# Leaf area index and soil water content responses to pre-commercial thinning in Norway spruce plantations under climate change

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**Abstract:** Global climate change (GCC) and increasing drought frequency pose a threat to the stability of European forests, particularly those of Norway spruce [*Picea abies* (L.) Karst.] plantations. We investigated how different precommercial thinning (PCT) intensities affect leaf area index (*LAI*) and its relationship to soil water content (*SWC*) in young spruce stands in northeastern Czechia. Three permanent research plots in a 13-year-old monoculture were subjected to mild PCT, heavy PCT, or left as an unthinned control in winter 2019/2020. Thinning caused an immediate decrease in *LAI*, with averages of 8.3  $\pm$  1.1 m<sup>2</sup>·m<sup>-2</sup> (mild), 3.8  $\pm$  0.5 m<sup>2</sup>·m<sup>-2</sup> (heavy) and 11.1  $\pm$  1.1 m<sup>2</sup>·m<sup>-2</sup> (control) in 2020. By 2023, *LAI* in the mildly thinned stand had largely converged with the control, whereas the heavily thinned stand maintained significantly lower *LAI*. The strongest relationship between *LAI* and *SWC* occurred in the heavily thinned plot ( $R^2 = 0.715$  in 2021), while correlations were weak or transient in the mildly thinned and control plots. These results indicate that PCT intensity influences both the magnitude and duration of *LAI* reduction and is associated with differences in stand water dynamics. Appropriately adjusted thinning may therefore modestly affect water availability and could contribute to adaptive management of spruce forests under GCC.

Keywords: biometeorology, forest management; Picea abies; silvicultural intervention; stand structure

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The Norway spruce [Picea abies (L.) Karst.] is one of the most economically and ecologically significant tree species in Europe (Ge et al. 2013) and dominates approximately 46% of the total forested area in the Czech Republic (MoA 2023). Particularly in regions where it has been planted outside its natural range or close to the lower limits of its ecological tolerance, its ecological stability has been increasingly challenged (Putalová et al. 2019; D'Andrea et al. 2023; Šimůnek et al. 2025). Global climate change (GCC), expressed through rising air temperatures, altered precipitation patterns and a higher frequency of extreme weather events, has made Norway spruce stands more vulnerable to drought, pest outbreaks, windthrow and dieback (Slodičák 2014; Hlásny et al. 2021; MoA 2023; Vacek et al. 2023).

Among adaptive forest management options, pre-commercial (PCT) and commercial thinning are key measures to enhance the resistance and sustainability of Norway spruce stands under GCC (Ge et al. 2013). Thinning is a fundamental silvicultural intervention that reduces stand density and competition for resources, improves the structural stability of trees and modifies stand microclimate, particularly light regime and water balance (Aussenac 2000; Slodičák, Novák 2006; Rambo, North 2009; Mihai et al. 2020). By selectively removing individual trees, thinning can reduce the risk of damage from wind, snow, and pest outbreaks and improve access to critical resources for the remaining trees (Ge et al. 2012; Sohn et al. 2013; Dušek et al. 2021). However, the effects of thinning on the leaf area index (LAI) and its subsequent impact on soil water content (SWC) are complex and strongly dependent on stand age, thinning intensity and climatic conditions (Bréda 2003; Gebhardt et al. 2014).

The *LAI* represents a critical ecological parameter, defined as the total one-sided leaf area per unit ground area (Watson 1947). It integrates canopy structure and function and strongly influences carbon and water exchange between the stand and the atmosphere (Chen et al. 1997; Asner et al. 2003; Leuschner et al. 2006; DeRose et al. 2012). As it responds sensitively to growth conditions through changes in leaf morphology, canopy structure and metabolism (Kull et al. 1999; Bussotti et al. 2000; Hallik et al. 2009), *LAI* can be regarded as an indicator of both stand productivity and the adaptive capacity of tree species (Bréda 2003).

From the hydrological perspective, *LAI* is closely linked to rainfall interception, transpiration, and the amount of precipitation that reaches the forest floor (Parker 2020; Jonckheere et al. 2004). High LAI values increase canopy interception and transpiration, which may reduce SWC, whereas a reduction in LAI following thinning generally increases throughfall and can temporarily enhance SWC (Parker 2020). At the same time, more open canopies may promote soil evaporation and stimulate understory vegetation and transpiration, so that the net effect of thinning on SWC depends on canopy opening, understory response and local climatic conditions (Sohn et al. 2013; Gebhardt et al. 2014; Zavadilová et al. 2023). This dynamic interplay between canopy structure and hydrological processes emphasises the importance of understanding how different thinning intensities modify LAI and, consequently, soil water dynamics, particularly in regions where water availability limits tree growth and forest productivity (Grier, Running 1977; Hlásny et al. 2014; Parker 2020; Vacek et al. 2023).

Given the critical role of *LAI* in mediating the water balance in forest ecosystems (Zhang et al. 2020), this study aims to investigate how *LAI* develops and its effects on *SWC* in pure Norway spruce pole stands managed in different ways. Specifically, the objectives of this study are to: (*i*) quantify the temporal dynamics of *LAI* following PCT of varying intensities, (*ii*) assess the effect of these silvicultural interventions on *SWC*, and (*iii*) evaluate the implications for stand management in regions prone to drought stress. The findings are expected to contribute to the optimisation of thinning regimes in Norway spruce stands, thereby supporting both economic productivity and ecological resistance under ongoing GCC.

# MATERIAL AND METHODS

**Study sites.** The study was conducted on three research plots in the Křivina area in northeast Bohemia, Czech Republic (50°12'55"N, 16°06'51"E) at 402 m a.s.l., which represents a lower limit of suitable growing conditions for Norway spruce in the country (Černý 2023). Spruce at this elevation is expected to experience increasing climatic stress, as it usually struggles below 650 m a.s.l. due to higher air temperature and reduced precipitation (Vejpustková 2022). The stands were estab-

lished by artificial regeneration using containerised planting stock on mechanically prepared soil (disk trenching) at an initial density of 3 500 seedlings per ha. During the measurement period (2019–2023), mean annual air temperature was 9.8 °C and total annual precipitation 570.5 mm, based on data from an automatic meteorological station (EMS, Czech Republic), which is operated by the Forest-

ry and Game Management Research Institute and located approximately 500 m from the site (Figure 1). This meteorological station was specifically installed for the experiment in a sufficiently large open area, where it recorded air temperature and precipitation at 10-min intervals. For the purposes of this study, these data were aggregated to daily and then monthly means and totals. Thus, the

