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The effect of thinning intensity on sap flow and growth of Norway spruce

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Abstract: Forest thinning can be used as an adaptive measure to improve the growth and resistance of Norway spruce forests affected by climate change. The impact of different thinning intensities on sap flow, growth, and tree water deficit of 40-year-old Norway spruce was tested. High thinning intensity (–61% of basal area) resulted in increased tree-level sap flow compared to the control (+27%), but it caused a decrease in the stand-level transpiration (–34%) due to reduced leaf area index. Low-intensity thinning (–28% basal area), high-intensity thinning, and control showed similar responses of sap flow to vapour pressure deficit and global radiation, suggesting unchanged isohydric behaviour. Both low- and high-intensity treatments displayed greater radial growth than the control. There were no differences in tree water deficit between the treatments. The low-intensity treatment can be considered the best water utilisation treatment with increased growth and unchanged transpiration at the tree level. The high-intensity treatment had similar radial growth as the low-intensity but lower stand-level transpiration, implying improved soil water availability. The study expands the ecophysiological understanding of thinning as a valuable silvicultural practice for adapting forest management of Norway spruce to the effects of climate change.

Keywords: increment; *Picea abies*; silviculture; transpiration; tree water deficit

Thinning is a common silvicultural technique used to manage growth and development of forests. Alteration of stand density and structure can improve growth and stress resistance of remaining trees due to reduced competition (Krajnc et al. 2019). Norway spruce (*Picea abies* (L.) Karst.) in Central Europe is especially affected by a combination of abiotic and biotic stresses which threaten

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its productivity and stability (Bosela et al. 2021; Sedmáková et al. 2022). The decrease in precipitation and higher evaporative demand in the past decades are already negatively affecting the growth of Norway spruce and pushing its ecological optimum to higher altitudes and latitudes (Krejza et al. 2021). Modern forestry should utilise thinning techniques as an adaptive measure to stabilise the existing Norway spruce stands. The use of thinning at a relatively young tree age can improve growth, allometry, and soil water availability, which can make the trees more resistant and resilient to expected climate change (Pretzsch, Mette 2008; Bhandari et al. 2021; Dušek et al. 2021). Heavy thinning can also improve understory conditions for the survival of natural regeneration or planted seedlings, with the aim of transforming a pure Norway spruce stand to a more heterogenous mixed stand (Lin et al. 2012; Reventlow et al. 2021).

Thinning affects the growth of Norway spruce in several ways. By reducing competition for resources such as light, water, and nutrients, thinning allows the remaining trees to grow more efficiently and with improved vigour (Jiménez et al. 2019; Houtmeyers, Brunner 2020). This can increase the trees' overall size and radial growth, as well as their resistance to environmental stressors and pathogens (Houtmeyers, Brunner 2020). Thinning from below (reduction of understory trees) increases the mean diameter and height of the remaining trees (Eliasson, Lageson 1999). Removal of the trees from this layer has a greater impact on soil-zone competition than on light competition (Kenkel 1988; Fernandez et al. 2012). Regardless, the understory trees exhibit a higher probability of mortality due to competitive pressure imposed by the trees in the uppermost canopy layer (Powers et al. 2010). Therefore, thinning from below can be seen as a great management tool to improve resistance and growth of the large trees from the canopy layer. The thinning intensity is also an important factor affecting the response of remaining trees to the silvicultural intervention. Higher-intensity thinning can have a more pronounced effect on the remaining large trees but can negatively affect total stand biomass production in the short-term (Mäkinen, Isomäki 2004).

