extend to a broader range of ecological conditions and involve site-specific factors such as horizontal precipitation. Despite these limitations, the management recommendations presented here provide practical guidance: moderate thinning appears most suitable for waterlogged sites, whereas heavy thinning can be considered for extreme sites (e.g. wind-exposed stands).

REFERENCES

- Adams H.D., Luce C.H., Breshears D.D., Allen C.D., Weiler M., Hale V.C., Smith A.M.S., Huxman T.E. (2012): Ecohydrological consequences of drought- and infestation-triggered tree die-off: Insights and hypotheses. *Ecohydrology*, 5: 145–159.
- Anderegg W.R., Hicke J.A., Fisher R.A., Allen C.D., Aukema J., Bentz B., Hood S., Lichstein J.W., Macalady A.K., McDowell N., Pan Y., Raffa K., Sala A., Shaw J.D., Stephenson N.L., Tague C., Zeppel M. (2015): Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytologist*, 208: 674–683.
- Baillie M.G.L., Pilcher J.R. (1973): A simple crossdating program for tree-ring research. *Tree-Ring Bulletin*, 33: 7–14.
- Beguiría S., Vicente-Serrano S.M., Reig F., Latorre B. (2014): Standardized precipitation evapotranspiration index (SPEI) revisited: Parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. *International Journal of Climatology*, 34: 3001–3023.
- Biondi F., Qeadan F. (2008): A theory-driven approach to tree-ring standardization: Defining the biological trend from expected basal area increment. *Tree-Ring Research*, 64: 81–96.
- Brang P., Spathelf P., Larsen J.B., Bauhus J., Bončina A., Chauvin C., Drössler L., García-Güemes C., Heiri C., Kerr G., Lexer M.J., Mason B., Mohren F., Mühlethaler U., Nocentini S., Svoboda M. (2014): Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. *Forestry*, 87: 492–503.
- Bunn A.G. (2008): A dendrochronology program library in R (dplR). *Dendrochronologia*, 26: 115–124.
- Bunn A.G., Korpela M., Biondi F., Campelo F., Mérian P., Qeadan F., Zang C. (2020): dplR: Dendrochronology Program Library in R. R Package Version 2020. Vienna, R Foundation. Available at: <https://github.com/OpenDendro/dplR>
- Buras A., Wilmking M. (2015): Correcting the calculation of Gleichläufigkeit. *Dendrochronologia*, 34: 29–30.
- Campelo F., Gutiérrez E., Ribas M., Sanchez-Salguero R., Nabais C., Camarero J.J. (2018): The facultative bimodal growth pattern in *Quercus ilex* – A simple model to predict sub-seasonal and inter-annual growth. *Dendrochronologia*, 49: 77–88.
- Caudullo G., Tinner W., De Rigo D. (2016): *Picea abies* in Europe: Distribution, habitat, usage and threats. *European Atlas of Forest Tree Species*, 114: 116.
- Cavin L., Mountford E.P., Peterken G.F., Jump A.S. (2013): Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. *Functional Ecology*, 27: 1424–1435.
- Černý J. (2023): Pre-commercial thinning in young Norway spruce stands as a tool mitigating global climate change? *Zprávy lesnického výzkumu*, 68: 149–158. (in Czech)
- Chen S., Shahi C., Chen H.Y., McLaren B. (2017): Economic analysis of forest management alternatives: Compositional objectives, rotation ages, and harvest methods in boreal forests. *Forest Policy and Economics*, 85: 124–134.
- Cook E.R., Peters K. (1981): The smoothing spline: A new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bulletin*, 41: 45–53.
- Cook E.R., Kairiukstis L.A. (1990): *Methods of Dendrochronology: Applications in the Environmental Sciences*. Dordrecht, Kluwer Academic Publishers: 394.
- Cornes R.C., van der Schrier G., van den Besselaar E.J.M., Jones P.D. (2018): An ensemble version of the E-OBS temperature and precipitation data sets. *Journal of Geophysical Research: Atmospheres*, 123: 9391–9409.
- Cosofret C., Bouriaud L. (2019): Which silvicultural measures are recommended to adapt forests to climate change? A literature review. *Bulletin of the Transilvania University of Brasov. Series II: Forestry Wood Industry Agricultural Food Engineering*, 12: 13–34.
- Coutts M.P., Philipson J.J. (1978): Tolerance of tree roots to waterlogging: II. Adaptation of Sitka spruce and lodgepole pine to waterlogged soil. *New Phytologist*, 80: 71–77.