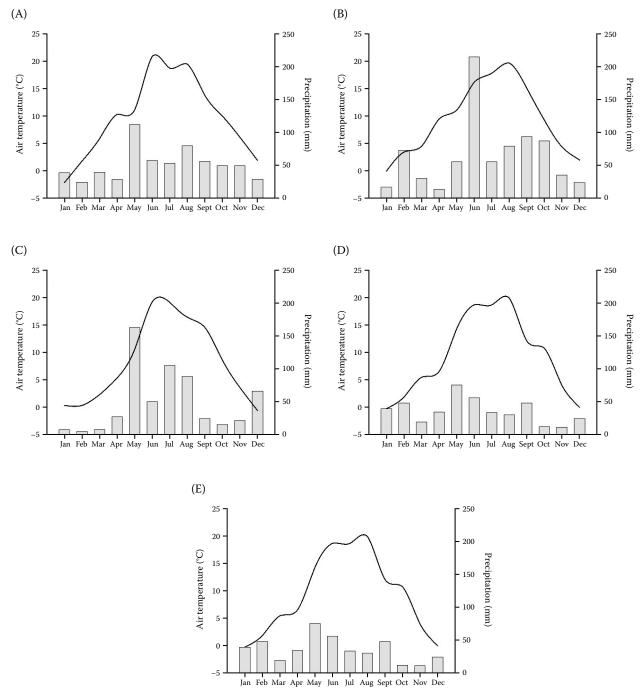


Figure 1. Mean monthly air temperature and monthly precipitation in an open area at the Křivina study site in (A) 2019, (B) 2020, (C) 2021, (D) 2022 and (E) 2023

2019-2023 series characterises the actual weather during LAI and SWC monitoring rather than, for example, a standard 30-year climate normal. According to the Köppen-Geiger classification, the area belongs to the temperate oceanic (Cfb) climate with a growing season of about 165–175 days (Peel et al. 2007). The terrain is flat (slope < 2°) with no pronounced aspect, and all three plots are located next to each other in the central part of the stand. The soil is a modal Cambisol developed on sandy marlstone and marlite, and the site is classified as a Querceto-Fagetum illimerosim trophicum (Černý 2023; Viewegh et al. 2003; Giagli et al. 2024). Soil conditions (horizon thickness, bulk density and basic chemical and nutrient properties) did not differ substantially among all three plots based on sampling and laboratory analyses (data not shown). The herbaceous layer was practically absent throughout the study period, with only small, scattered moss patches occurring locally in the heavily thinned plot C, and no continuous herb layer developed on any of the plots.

In 2018, three rectangular plots (40 × 65 m each) were established within a 13-year-old pure Norway spruce stand. All trees were individually numbered and measured annually for diameter at breast height (*DBH*) and total height (*H*). In winter 2019/2020, PCT of different intensities was applied: mild PCT (plot A; final stand density 2 062 trees·ha<sup>-1</sup>), heavy PCT (plot C; 1 369 trees·ha<sup>-1</sup>) and unthinned stand (plot B; 3 512 trees·ha<sup>-1</sup>). PCT was carried out by negative selection, primarily removing suppressed trees in the lower canopy. Stand edges were left intact to ensure mechanical stability, and all logging residues were removed (Černý 2023).

Annual inventories were conducted each September from 2019 to 2023. *DBH* was measured as the mean of two perpendicular readings to the nearest 0.1 cm, and tree height was recorded for all trees. From 2021 onwards, the height of the live crown base was also measured to 0.1 m using a Vertex IV hypsometer (Haglöf, Sweden). Basic stand characteristics are summarised in Table 1.

**Measurement of microclimate and** *LAI* **calculation.** For this study, photosynthetically active radiation (*PAR*) was measured between 2019 and 2023 above and below the canopy. Above-canopy *PAR* was recorded in a nearby open area (Fleck et al. 2020). Below the canopy, eighteen EMS 12S sensors (EMS, Czech Republic) with a reliable cosine-corrected response up to a zenith angle of 85° (i.e. an effective sensors)

sor field of view of about 170°) were installed in each plot (A, B, C) in a regular  $10 \times 10$  m grid in the central part of each plot to provide dense spatial coverage and minimise edge effects. All sensors were mounted on vertical steel posts, with the sensor heads at 60 cm above the ground level between trees (not directly adjacent to stems). SWC was measured with ten Campbell CS650 sensors (Campbell Scientific, USA) at a depth of 15 cm within the same central plot area. All PAR and SWC sensors were connected to an automatic data-logging system (EMS, Czech Republic), which controlled the measurements and data storage. All sensors operated continuously, and data were logged every 10 min and stored in a cloud database. The daily average PAR for each sensor was calculated as the arithmetic mean of all the 10-minute PAR records for a given calendar day. Analogously, the daily mean SWC was obtained from the 10-minute SWC records. For this study, we used daily means for the growing season (April 1 - October 31). In 2019, instrumentation began on 19 June; therefore, the period from 19 June to 31 October was analysed. Thus, we obtained one stand-level value of PAR transmittance and one stand-level value of SWC for each day and plot, based on averaging across all sensors. Technical specifications and user manuals for all instruments are available from the manufacturers' websites (EMS, Czech Republic; Campbell Scientific, USA).

For each plot and day, daily mean *PAR* values from the eighteen below-canopy sensors were averaged to obtain a stand-level mean understory irradiance. *LAI* was then calculated using the modified Lambert-Beer law (Bréda 2003; Hirose 2005), as shown by Equation (1):

$$LAI = -\ln\frac{I}{I_0} \times k^{-1} \tag{1}$$

where:

*LAI* – leaf area index;

I – daily average photosynthetically active radiation (PAR) measured below the canopy;

 $I_0$  — daily average PAR measured above the canopy;

 extinction coefficient, set to 0.33 for pure Norway spruce stands (Bréda 2003).

For each plot and year, we also derived the maximum leaf area index ( $LAI_{\rm max}$ ), defined as the highest daily LAI value recorded during the growing season. In this study, both LAI and  $LAI_{\rm max}$  are considered as canopy metrics at the stand level.

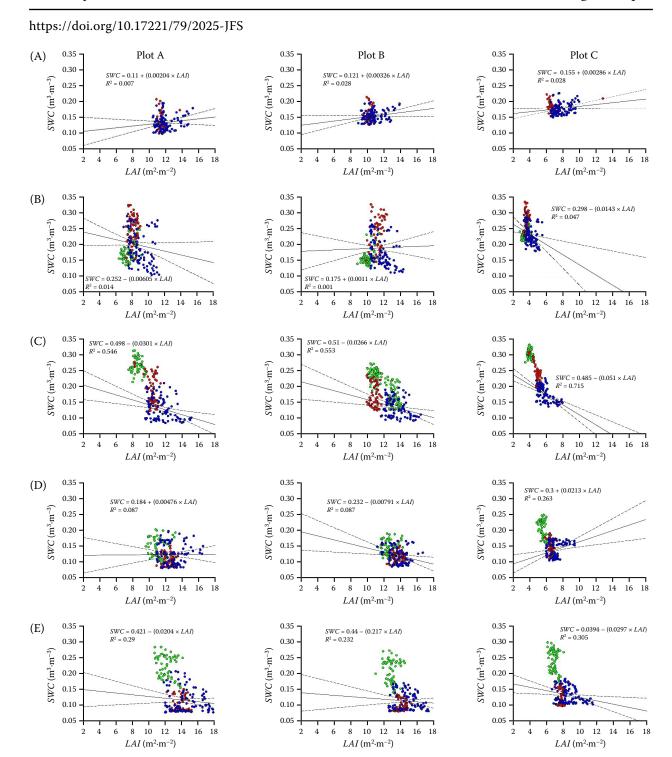


Figure 2. Linear relationship between leaf area index and soil water content in young Norway spruce stands with different intensities of PCT in 2019: (A) before PCT application, (B) 2020, (C) 2021, (D) 2022 and (E) 2023