Sap flow is the movement of water and nutrients from the roots to the branches and leaves, driven mostly by changes in the water pressure through the soil-plant-atmosphere continuum (Zhang et al. 1997; Yang et al. 2022). Thinning can increase sap flow by reducing competition for resources and allowing for increased light penetration and greater leaf area per tree (Kellomäki et al. 2023). Greater nutrient availability due to lower competition can also lead to formation of more efficient tracheids capable of greater sap flow (Ward et al. 2008). At the same time, thinning can also reduce stand-level respiration as the total leaf area or leaf area index is reduced and leads to less water being lost in the process (Forrester et al. 2013; Wang et al. 2019). Lower stand-level transpiration in stands with higher thinning intensity can lead to greater soil water reserves under higher evaporative demand, compared to unthinned stands (Rimal et al. 2022). In addition to measuring tree water status through sap flow, the automatic dendrometer that records stem radial variations (SRV) is a valuable tool for monitoring tree growth patterns and diurnal water changes in the stem (Krejza et al. 2021; Szatniewska et al. 2022). Dendrometers can provide a useful method for assessing tree water status (i.e. tree water deficit; TWD), which can indicate stress and potentially compromised vitality status of forest trees (Zavadilova et al. 2023). During prolonged droughts, trees use more of their stored water to maintain their essential functions (Salomón et al. 2022). As the stored water is depleted, TWD becomes more pronounced, leading to reduced growth, hydraulic constraints, and even death in extreme cases (Preisler et al. 2021). Changes in stand density (i.e. thinning) may have favourable effects on soil water availability and consequently improve water status and reduce the remaining trees' dependence on stored trunk water (Jiménez et al. 2019). Investigation of multiple environmental factors can improve current ecophysiological knowledge, which can enable us to use proper management strategies to achieve higher resistance and productivity of forest ecosystems.

In this study, we analysed stem radial growth and sap flow dynamics in *Picea abies* trees two years after different thinning intensities. We aimed to validate the following hypotheses: (*i*) thinning will have a positive impact on radial growth and a tree-level sap flow, and (*ii*) will cause a decrease in stand-level transpiration. Moreover, we wanted to test if (*iii*) the unthinned plot will experience a greater TWD due to higher competition for soil water sources than the thinning treatments and will use more stored stem water for the sap flow. The relevance of these objec-

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tives is enhanced by the site conditions that represent a lower altitude edge (625 m a.s.l.) for Norway spruce cultivation in the region.

MATERIAL AND METHODS

Study site description. The study site was located near Rajec, Czech Republic (49°26'45''N, 16°41'49''E; 625 m a.s.l.). The soil type was modal podzol with maximum soil depth of 60–80 cm. The stand was established in 1979 by afforestation of a previously clear-cut Norway spruce forest. Three-year-old seedlings were planted during the spring of 1979 in a 2 m × 1 m spread (Krejza 2016). The pure Norway spruce stand was divided into three equally large plots of 625 m^2. Two plots were thinned from below during the spring of 2018 with two different thinning intensities (30% and 60% of basal area removed). The third plot was left unthinned as a control treatment. The diameter at breast height (*DBH*) measurements were conducted during the 2020 vegetation season, two years post-thinning on each plot (Figure 1, Table 1). The leaf area index (*LAI*) was measured in July 2020 by the SS1 SunSCAN (Delta-T Devices Ltd., the United Kingdom) at five different positions at each plot to cover the heterogeneity of the canopy stands (Table 1). The broader area is covered mostly by coniferous species (77%), of which Norway spruce is most abundant (54%), but based on phytocenological classification, the natural cover was historically dominated by European beech (Světlík 2016). According to climatic conditions, altitude, and the southern slope of the stand, the site is not suitable for Norway spruce under the prospects of climate change. The evidence of that is a massive bark beetle infestation in the neighbouring old Norway spruce stand that was clear-cut and is being afforested with mixed broadleaved and coniferous species.

Meteorological measurements. Meteorological data were measured on the site above the canopy at 40 m height on a meteorological tower with the sensor for relative air humidity and air temperature (EMS 33, Czech Republic), incoming global radiation (CNR 1, Kipp & Zonen, the Netherlands), and precipitation (386 C, MetOne, USA; Figure 2). The mean annual temperature in 2020 was 9 °C which is 1.2 °C above the long-term yearly average (7.8 °C; Krejza et al. 2022). The amount of precipitation in 2020 was 879 mm, 200 mm more than the long-term annual average (679 mm; Krejza et al. 2022).