- D'Amato A.W., Bradford J.B., Fraver S., Palik B.J. (2013): Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. *Ecological Applications*, 23: 1735–1742.
- D'Andrea G., Šimůnek V., Pericolo O., Vacek Z., Vacek S., Corleto R., Olejár L., Ripullone F. (2023): Growth response of Norway spruce [*Picea abies* (L.) Karst.] in central Bohemia (Czech Republic) to climate change. *Forests*, 14: 1215.
- Dodan M., Perić S. (2019): Windthrow resistance of Norway spruce [*Picea abies* (L.) Karst.] forest cultures – Preliminary results. *South-East European Forestry: SEEFOR*, 10: 77–88.
- Dušek D., Novák J., Slodičák M. (2014): Response of young spruce stands on thinning in stands affected by long-term decline. *Zpravy lesnického výzkumu*, 59: 104–108. (in Czech)
- Dymond S., Kolka R.K., Bolstad P.V., Gill K., Curzon M., D'Amato A.W. (2015): Excess growing-season water limits lowland black spruce productivity. In: *AGU Fall Meeting Abstracts*, Vol. 2015, San Francisco, Dec 14–18, 2015: GC33B-1277.
- Eckstein D., Bauch J. (1969): Beitrag zur Rationalisierung eines dendrochronologischen Verfahrens und zur Analyse seiner Aussagesicherheit. *Forstwissenschaftliches Centralblatt*, 88: 230–250. (in German)
- Fritts H.C. (1971): Dendroclimatology and Dendroecology. *Quaternary Research*, 1: 419–449.
- Fritts H.C. (1976): *Tree Rings and Climate*. New York, Academic Press: 567.
- Fuchs Z., Vacek Z., Vacek S., Černý J., Cukor J., Šimůnek V., Gallo J., Hájek V. (2025): Growth responses of European beech (*Fagus sylvatica* L.) and Oriental beech (*Fagus orientalis* Lipsky) along an elevation gradient under global climate change. *Forests*, 16: 655.
- Gazol A., Camarero J.J., Anderegg W.R.L., Vicente-Serrano S.M. (2017): Impacts of droughts on the growth resilience of Northern Hemisphere forests. *Global Ecology and Biogeography*, 26: 166–176.
- Hlásný T., Zimová S., Merganičová K., Štěpánek P., Modlinger R., Turčáni M. (2021): Devastating outbreak of bark beetles in the Czech Republic: Drivers, impacts, and management implications. *Forest Ecology and Management*, 490: 119075.
- Huber C., Langmaier M., Stadlmann A., Hochbichler E., Grabner M., Teischinger A., Konnerth J., Grabner M., Müller U., Pramreiter M. (2023): Potential alternatives for Norway spruce wood: A selection based on defect-free wood properties. *Annals of Forest Science*, 80: 41.
- IUSS Working Group WRB (2022): World Reference Base for Soil Resources. *International Soil Classification System for Naming Soils and Creating Legends for Soil Maps*. 4th Ed. Vienna, International Union of Soil Sciences (IUSS): 236.
- Jaime L., Batllori E., Lloret F. (2024): Bark beetle outbreaks in coniferous forests: A review of climate change effects. *European Journal of Forest Research*, 143: 1–17.
- Jansson G., Danusevičius D., Grotehusman H., Kowalczyk J., Krajmerova D., Skroppa T., Wolf H. (2013): Norway Spruce [*Picea abies* (L.) H. Karst.]. In: Pâques L. (ed.): *Forest Tree Breeding in Europe: Current State-of-the-Art and Perspectives*. Dordrecht, Springer: 123–176.
- Jevšenak J. (2020): New features in the dendroTools R package: Bootstrapped and partial correlation coefficients for monthly and daily climate data. *Dendrochronologia*, 63: 125753.
- Jevšenak J., Saražin J. (2023): *Pinus halepensis* is more drought tolerant and more resistant to extreme events than *Pinus nigra* at a sub-Mediterranean flysch site. *Trees*, 37: 1281–1286.
- Klesse S., Etzold S., Frank D. (2016): Integrating tree-ring and inventory-based measurements of aboveground biomass growth: Research opportunities and carbon cycle consequences from a large snow breakage event in the Swiss Alps. *European Journal of Forest Research*, 135: 297–311.
- Klimo E., Kulhavý J. (2006): Norway spruce monocultures and their transformation to close-to-nature forests from the point of view of soil changes in the Czech Republic. *Ekológia (Bratislava)*, 25: 27–43.
- Leppä K., Hökkä H., Laiho R., Launiainen S., Lehtonen A., Mäkipää R., Peltoniemi M., Saarinen M., Sarkkola S., Nieminen M. (2020): Selection cuttings as a tool to control water table level in boreal drained peatland forests. *Frontiers in Earth Science*, 8: 576510.
- Lloret F., Keeling E.G., Sala A. (2011): Components of tree resilience: Effects of successive low-growth episodes in old ponderosa pine forests. *Oikos*, 120: 1909–1920.
- Mäkinen H., Isomäki A. (2004): Thinning intensity and long-term changes in increment and stem form of Norway spruce trees. *Forest Ecology and Management*, 201: 295–309.
- Maxwell R.S., Larsson L.A. (2021): Measuring tree-ring widths using the CooRecorder software application. *Dendrochronologia*, 67: 125841.
- Mikulénka P., Prokúpková A., Vacek Z., Vacek S., Bulušek D., Simon J., Šimůnek V., Hájek V. (2020): Effect of climate and air pollution on radial growth of mixed forests: *Abies alba* Mill. vs. *Picea abies* (L.) Karst. *Central European Forestry Journal*, 66: 23–36.
- Nehrbass-Ahles C., Babst F., Klesse S., Nötzli M., Bouriaud O., Neukom R., Dobbertin M., Frank D. (2014): The influence of sampling design on tree-ring-based quantification of forest growth. *Global Change Biology*, 20: 2867–2885.
- Nolet P., Kneeshaw D., Messier C., Bêland M. (2018): Comparing the effects of even- and uneven-aged silviculture on ecological diversity and processes: A review. *Ecology and Evolution*, 8: 1217–1226.