Each point represents one daily mean pair of LAI and SWC values for a given plot (A, B, C) during the growing season in the respective year, and is coloured according to its day-of-year category: green – early-season (1 April–31 May), red – mid-season (1 June–31 July) and blue – late-season (1 August–31 October); A – mild pre-commercial thinning (PCT); B – unthinned control; C – heavy PCT; SWC – soil water content (m3·m–3); LAI – leaf area index (m2·m–2); R2 – coefficient of determination

*LAI* and *SWC* values are shown for the growing season (1 April–31 October), except in 2019 when measurements began on 19 June and continued to 31 October, only the mid- and late-season categories are present in panel a); therefore, the 2019 relationships are not fully comparable with those for 2020–2023

Table 1. Basic characteristics of the studied Norway spruce stands with different tending in 2019–2023

Year	Silvicultural variant	Age (year)	Stand density (trees⋅ha <sup>-1</sup> )	DBH (cm)	<i>BA</i> <sub>1.3</sub> (m <sup>2</sup> ·ha <sup>-1</sup> )	<i>Н</i> (m)	LCB (m)	<i>LAI</i> (m <sup>2</sup> ·m <sup>-2</sup> )	SWC (m³·m⁻³)
2019	A	14	3 569	8.5 ± 2.5	21.95	$7.3 \pm 1.4$	_	11.9 ± 1.0	$0.13 \pm 0.03$
	В		3 527	$7.9 \pm 2.4$	18.90	$7.0 \pm 1.5$	_	$10.7 \pm 1.0$	$0.15 \pm 0.02$
	С		3 685	$7.7 \pm 2.3$	18.74	$6.8 \pm 1.4$	_	$7.5 \pm 1.1$	$0.18\pm0.02$
2020	A	15	2 062	$10.4 \pm 2.2$	18.26	$9.0 \pm 1.0$	_	$8.3 \pm 1.1$	$0.20 \pm 0.05$
	В		3 519	$8.5 \pm 2.5$	21.52	$8.7 \pm 1.0$	_	11.1 ± 1.1	$0.19 \pm 0.05$
	С		1 369	$10.0\pm1.8$	11.40	$8.8 \pm 1.0$	_	$3.8 \pm 0.5$	$0.24 \pm 0.03$
2021	A	16	2 058	11.5 ± 2.4	22.42	9.4 ± 1.1	$1.8 \pm 0.4$	$10.4 \pm 1.6$	$0.19 \pm 0.07$
	В		3 512	$9.2 \pm 2.8$	25.29	$8.4 \pm 1.7$	$1.6 \pm 0.5$	$12.7 \pm 1.4$	$0.17 \pm 0.05$
	С		1 365	$11.4 \pm 2.1$	14.36	$9.1 \pm 1.1$	$1.4\pm0.4$	$5.1\pm1.0$	$0.23 \pm 0.06$
2022	A	17	2 058	12.2 ± 2.5	24.97	10.1 ± 1.3	$2.1 \pm 0.6$	12.2 ± 1.3	$0.13 \pm 0.03$
	В		3 492	$9.6 \pm 2.9$	27.49	$8.9 \pm 1.8$	$2.3 \pm 0.7$	$13.4 \pm 1.0$	$0.13 \pm 0.03$
	С		1 362	$12.5 \pm 2.2$	17.12	$9.8 \pm 1.2$	$1.6 \pm 0.4$	$6.6 \pm 0.9$	$0.16 \pm 0.04$
2023	A	18	2 023	12.6 ± 2.5	26.13	10.9 ± 3.9	$2.8 \pm 0.7$	13.7 ± 1.6	$0.14 \pm 0.06$
	В		3 442	$9.9 \pm 3.0$	28.88	$9.4 \pm 1.8$	$2.8 \pm 0.9$	$14.0 \pm 1.2$	$0.14 \pm 0.05$
	С		1 331	$13.1 \pm 2.3$	18.35	$10.6 \pm 1.2$	$1.9 \pm 0.5$	$7.9 \pm 1.1$	$0.16 \pm 0.06$

A – mild pre-commercial thinning (PCT); B – unthinned control; C – heavy PCT; DBH – diameter at breast height;  $BA_{1.3}$  – stand basal area at breast height; H – tree height; LCB – height of live crown base; LAI – stand-level leaf area index; SWC – soil water content

Stand variables were measured during annual inventories in September; *LAI* and *SWC* values represent the seasonal averages (1 April–31 October), except in 2019 when measurements began on 19 June (19 June–31 October); therefore, *LAI* and *SWC* values should be interpreted with caution when making year-on-year comparisons

To assess the influence of *LAI* on *SWC*, we calculated daily averages from the ten *SWC* sensors below the canopy for each plot, and these values were used in the subsequent regression analyses.

Statistical analyses. All data analyses were conducted in SigmaPlot® (Version 13, 2014). Data were first tested for normality (Shapiro-Wilk test) and homogeneity of variance (Bartlett test). When these assumptions were met, we applied one-way analysis of variance (ANOVA) with Tukey's honestly significant difference (HSD) for post hoc pairwise comparisons. When the assumptions were violated, we performed a nonparametric Kruskal-Wallis test (Siegel, Castellan 1988). Statistical significance was set at P < 0.05. To evaluate the influence of LAIon SWC, linear regression models were fitted for each silvicultural variant (A, B, C) and year (2019-2023). Paired daily mean *LAI* and *SWC* values were used for each plot, and the coefficients of determination  $(R^2)$  were calculated. To visualise the potential seasonal structure of these relationships, the days were also categorised by day of year (DOY) to represent successive parts of the growing season. These categories are indicated by different colours of points in Figure 2.

# **RESULTS**

In 2019, before PCT, LAI was highest in plot A (mild PCT), intermediate in plot B (unthinned control), and lowest in plot C (heavy PCT), with  $LAI_{\rm max}$  occurring in mid-October for plot A and in mid-June for plots B and C (Figures 3A, 4A). In the same year, the seasonal mean SWC showed the opposite pattern, being lowest in plot A and highest in plot C (0.13, 0.15 and 0.18 m³·m⁻³ in A, B and C, respectively) (Table 1, Figure 3A).