Sap flow measurements. We measured the sap flow using EMS81 (EMS Brno, Czech Republic) modules on four trees per treatment during

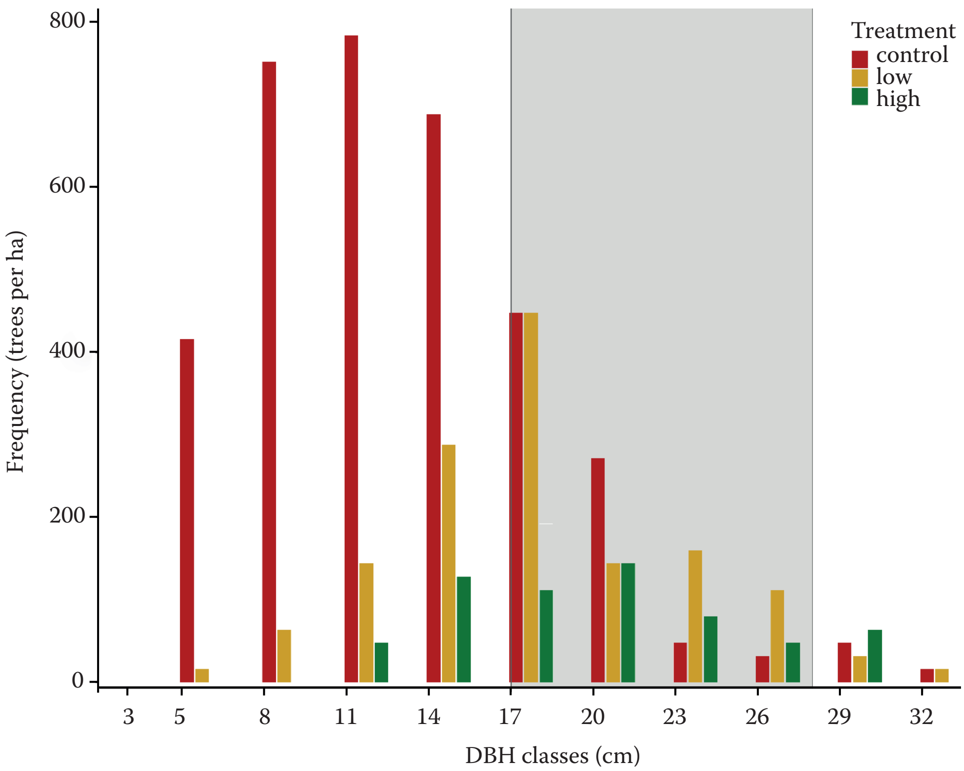

Figure 1. Tree diameter structure of the stands; grey area indicates DBH classes of selected trees for sap flow measurements

DBH – diameter at breast height

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Table 1. Overview of the stand structure, Leaf Area Index and average (mean ± SE) sap flow at tree and stand-level for all three treatments

Thinning intensity	Stand density (tree·ha^{-1})	Stand *BA* (m^2·ha^{-1})	Mean *DBH* (cm)	*LAI*	Mean sap flow (sampled trees) (kg·year^{-1}·tree^{-1})	Stand transpiration (mm·year^{-1})
Control	3 504	3.506	13 ± 5.2	5.02 ± 0.90	1 900 ± 375	227
Low	1 424	2.514	18 ± 5.1	3.95 ± 1.42	1 889 ± 813	219
High	624	1.358	20 ± 5.2	3.08 ± 0.75	2 507 ± 888	149

BA – basal area; *DBH* – diameter at breast height; *LAI* – Leaf Area Index

the 2020 growing season. The measurement principle is based on the Tissue Heat Balance method (Čermák et al. 2004). The post-processing of data includes establishing a baseline that eliminates noise caused by heat losses in the system under zero-flow conditions (Kučera et al. 2020). Moreover, the 23 days (12% of data) where precipitation exceeded 10 mm·day^{-1} were excluded according to the declining regression curve between sap flow and rainfall. The collected 10-min data were averaged to hourly and then aggregated to daily values. The tree sap flow (Q_{tree}) was standardised per one cm of the tree circumference (Q, kg·day^{-1}·cm^{-1}). Tree-level sap flow was also upscaled to stand-level sap flow via a scaling factor calculated from the ratio of the sampled trees' sap flow and the sap flow of all trees in the selected diameter classes (Čermák et al. 2004). The scaling curves are visualised for all three plots in supplementary files [Figure S1 in the Electronic Supplementary Material (ESM)].