<https://doi.org/10.17221/55/2025-JFS>

- Novák J., Dušek D., Slodičák M., Kacálek D. (2017): Importance of the first thinning in young mixed Norway spruce and European beech stands. *Journal of Forest Science*, 63: 254–262.
- Parmenter R.R., Losleben M.V. (2023): Influence of mixed conifer forest thinning and prescribed fire on soil temperature and moisture dynamics in proximity to forest logs: A case study in New Mexico, USA. *Forests*, 14: 1117.
- Peel M.C., Finlayson B.L., McMahon T.A. (2007): Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, 11: 1633–1644.
- Podrázský V. (2006): Effects of thinning regime on the humus form state. *Ekológia (Bratislava)* 25: 298–305.
- Podrázský V., Novák J., Moser W.K. (2005): Vliv výchovných zásahů na množství a charakter nadložního humusu v horském smrkovém porostu. *Zprávy lesnické výzkumu*, 50: 222–225. (in Czech)
- Podrázský V., Remeš J. (2007): Změny kvality a množství nadložního humusu při přirozeném zmlazení bukových porostů na území Školního lesního podniku Kostelec nad Černými lesy. *Zprávy lesnického výzkumu*, 52: 118–122. (in Czech)
- Poleno Z., Vacek S., Podrázský V. (2009): Pěstování lesů III: Praktické postupy pěstování lesů. Kostelec nad Černými lesy, Lesnická práce: 951. (in Czech)
- Pretzsch H., Grams T., Häberle K.H., Pritsch K., Bauerle T., Rötzer T. (2020): Growth and mortality of Norway spruce and European beech in monospecific and mixed-species stands under natural episodic and experimentally extended drought. Results of the KROOF throughfall exclusion experiment. *Trees*, 34: 957–970.
- Razavi S., Vogel R. (2018): Prewhitening of hydroclimatic time series? Implications for inferred change and variability across time scales. *Journal of Hydrology*, 557: 109–115.
- R Core Team (2024): R: A Language and Environment for Statistical Computing. Vienna, R Foundation for Statistical Computing. Available at: <https://www.R-project.org/>
- Schuster R., Oberhuber W. (2013): Age-dependent climate–growth relationships and regeneration of *Picea abies* in a drought-prone mixed-coniferous forest in the Alps. *Canadian Journal of Forest Research*, 43: 609–618.
- Schuldt B., Buras A., Arend M., Vitasse Y., Beierkuhnlein C., Damm A., Gharun M., Grams T.E.E., Hauck M., Hajek P., Hartmann H., Hiltbrunner E., Hoch G., Holloway-Phillips M., Körner C., Larysch E., Lübke T., Nelson D.B., Rammig A., Rigling A., Rose L., Ruehr N.K., Schumann K., Weiser F., Werner C., Wohlgemuth T., Zang C.S., Kahmen A. (2020): A first assessment of the impact of the extreme 2018 summer drought on Central European forests. *Basic and Applied Ecology*, 45: 86–103.
- Skrøppa T. (2003): EUFORGEN Technical Guidelines for Genetic Conservation and Use for Norway Spruce (*Picea abies*). Rome, International Plant Genetic Resources Institute: 6.
- Sohn J.A., Hartig F., Kohler M., Huss J., Bauhus J. (2016): Heavy and frequent thinning promotes drought adaptation in *Pinus sylvestris* forests. *Ecological Applications*, 26: 2190–2205.
- Souček J., Tesař V. (2008): Metodika přestavby smrkových monokultur na stanovištích přirozených smíšených porostů. *Lesnický průvodce 4/2008*. Strnady, Forestry and Game Management Research Institute: 37. (in Czech)
- Spathelf P., Bolte A., van der Maaten E. (2015): Is Close-to-Nature Silviculture (CNS) an adequate concept to adapt forests to climate change? *Landbauforschung Volkenrode*, 65: 161–170.
- Speer J.H. (2010): *Fundamentals of Tree-Ring Research*. Tucson, University of Arizona Press: 333.
- Spiecker H. (2000): The growth of Norway spruce [*Picea abies* (L.) Karst.] in Europe within and beyond its natural range. In: Hasenauer H. (ed.): *Forest Ecosystem Restoration. Proceedings of the International Conference*, Vienna, Apr 10–12, 2000: 247–256.
- Stokes M.A., Smiley T.L. (1996): *An Introduction to Tree-Ring Dating*. Tucson, University of Arizona Press: 73.
- Šimůnek V., Stejskal J., Čepel J., Korecký J., Vacek Z., Vacek S., Bílek L., Švanda M. (2023): Different adaptive potential of Norway spruce ecotypes in response to climate change in Czech long-term lowland experiment. *Forests*, 14: 1922.
- Štefančík I. (2013): Quantitative production of spruce stands with different initial spacing and tending regime. *Zprávy lesnického výzkumu*, 58: 37–49. (in Slovak)
- Toraño Caicoya A., Biber P., Poschenrieder W., Schwaiger F., Pretzsch H. (2018): Forestry projections for species diversity-oriented management: An example from Central Europe. *Ecological Processes*, 7: 23.
- Tulík M., Grochowina A., Jura-Morawiec J., Bijak S. (2020): Groundwater level fluctuations affect the mortality of black alder (*Alnus glutinosa* Gaertn.). *Forests*, 11: 134.
- Vacek Z., Prokúpková A., Vacek S., Cukor J., Bílek L., Gallo J., Bulušek D. (2020): Silviculture as a tool to support stability and diversity of forests under climate change: Study from Krkonoše Mountains. *Central European Forestry Journal*, 66: 116–129.
- Vacek Z., Vacek S., Cukor J. (2023): European forests under global climate change: Review of tree growth processes, crises and management strategies. *Journal of Environmental Management*, 332: 117353.
- Van der Maaten-Theunissen M., Trouillier M., Schwarz J., Skiadaresis G., Thurm E.A., van der Maaten E. (2021): pointRes 2.0: New functions to describe tree resilience. *Dendrochronologia*, 70: 125899.