After PCT 2020, mean LAI dropped markedly in mildly and heavily thinned plots  $(8.3 \pm 1.1 \text{ m}^2 \cdot \text{m}^{-2} \text{ and } 3.8 \pm 0.5 \text{ m}^2 \cdot \text{m}^{-2}$ , respectively), while it slightly increased in the unthinned control  $(11.1 \pm 1.1 \text{ m}^2 \cdot \text{m}^{-2}; \text{ Figures } 3B, 4B)$ . In contrast, the seasonal mean SWC increased in both thinned plots, with the highest

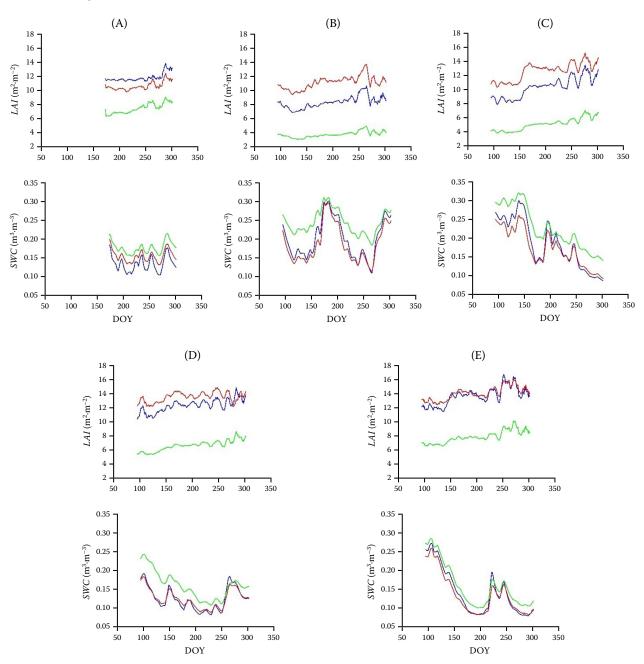


Figure 3. Seasonal dynamics of stand-level LAI (m<sup>2</sup>·m<sup>-2</sup>) and SWC (m<sup>3</sup>·m<sup>-3</sup>) in young Norway spruce stands with different intensities of PCT at the Křivina study site in 2019: (A) the growing season before PCT application, (B) 2020, (C) 2021, (D) 2022, and (E) 2023

A – mild pre-commercial thinning (PCT); B – unthinned control; C – heavy PCT; DOY – day of the year; *LAI* – stand-level leaf area index; *SWC* – soil water content

In 2019 (A), the monitoring period was shorter (19 June–31 October) because the sensors were installed in all research plots after the beginning of the growing season

SWC in heavily thinned plot C (0.24 m $^3$ ·m $^{-3}$ ) (Table 1, Figure 3B).

In the subsequent years (2021–2023), *LAI* increased again in all plots, but trajectories differed between treatments. In 2021 and 2022, plots A and B

showed a higher mean LAI than the heavily thinned plot C (Figures 3C–D, 4C–D). By 2023, the mean LAI in plots A and B converged (13.7  $\pm$  1.6 m<sup>2</sup>·m<sup>-2</sup> and 14.0  $\pm$  1.2 m<sup>2</sup>·m<sup>-2</sup>), whereas plot C remained significantly lower (7.9  $\pm$  1.1 m<sup>2</sup>·m<sup>-2</sup>) (Figures 2E, 3E).

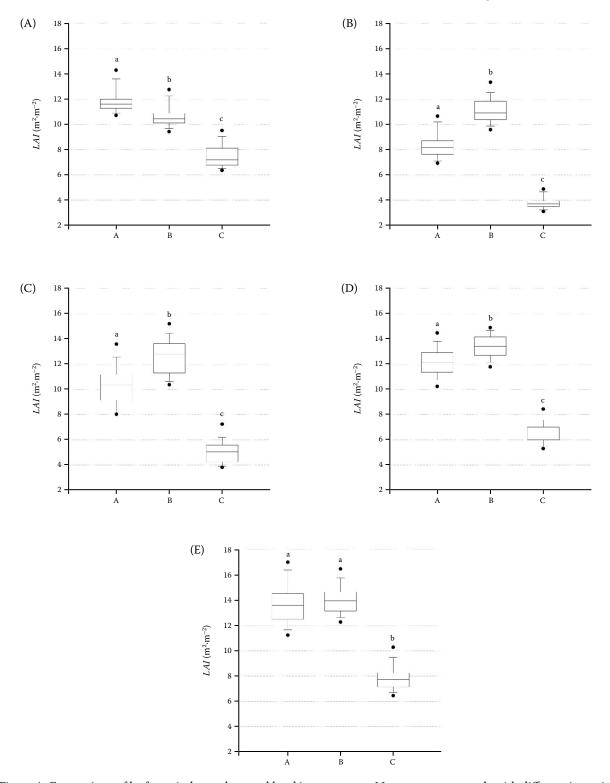


Figure 4. Comparison of leaf area index at the stand level in pure young Norway spruce stands with different intensities of PCT at the Křivina study site in (A) 2019, (B) 2020, (C) 2021, (D) 2022, and (E) 2023

A – mild pre-commercial thinning (PCT); B – unthinned control; C – heavy PCT; LAI – stand-level leaf area index; lower-case letters – statistically significant differences between silvicultural treatments (P < 0.05)

*LAI* values represent seasonal averages for the growing season (1 April–31 October), except in 2019 when measurements began on 19 June (19 June–31 October); therefore, *LAI* values for 2019 should be interpreted with caution when making year-on-year comparisons

During the same period, the seasonal mean SWC was consistently highest in plot C (0.23, 0.16 and 0.16 m<sup>3</sup>·m<sup>-3</sup>) (Table 1, Figure 3C–E). Overall, SWC was relatively high in 2020–2021, but lower in 2022 and 2023 (Table 1, Figure 3D–E).

Across 2019–2022, *LAI* differed significantly among all three thinning variants, while in 2023, significant differences were found only between the heavily thinned plot C and both the mildly thinned plot A and the control plot B (Figure 4).

In 2019, before PCT, relationships between LAI and SWC were very weak for all three plots (Figure 2A). In 2020, the first growing season after PCT, correlations between LAI and SWC remained low in the mildly thinned plot A and the control plot B (Figure 2B). In 2021, the effect of PCT on the LAI-SWC relationship became more evident, particularly in the heavily thinned plot C, where a strongly positive relationship was observed ( $R^2 = 0.715$ ; Figure 2C). In 2022,  $R^2$  values in plots A and B decreased again to very low levels, whereas plot C maintained higher  $R^2$  values, indicating a persistent influence of its more open canopy structure on SWC (Figure 4D-E). Overall, heavy PCT had the greatest and longest-lasting effect on the relationship between LAI and SWC, with the strongest influence observed in 2021 and a weaker but still noticeable effect in 2023 (Figure 2A-E).