Stem variation measurements. Stem radial variation (*SRV*) was obtained by measuring changes in tree circumference by automatic band dendrometers (DRL26, EMSBrno, Czech Republic) on four trees per treatment. The tree periderm was carefully removed before installing dendrometers to reduce the impact of hydroscopic shrinkage and swelling of the tree's outer bark. To measure the water-related changes in the stem, *TWD* (in mm) was calculated using dendrometer records that were de-trended for growth (Ehrenberger et al. 2012; Zweifel 2016). In the first step, a growth line was constructed by drawing lines between the daily maximum stem circumference values and the next equal stem circumference value, ignoring periods of incomplete stem circumference recov-

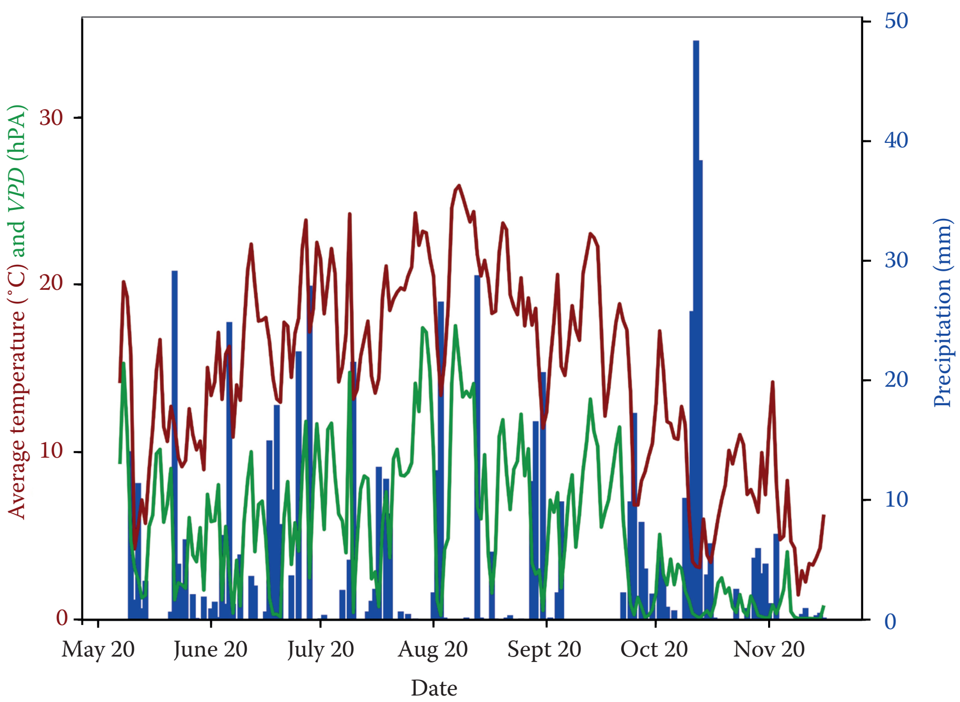

Figure 2. Daily dynamics of mean air temperature (red), vapour pressure deficit (*VPD*) (green) and precipitation (blue) during the vegetation season of 2020 at the experimental site

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ery due to stem shrinkage induced by water shortage. In the second step, the *TWD* was calculated as a difference between the actual *SRV* and growth line. The normalisation of the dendrometer data was not necessary as the difference in the average *DBH* of all the sampled trees was found to be statistically insignificant among plots.

Statistical analyses. All statistical analyses were conducted with R software (Version 4.2, 2022). Two-way ANOVA was used to test the sap flow differences between treatments and DBH classes. As the assumptions of homogeneity and normality were not met for the dendrometer data, we used Kruskal-Wallis' test for the analysis of variance. Differences between treatments and DBH classes were further analysed with nonparametric Fisher's LSD (least significant difference) test for multiple pairwise comparisons and the parametric Tukey's HSD (honest significant difference) test for mean comparisons. Both post-hoc tests were conducted with the Holm method (Holm 1979) for adjustment of the *P*-value. All statistical analyses were conducted at a significance level of $\alpha = 0.05$. Relationships between environmental conditions and sap flow were tested by linear and logarithmic regressions.