- Vejpustková M., Čihák T. (2019): Climate response of Douglas fir reveals recently increased sensitivity to drought stress in Central Europe. *Forests*, 10: 97.
- Vicente-Serrano S.M., Beguería S., López-Moreno J.I. (2010): A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. *Journal of Climate*, 23: 1696–1718.
- Vicente-Serrano S.M., Beguería S., Lorenzo-Lacruz J., Camarero J.J., López-Moreno J.I., Azorin-Molina C., Revuelto J., Morán-Tejeda E., Sanchez-Lorenzo A. (2012): Performance of drought indices for ecological, agricultural, and hydrological applications. *Earth Interactions*, 16: 1–27.
- Viewegh J., Kusbach A., Mikeska M. (2003): Czech forest ecosystem classification. *Journal of Forest Science*, 49: 74–82.
- Vose J.M., Clark J.S., Luce C.H., Patel-Weynand T. (2016): Effects of Drought on Forests and Rangelands in the United States: A Comprehensive Science Synthesis. Vol. 93. Washington, D.C., United States Department of Agriculture, Forest Service: 289.
- Wang A.F., Roitto M., Lehto T., Zwiazek J., Calvo-Polanco M., Repo T. (2013): Waterlogging under simulated late-winter conditions had little impact on the physiology and growth of Norway spruce seedlings. *Annals of Forest Science*, 70: 781–790.
- Westin J., Haapanen M. (2013): Norway spruce – *Picea abies* (L.) Karst. In: Mullin T.J., Lee S.J. (eds): Best Practice for Tree Breeding in Europe. Uppsala, Skogforsk: 29–49.
- Zang C., Hartl-Meier C., Dittmar C., Rothe A., Menzel A. (2014): Patterns of drought tolerance in major European temperate forest trees: Climatic drivers and levels of variability. *Global Change Biology*, 20: 3767–3779.
- Zavadilová I., Szatniewska J., Stojanović M., Fleischer P., Vágner L., Pavelka M., Petřík P. (2023): The effect of thinning intensity on sap flow and growth of Norway spruce. *Journal of Forest Science*, 69: 205–216.

Received: July 20, 2025

Accepted: September 11, 2025

Published online: October 21, 2025