# DISCUSSION

Norway spruce is the most widely distributed tree species in the Czech Republic, accounting for approximately 46% of forests (MoA 2023) and remains an important component of forest ecosystems in Central Europe (Bošeľa et al. 2021). However, GCC already results in irregular precipitation during the growing period, prolonged droughts, the spread of insects and wood-decaying fungi, and a high risk that young stands will not reach maturity, particularly at low elevations and outside the natural range of the species (Čermák 2014; Hlásny et al. 2014, 2021; D'Andrea et al. 2023; Šimůnek et al. 2025). Despite these risks, management strategies still prioritise Norway spruce, recommending a proportion of 28.3% compared to 22.5% for European beech (Fagus sylvatica L.). However, beech historically covered around 40.2% of the forest area, whereas spruce accounted for just 11.2% (MoA 2023).

One adaptation pathway is to reduce drought risk through functionally diverse mixed stands, where tree species differ in resource use and interact in ways that can increase resistance to climatic stress (Jaworski, Pach 2014; Steckel et al. 2020; Vacek et al. 2021, 2023; Vospernik et al. 2023). The use of tree species exploiting different soil horizons and ecological niches, such as combining Norway spruce with silver fir (Abies alba Mill.) and European beech, helps to alleviate belowground competition and stabilise stand structure (Vacek 2017; Poleno et al. 2009; Vacek et al. 2014, 2021). Historical beech-fir-spruce old-growth forests in Central Europe illustrate that such mixtures can be structurally stable over long periods, although recent studies have reported a trend towards declining conifer abundance and increasing dominance of beech across Europe (Diaci et al. 2008, 2011; Vrška et al. 2009; Janík et al. 2014; Jaloviar et al. 2017; Parobeková et al. 2018). Species-specific responses to climate and anthropogenic disturbances further underline the value of structurally diverse, closeto-nature beech-fir-spruce forests, which have shown high stability under appropriate management (Bouriaud, Popa 2009; Gazol et al. 2015; Vacek et al. 2015). On Slovak sites, leaf area per tree, stand LAI and stem radial increment per unit leaf area were similar between beech and spruce, indicating near-maximal light-use efficiency, although greater morphological plasticity of beech may confer a competitive advantage under changing climatic conditions (Konôpka et al. 2016). At the stand level, mixed stands can also be more productive, as shown for Scots pine with admixed spruce and for silver fir mixed with spruce, where growth and stem-wood production increased relative to monoculture (Vallet, Pérot 2011; Bielak et al. 2014).

Nevertheless, species mixtures are not universally beneficial. On sandy soils with deep groundwater tables, mixing Scots pine and Norway spruce can be problematic because spruce in the understory may form a shallow, wide-spreading root system and high interception surface that strongly reduces throughfall and induces water stress in the overstory pine. Following the removal of this biological barrier, the Scots pine significantly increased its radial growth (Špulák 2023). Large-scale analyses have also shown that tree neighbourhood diversity may have negligible or adverse effects on drought resistance, as trees compete strongly regardless of species composition (Gillerot et al. 2020). Thus,

the main advantage of mixtures may lie in diversifying risk and enhancing non-producing forest functions, while additional measures such as targeted thinning remain necessary for adapting Norway spruce to GCC.

Another adaptation option within existing spruce young stands is to reduce canopy interception so that a larger fraction of precipitation reaches the forest floor. Under conditions of low precipitation, the assimilation apparatus can intercept almost all incoming rainfall, meaning that intercepted water has no direct usable potential for trees (Šrámek et al. 2023). In spruce stands, interception losses can exceed 36% over the year and canopy interception capacity can reach up to 5 mm per rainfall event, depending on the duration and intensity of precipitation (Dohnal et al. 2014). At the same Křivina site as our experiment, PCT and the associated reduction in LAI significantly increased throughfall: in the unthinned stand, the lowest measured throughfall was 56.5% of open-area precipitation, whereas it reached 74.9% and 87.0% in the mildly and heavily thinned stands, respectively (Pavlištová 2022). Our results on LAI and SWC build on these findings by demonstrating that reductions in canopy interception result in modest, yet measurable, increases in soil water availability in heavily thinned stands.

From a methodological perspective, we obtained our LAI values using an indirect optical approach. In this approach, stand-level *LAI* is derived from the ratio of incident and transmitted photosynthetically active radiation, as measured by line quantum sensors, using the modified Beer-Lambert law (Bréda 2003; Hirose 2005; Welles, Cohen 1996). Indirect optical methods based on canopy transmittance or gap fraction, such as LAI-2200 PCA, LaiPen, digital hemispherical photography, and line quantum sensors, are widely used in forest hydrology and ecophysiology because they are non-destructive and enable repeated LAI monitoring at stand level (Jonckheere et al. 2004; Černý, Pokorný 2021; Černý et al. 2018, 2019; Fang et al. 2019). Unlike portable canopy analysers or hemispherical photography, which provide LAI snapshots at specific times and locations, the fixed grid of EMS 12S sensors used in this study yielded continuous, spatially averaged information on canopy transmittance throughout the growing season. This design is particularly advantageous for analysing intra-annual LAI dynamics and its co-variation with SWC. However, our estimates are subject to the common limitations of indirect optical methods. They provide an approximation of the effective leaf area index and may underestimate the actual needle area in spruce stands due to foliage clumping and the presence of woody elements. Furthermore, they depend on an assumed species-specific extinction coefficient (Bréda 2003; Černý 2021; Jonckheere et al. 2004). Nevertheless, comparisons between line quantum sensors, LAI-2200 PCA and destructive sampling in Norway spruce stands suggest that relative differences in LAI between treatments and years can be reliably captured when appropriate extinction coefficients and correction factors are used (Černý 2021; Černý et al. 2019). We therefore primarily interpret our LAI values in a relative sense among plots and years, while acknowledging some uncertainty in their absolute magnitude.

Over the course of the growing season, the relationship between LAI and SWC showed a clear seasonal structure. The colour coding in Figure 2 indicates that the most variation in SWC reflects progressive drying from the beginning to the end of the season. In contrast, LAI in these young spruce stands changes only slowly due to their evergreen nature (Pokorný et al. 2008). Therefore, the regressions in Figure 2 should be interpreted primarily as the seasonal correlation between canopy density and soil water under the stand structure and climatic conditions of a given year, rather than as universally transferable response functions. The strongest and most persistent relationships occurred in the heavily thinned stand C, particularly in 2021, when a lower LAI and a more open canopy were consistently associated with a higher SWC throughout much of the season. In the mildly thinned and control plots, by contrast, relationships were mostly weak to moderate. This suggests that once canopy closure is largely complete, intraannual variation in SWC is driven more by weather than by relatively small differences in LAI. Taken together, these patterns of intra-annual variation support the view that heavy PCT creates a more persistent coupling between canopy structure and soil water, but that the strength of this coupling depends on both stand structure and year-specific climatic conditions.