RESULTS AND DISCUSSION

Effect of thinning on standardised sap flow and stand transpiration. The effects of thinning on sap flow and transpiration in Norway spruce are complex and can depend on various factors such as the intensity of thinning, the age and size of the remaining trees, and local environmental conditions (Lagergren et al. 2008; Clausnitzer et al. 2011). In this study, the thinning treatment had a significant impact on standardised sap flow (*Q*) in stands with high-intensity thinning but not low-intensity thinning (Figure 3A, Table S1 in the ESM). High-intensity treatment showed overall higher maximum values of *Q* throughout the vegetation season compared to control and low-intensity treatment (Figure 3B), comparable with results observed by McJannet and Vertessy (2001) and Park et al. (2018).

The main factor which could explain the increase of individual tree *Q* in the high-intensity treatment is the lower competition for soil water and nutrient availability due to the removal of smaller trees. Another explanatory factor could be increased light availability. However, most of the trees removed during thinning were chosen from the understory; hence, the soil-water competition alternations are probably a more dominant factor affecting the *Q* changes. Greater access to soil water resources could be directly reflected in higher transpiration and, therefore, higher *Q* rates (Clausnitzer et al. 2011; Szatniewska et al. 2022). Higher competition leads to lower *Q* values and reduced competition via thinning can lead to a rapid increase of *Q* in the following vegetation season (Lagergren, Lindroth 2004; Gebauer et al. 2011). Trees with the dominant social position and reduced competition pressure can show larger xylem conductivity, as indicated by Zhang et al. (2019). Given the warmer and wetter vegetation season in 2020 compared to the long-term average, changes in *Q* may have been notably influenced by the higher nutrient availability. Nutrient limitation of Norway spruce can lead to the reduction of total leaf area and, consequently, lower transpiration and tree level *Q* (Phillips et al. 2001). Better access to nutrients can also lead to the development of wider tracheids of Norway spruce which could support larger *Q* rates (Ward et al. 2008). The lower-intensity thinning had no significant effect on tree level *Q*, which corresponds to the non-significant effect of similar thinning (50% stand density) on tree level *Q* observed in Gebauer et al. (2011).

The results of *Q* per DBH classes showed that 23 cm and 26 cm DBH classes of high-intensity treatments had significantly higher *Q* than corresponding DBH classes from the control treatment (Figure 4). The smaller 17 cm and 20 cm DBH classes showed no significant difference between high-intensity and control treatments. Moreover, all four DBH classes showed no significant difference in *Q* between low-intensity thinning and control treatment. The high-intensity thinning effect had a stronger impact on the larger trees than the smaller trees. As the taller trees with greater *DBH* occupy higher canopy layers, they might exert higher competitive pressure on smaller trees after thinning. The *Q* results represent the state of the stand two years after thinning. Therefore, the reduction of stand density can have a long-lasting effect on the larger trees via changes in competition.

The linear regression analysis between vapour pressure deficit (*VPD*), global radiation (*GR*), and *Q* revealed that all three treatments reacted similarly to the changing *VPD* and *GR* during the vegetation season (Figure 5). There were no significant chang-

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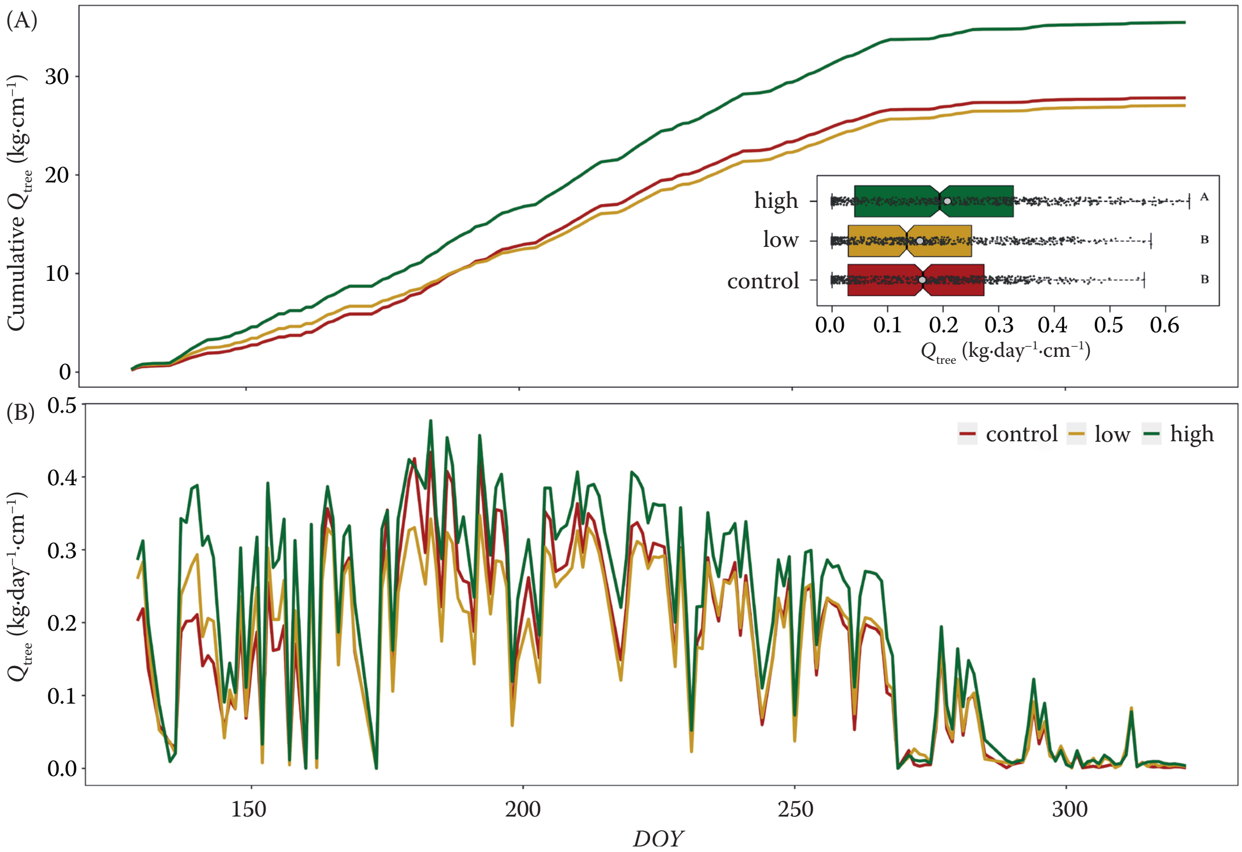

Figure 3. (A) Cumulative standardized sap flow (Q) and (B) daily dynamics of Q for control, low thinning intensity and high thinning intensity; the embedded graph in the upper section shows boxplots of the Q with capital letters showing the results of the post-hoc test; white dot in the boxplot refers to the mean value and the black line to the median

DOY – day of the year

es among slopes or intercepts of *VPD* and *GR* response between the treatments. All three treatments showed a relative reduction of sap flow after the 10 hPa *VPD* threshold captured by logarithmic function (Figure 5A) and responded linearly to increasing *GR* (Figure 5B). The results match the overall charac-