Despite the substantial changes in throughfall, several studies, including ours, indicate that the effect of PCT on *SWC* is modest. Dušek et al. (2021) reported only about a 0.9% average increase (maxi-

mum 1.8%) in SWC after thinning in young Norway spruce stands. In our study, the overall correlations between LAI and SWC were weak to moderate and were consistently strongest in the heavily thinned stand. In the stand, AI explained up to 71.5% of SWC variability in 2021 and remained more strongly related to SWC than in the mildly thinned and control stands in subsequent years. These findings are consistent with Thomas and Packam (2007), who reported that stands with more open canopies and lower LAI intercept less rainfall but are more exposed to soil evaporation due to increased solar radiation and wind. Heavy thinning can also enhance direct soil evaporation and strongly stimulate understory vegetation development and transpiration, particularly where species with high transpiration potential, such as wood small-reed [Calamagrostis epigeios (L.) Roth], are abundant. In extreme cases, the herb layer may account for up to 50% of total stand transpiration, reducing water availability for trees and fine-root development (Gebhardt et al. 2014). On our site, however, the herbaceous layer was practically absent throughout the study period. Only a few small moss patches occurred locally in the heavily thinned plot C, and no continuous herb layer developed. For this reason, we did not quantify herbaceous vegetation and considered its direct effect on SWC to be negligible here. By contrast, on sites with a well-developed herb layer, it may substantially contribute to evapotranspiration and soil water dynamics (Balandier et al. 2022).

Process-based studies show that thinning generally reduces stand-level transpiration of Norway spruce by decreasing LAI, but the magnitude and persistence of this reduction strongly depend on thinning intensity (Zavadilová et al. 2023). Chroust (1997) observed that a 61% reduction in stand basal area, accompanied by a decrease in LAI to 3.1  $\pm$  0.8 m<sup>2</sup>·m<sup>-2</sup>, caused a 34% reduction in total stand transpiration. At the same time, reduced competition, increased water availability and greater crown illumination of remaining trees led to a 27% increase in sap flow, enhancing photosynthetic uptake and promoting radial and height growth (Chroust 1997; Černý et al. 2020). A milder intervention with a 30% reduction in basal area and LAI of 4.0 ± 1.4 m<sup>2</sup>·m<sup>-2</sup> reduced stand transpiration by only 4% and did not significantly increase sap flow, yet total growth volume was similar to that in the heavily thinned stands (Chroust 1997). It should also be noted that there were slight differences in stand density and LAI among the three plots before the PCT treatments, reflecting small-scale variability within the same even-aged stand. Therefore, our analysis primarily focused on the relative changes in LAI and the LAI-SWC relationships within each plot after PCT application, rather than on the absolute differences among plots. Together with our results, this suggests that mildly thinned stands may use water and radiation more efficiently at the stand level, whereas heavy thinning trades stronger individual-tree growth and somewhat improved soil water dynamics against higher soil evaporation and a greater risk of competitive understory proliferation. Overall, our results therefore indicate that heavy PCT creates a more persistent reduction in LAI and a clearer link to SWC than mild thinning. However, the absolute gain in soil water is relatively small and must be balanced against the risk of higher soil evaporation and understory competition on some sites.

### **CONCLUSION**

In young Norway spruce stands, PCT significantly modified LAI but only weakly affected SWC. Across all observed years and treatments, the correlation between LAI and SWC was consistently strongest in the heavily thinned stand, where LAI explained up to 71.5% of SWC variability in 2021; the strength of this relationship decreased in 2022-2023 but remained higher than in the mildly thinned and control stands. Moderate relationships were present in all three stands in 2023. Mild PCT caused a short-term reduction in LAI, but canopy regrowth led to LAI values converging with the unthinned control within about two growing seasons. Its influence on SWC was relatively small and difficult to distinguish from year-to-year variability in the unthinned control. Heavy PCT maintained consistently lower LAI and a clearer LAI-SWC relationship throughout the study period, yet differences in SWC among treatments were small. A key limitation of this study is its focus on a single locality and stand type. Further research on multiple sites and age classes is needed to verify the persistence and magnitude of LAI-SWC responses to different thinning intensities and to better understand their intra-annual dynamics.

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#### **REFERENCES**

- Asner G.P., Scurlock J.M.O., Hicke J.A. (2003): Global synthesis of leaf area index observations: Implications for ecological and remote sensing studies. Global Ecology and Biogeography, 12: 191–205.
- Aussenac G. (2000): Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. Annals of Forest Science, 57: 287–301.
- Balandier P., Gobin R., Prévosto B., Korboulewsky N. (2022): The contribution of understorey vegetation to ecosystem evapotranspiration in boreal and temperate forests: A literature review and analysis. European Journal of Forest Research, 141: 979–997.
- Bielak K., Dudzinska M., Pretzsch H. (2014): Mixed stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce [*Picea abies* (L.) Karst] can be more productive than monocultures. Evidence from over 100 years of observation of long-term experiments. Forest Systems, 23: 573–589.
- Bouriaud O., Popa I. (2009): Comparative dendroclimatic study of Scots pine, Norway spruce, and silver fir in the Vrancea Range, Eastern Carpathian Mountains. Trees Structure and Function, 23: 95–106.
- Bréda N.J.J. (2003): Ground-based measurements of leaf area index: A review of methods, instruments and current controversies. Journal of Experimental Botany, 54: 2403–2417.
- Bussotti F., Borghini F., Celesti C., Leonzio C., Bruschi P. (2000): Leaf morphology and macronutrients in broadleaved trees in central Italy. Trees – Structure and Function, 14: 361–368.
- Čermák P. (2014): Jak reaguje smrk na klimatické změny. In: Novák J., Dušek D. (eds.): Chřadnutí smrku v oblasti severní a střední Moravy. Budišov nad Budišovkou, Forestry and Game Management Research Institute, Opočno Research Station: 9–15. (in Czech)
- Černý J. (2023): Výchovný zásah v mladých smrkových porostech jako nástroj mitigace globální klimatické změny? Reports of Forestry Research/Zprávy lesnického výzkumu, 68: 149–158. (in Czech)
- Černý J., Pokorný R. (2021): Field measurement of effective leaf area index using optical device in vegetation canopy. Journal of Visualized Experiments, 173: e62802.
- Černý J., Krejza J., Pokorný R., Bednář P. (2018): LaiPen LP 100 A new device for estimating forest ecosystem leaf area index compared to the etalon: A methodologic case study. Journal of Forest Science, 64: 455–468.