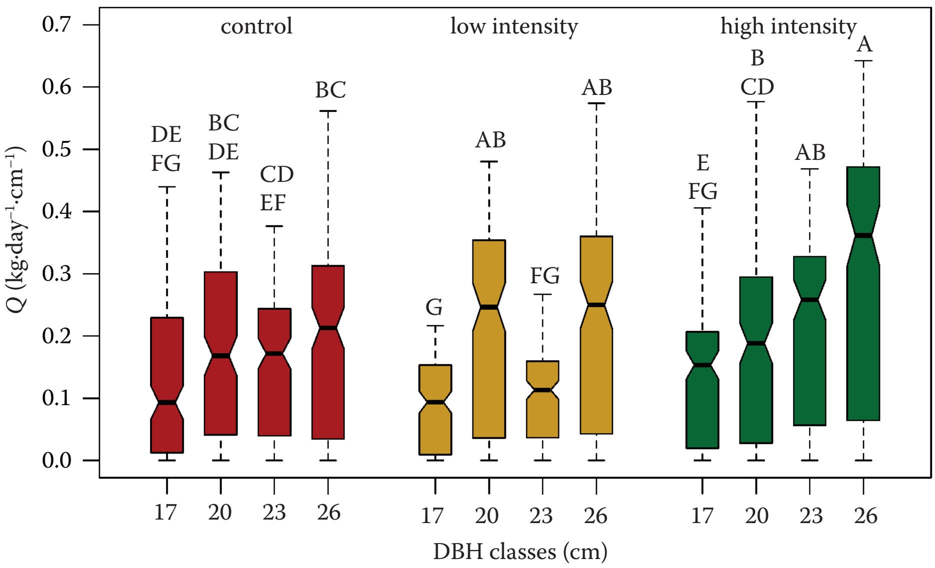

Figure 4. Box plots of standardized sap flow (Q) for respective diameter at breast height classes (*DBH*) and thinning treatments; capital letters represent significantly distinguishable groups based on post-hoc tests

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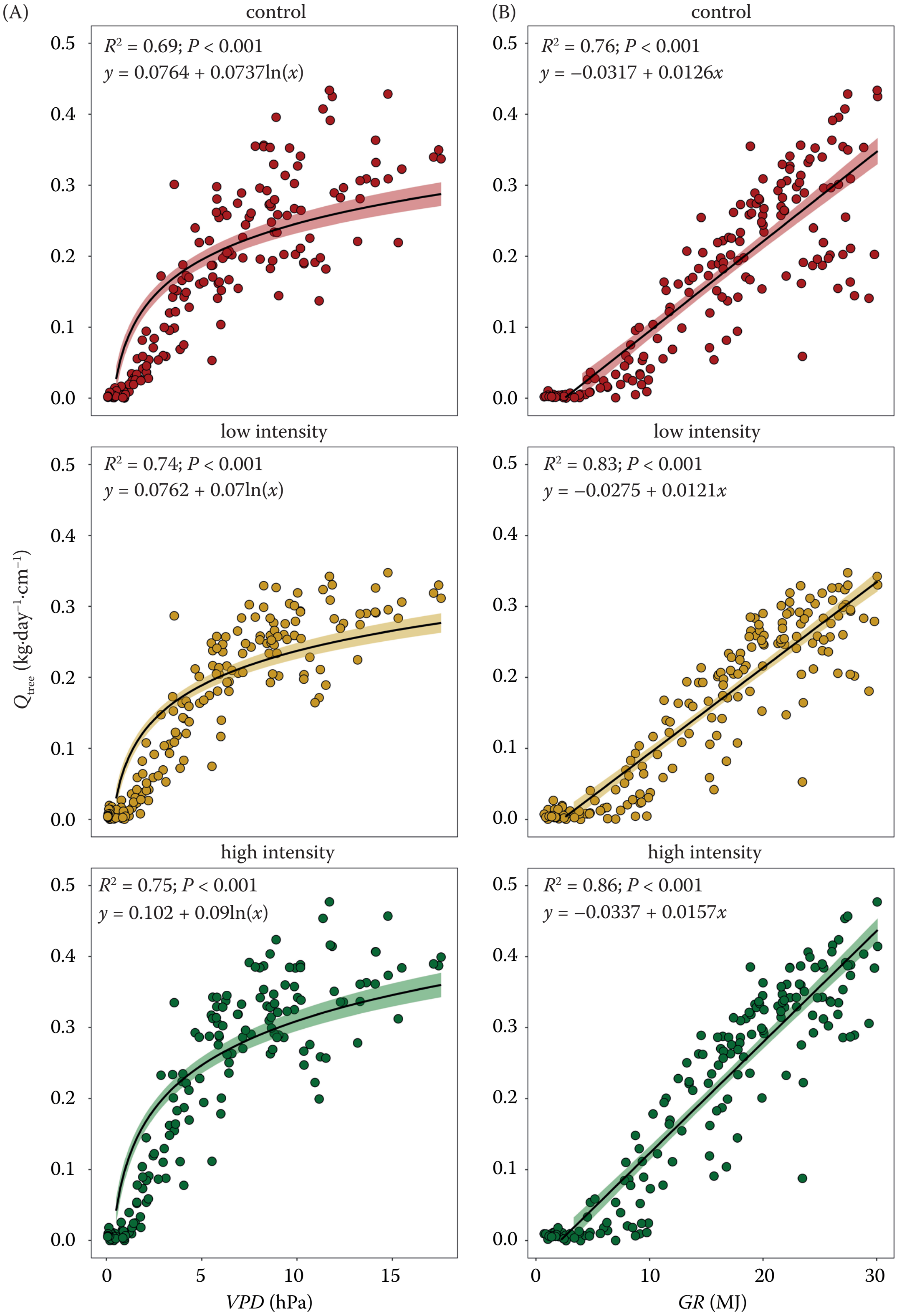