- Černý J., Pokorný R., Haninec P., Bednář P. (2019): Leaf area index estimation using three distinct methods in pure deciduous stands. Journal of Visualized Experiments, 150: e59757.
- Černý J., Pokorný R., Vejpustková M., Šrámek V., Bednář P. (2020): Air temperature is the main driving factor of radiation use efficiency and carbon storage of mature Norway spruce stands under global climate change. International Journal of Biometeorology, 64: 1599–1611.
- Chen J.M., Rich P.M., Gower S.T., Norman J.M., Plummer S. (1997): Leaf area index of boreal forests: Theory, techniques, and measurements. Journal of Geophysical Research: Atmospheres, 102: 29429–29443.
- Chroust L. (1997): Ekologie výchovy lesních porostů. Opočno, Forestry and Game Management Research Institute: 277. (in Czech)
- 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.
- DeRose R.J., Seymour R.S. (2012): Leaf Area and structural changes after thinning in even-aged *Picea rubens* and *Abies balsamea* stands in Maine, USA. International Journal of Forestry Research, 2012: 181057.
- Diaci J., Rozenbergar D., Mikac S., Anić I., Hartman T., Bončina A. (2008): Long-term changes in tree species composition in old-growth Dinaric beech-fir forest. Glasnik za šumske pokuse, 42: 13–27.
- Diaci J., Rozenbergar D., Anić I., Mikac S., Saniga M., Kucbel S., Visnjic C., Ballia D. (2011): Structural dynamics and synchronous silver fir decline in mixed old-growth mountain forests in Eastern and Southeastern Europe. Forestry, 84: 479–491.
- Dohnal M., Černý T., Votrubová J., Tesař M. (2014): Rainfall interception and spatial variability of throughfall in spruce stand. Journal of Hydrology and Hydromechanics, 62: 277–284.
- Dušek D., Novák J., Černý J., Kacálek D. (2021): Vliv prvních výchovných zásahů v mlazinách na obsah vody ve svrchní vrstvě minerální půdy. Reports of Forestry Research/Zprávy lesnického výzkumu, 66: 270–276. (in Czech)
- Fang H., Baret F., Plummer S., Schaepman-Strub G. (2019): An overview of global leaf area index (*LAI*): Methods, products, validation, and applications. Reviews of Geophysics, 57: 739–799.
- Fleck S., Raspe S., Čater M., Schlappi P., Ukonmaanaho L., Greve M., Hertel C., Weiss M., Rumpf S., Thimonier A., Chianucci F., Beckschäfer P. (2020): Part XVII: Leaf area measurements. In: UNECE ICP Forests Programme Coordinating Centre (eds): Manual of Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests. Eberswalde, Thünen Institute of Forest Ecosystems: 3–43.

- Gazol A., Camarero J.J., Gutiérrez E., Popa I., Andreu-Hayles L., Motta R., Nola P., Ribas M., Sangüesa-Barreda G., Urbinati C., Carrer M. (2015): Distinct effects of climate warming on populations of silver fir (*Abies alba*) across Europe. Journal of Biogeography, 42: 1150–1162.
- Ge Z.M., Kellomäki S., Peltola H., Zhou X., Wang K.Y., Väisänen H. (2012): Effects of varying thinning regimes on carbon uptake, total stem wood growth, and timber production in Norway spruce (*Picea abies*) stands in southern Finland under the changing climate. Annals of Forest Science, 68: 371–383.
- Ge Z.M., Kellomäki S., Peltola H., Zhou X., Väisänen H. (2013): Adaptive management to climate change for Norway spruce forests along a regional gradient in Finland. Climatic Change, 118: 275–289.
- Gebhardt T., Häberle K., Matyssek R., Schulz C., Ammer C. (2014): The more, the better? Water relations of Norway spruce stands after progressive thinning. Agricultural and Forest Meteorology, 197: 235–243.
- Giagli K., Vavrčík H., Tsalagkas D., Černý J., Leugner J., Hacurová J., Gryc V. (2024): Effect of different stand densities on xylem and phloem formation in Norway spruce plantations. IAWA Journal, 45: 227–242.
- Gillerot L., Forrester D., Bottero A., Rigling A., Lévesque M. (2020): Tree neighbourhood diversity has negligible effects on drought resilience of European beech, silver fir and Norway spruce. Ecosystems, 24: 20–36.
- Grier C.G., Running S.W. (1977): Leaf area of mature Northwestern coniferous forests: Relation to site water balance. Ecology, 58: 893–899.
- Hallik L., Niinemets Ü., Wright I.J. (2009): Are species shade and drought tolerance reflected in leaf-level structural and functional differentiation in Northern Hemisphere temperate woody flora? New Phytologist, 184: 257–274.
- Hirose T. (2005): Development of the Monsi–Saeki Theory on Canopy Structure and Function. Annals of Botany, 95: 483–494.
- Hlásny T., Mátyás C., Seidl R., Kulla L., Merganičová K., Trombik J., Dobor L., Barcza Z., Konôpka B. (2014): Climate change increases the drought risk in Central European forests: What are the options for adaptation? Central European Forestry Journal, 60: 5–18.
- Hlásny 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.
- Jaloviar P., Saniga M., Kucbel S., Pittner J., Vencurik J., Dovciak M. (2017): Seven decades of change in a European old-growth forest following a stand-replacing wind disturbance: A long-term case study. Forest Ecology and Management, 399: 197–205.

- Janík D., Adam D., Hort L., Král K., Šamonil P., Unar P., Vrška T. (2014): Tree spatial patterns of *Abies alba* and *Fagus sylvatica* in the Western Carpathians over 30 years. European Journal of Forest Research, 133: 1015–1028.
- Jaworski A., Pach M. (2014): A comparison of lower montane natural forest (*Abies, Fagus, Picea*) in Oszast Reserve and spruce monocultures in the Żywiecki Beskid and Śląski Beskid. Forest Research Papers, 75: 13–32.
- Jonckheere I., Fleck S., Nackaerts K., Muys B., Coppin P., Weiss M., Baret F. (2004): Review of methods for *in situ* leaf area index determination. Part I: Theories, sensors and hemispherical photography. Agricultural and Forest Meteorology, 121: 19–35.
- Konôpka B., Pajtík J., Marušák R., Bošeľa M., Lukac M. (2016): Specific leaf area and leaf area index in developing stands of *Fagus sylvatica* L. and *Picea abies* Karst. Forest Ecology and Management, 364: 52–59.
- Kull O., Broadmeadow M., Kruijt B., Meir P. (1999): Light distribution and foliage structure in an oak canopy. Trees Structure and Function, 14: 55–64.
- Leuschner C., Voß S., Foetzki A., Clases Y. (2006): Variation in leaf area index and stand leaf mass of European beech across gradients of soil acidity and precipitation. Plant Ecology, 186: 247–258.
- Mihai G., Teodosiu M., Birsan M.V., Alexandru A.M., Mirancea I., Apostol E.N., Garbacea P., Ionita L. (2020): Impact of climate change and adaptive genetic potential of Norway spruce at the south—eastern range of species distribution. Agricultural and Forest Meteorology, 291: 108040.
- MoA (2023): Zpráva o stavu lesa a lesního hospodářství České republiky v roce 2022. Prague, Ministry of Agriculture of the Czech Republic: 134. (in Czech)
- Parker G.G. (2020): Tamm review: Leaf Area Index (*LAI*) is both a determinant and a consequence of important processes in vegetation canopies. Forest Ecology and Management, 477: 118496.
- Parobeková Z., Pittner J., Kucbel S., Saniga M., Filípek M., Sedmáková D., Vencurik J., Jaloviar P. (2018): Structural diversity in a mixed spruce-fir-beech old-growth forest remnant of the Western Carpathians. Forests, 9: 379.
- Pavlištová H. (2022): Variabilita podkorunových srážek ve smrkových tyčkovinách v závislosti na intenzitě výchovného zásahu. [BSc. Thesis] Brno, Mendel University in Brno. (in Czech)
- 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.
- Pokorný R., Tomášková I., Havránková K. (2008): Temporal variation and efficiency of leaf area index in young mountain Norway spruce stand. European Journal of Forest Research, 127: 359–367.

- Poleno Z., Vacek S., Podrázský V., Remeš J., Štefančík I., Mikeska M., Kobliha J., Kupka I., Malík V., Turčáni M., Dvořák J., Zatloukal V., Bílek L., Baláš M., Simon J. (2009): Pěstování lesů III: Praktické postupy pěstování lesů. Kostelec nad Černými lesy, Lesnická práce: 952. (in Czech)
- Putalová T., Vacek Z., Vacek S., Štefančík I., Bulušek D., Král J. (2019): Tree-ring widths as an indicator of air pollution stress and climate conditions in different Norway spruce forest stands in the Krkonoše Mts. Central European Forestry Journal, 65: 21–33.
- Rambo T.R., North M.P. (2009): Canopy microclimate response to pattern and density of thinning in a Sierra Nevada forest. Forest Ecology and Management, 257: 435–442.
- Siegel S., Castellan Jr N.J. (1988): Nonparametric Statistics for the Behavioral Sciences. 2<sup>nd</sup> Ed. New York, McGraw-Hill Book Company: 399.
- Šimůnek V., Vacek Z., Vacek S., Švanda M., Podrázský V., Cukor J., Gallo J., Zahradník P. (2025): Bark beetle-induced salvage logging cycle is caused by weather patterns linked to the NAO and solar cycle in Central Europe. Forest Ecosystems, 13: 100328.
- Slodičák M. (2014): Příčiny chřadnutí smrku na Opavsku. In: Novák J., Dušek D. (eds): Chřadnutí smrku v oblasti severní a střední Moravy. Budišov nad Budišovkou, Forestry and Game Management Research Institute, Opočno Research Station: 5–8. (in Czech)
- Slodičák M., Novák J. (2006): Silvicultural measures to increase the mechanical stability of pure secondary Norway spruce stands before conversion. Forest Ecology and Management, 224: 252–257.
- Sohn J.A., Gebhardt T., Ammer C., Bauhus J., Häberle K.H., Matyssek R., Grams T.E.E. (2013): Mitigation of drought by thinning: Short-term and long-term effects on growth and physiological performance of Norway spruce (*Picea abies*). Forest Ecology and Management, 308: 188–197.
- Špulák O. (2023): Stabilization of the pine increment during recent years of low precipitation and high temperatures by removal of the spruce lower storey. Forest Ecology and Management, 545: 121300.
- Šrámek V., Pokorný R., Kupec P. (2023): Voda v lesních ekosystémech. Strnady, Forestry and Game Management Research Institute: 108. (in Czech)
- Steckel M., del Río M., Heym M., Aldea J., Bielak K., Brazaitis G., Černý J., Coll L., Collet C., Ehbrecht M., Jansons A., Nothdurft A., Pach M., Pardos M., Ponette Q., Reventlow D.O.J., Sitko R., Svoboda M., Vallet P., Wolff B., Pretzsch H. (2020): Species mixing reduces drought susceptibility of Scots pine (*Pinus sylvestris* L.) and oak [*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.] Site water supply and fertility modify the mixing effect. Forest Ecology and Management, 461: 117908.

- Thomas P., Packham J.R. (2007): Ecology of Woodlands and Forests: Description, Dynamics and Diversity. Cambridge, Cambridge University Press: 528.
- Vacek Z. (2017): Structure and dynamics of spruce-beechfir forests in Nature Reserves of the Orlické hory Mts. in relation to ungulate game. Central European Forestry Journal, 63: 23–34.
- Vacek Z., Vacek S., Bílek L., Král J., Remeš J., Bulušek D., Králíček I. (2014): Ungulate impact on natural regeneration in spruce-beech-fir stands in Černý důl Nature Reserve in the Orlické hory Mountains, case study from Central Sudetes. Forests, 5: 2929–2946.
- Vacek S., Vacek Z., Bulušek D., Bílek L., Schwarz O., Simon J., Štícha V. (2015): The role of shelterwood cutting and protection against game browsing for the regeneration of silver fir. Austrian Journal of Forest Science, 132: 81–102.
- Vacek Z., Prokůpková A., Vacek S., Bulušek D., Šimůnek V., Hájek V., Králíček I. (2021): Effect of Norway spruce and European beech mixing in relation to climate change: Structural and growth perspectives of mountain forests in Central Europe. Forest Ecology and Management, 488: 119019.
- 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.
- Vallet P., Pérot T. (2011): Silver fir stand productivity is enhanced when mixed with Norway spruce: Evidence based on large-scale inventory data and a generic modelling approach. Journal of Vegetation Science, 22: 932–942.
- Vejpustková M. (2022): Klimatické faktory limitující růst smrku na území České republiky v období 1968–2013. Reports on Forestry Research/Zprávy lesnického výzkumu, 67: 60–71. (in Czech)
- Viewegh J., Kusbach A., Mikeska M. (2003): Czech forest ecosystem classification. Journal of Forest Science, 49: 74–82.
- Vospernik S., Heym M., Pretzsch H., Pach M., Steckel M., Aldea J., Brazaitis G., Bravo-Oviedo A., del Río M., Löf M., Pardos M., Bielak K., Bravo F., Coll L., Černý J., Drössler L., Ehbrecht M., Jansons A., Korboulewsky N., Jourdan M., Nord-Larsen T., Nothdurft A., Ruiz-Peinado R., Ponette Q., Sitko R., Svoboda M., Wolff B. (2023): Tree species growth response to climate in mixtures of *Quercus robur/Quercus petraea* and *Pinus sylvestris* across Europe A dynamic, sensitive equilibrium. Forest Ecology and Management, 530: 120753.
- Vrška T., Adam D., Hort L., Kolář T., Janík D. (2009): European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) rotation in the Carpathians A developmental cycle or a linear trend induced by man? Forest Ecology and Management, 258: 347–356.

Watson D.J. (1947): Comparative physiological studies in the growth of field crops: I. Variation in net assimilation rate and leaf area between species, varieties, and within and between years. Annals of Botany, 11: 41–76.

Welles J.M., Cohen S. (1996): Canopy structure measurement by gap fraction analysis using commercial instrumentation. Journal of Experimental Botany, 47: 1335–1342.

Zavadilová I., Szatniewska J., Stojanović M., Fleischer P., Pavelka M., Petrík P. (2023): The effect of thinning intensity

on sap flow and growth of Norway spruce. Journal of Forest Science, 69: 205–216.

Zhang X., Maggioni V., Rahman A., Houser P., Xue Y., Sauer T., Kumar S., Mocko D. (2020): The influence of assimilating leaf area index in a land surface model on global water fluxes and storages. Hydrology and Earth System Sciences, 24: 3775–3788.

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