Figure 5. Regression between standardized sap flow and (A) vapour pressure deficit, and (B) global radiation for all thinning treatments (red – control, yellow – low thinning intensity, green – high thinning intensity)

Q – sap flow; *VPD* – vapour pressure deficit; *GR* – global radiation

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terisation of Norway spruce as an isohydric species (Pashkovskiy et al. 2019; Zavadilová et al. 2023).

Upscaled *Q* data showed that the high-intensity treatment had 34% lower than the control and the low-intensity treatment had 4% lower stand transpiration (Figure 6). The lower stand-level *Q* of the high-intensity treatment can be explained by the smaller leaf area, which was also reflected in lower *LAI* (3.1), compared to low-intensity (4.0) and the control (5.0) (Table 1). Rimal et al. (2022) similarly showed that thinning of Norway spruce led to reduced *LAI* of remaining trees and corresponded to lower transpiration derived from the model. The individual-level increase of *Q* for the high-intensity treatment is balanced at the stand level due to a decrease of *LAI*, reducing total water use of the stand. Tsamir et al. (2019) similarly found that stand transpiration decreased with thinning intensity while tree transpiration increased. The study by Gebhardt et al. (2014) also demonstrated that high-intensity thinning reduced total stand evapotranspiration and led to greater soil water availability even three years after thinning. The proportional decrease of stand transpiration to a reduction of the basal area through thinning indicates that our findings align with Wang et al. (2019).

Thinning in a pine-spruce forest led to a significant reduction of the stand-level canopy transpiration but quickly recovered in the following year (Clausnitzer et al. 2011). Our results contradict this previous observation as results were measured two years after thinning took place, and we still observe significant differences for the high-intensity treatment.

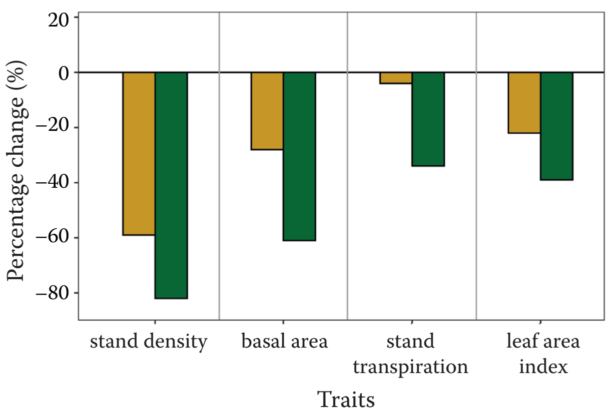

Figure 6. Reduction in thinning treatment of stand density, basal area, annual stand transpiration and Leaf Area Index compared to the control plot (Table 1), values represent means of percentual changes

Effect of thinning on growth and tree water deficit. Both low-intensity and high-intensity treatments showed significantly greater radial growth compared to the control treatment when measured two years after the thinning (Figure 7A). Improved radial growth after thinning is a general fact stemming from lower competition, better light conditions, and possibly greater nutrient access for the remaining trees (Jaakkola et al. 2005; Gspaltl et al. 2013; Bianchi et al. 2022). These positive effects for Norway spruce span both short-term and long-term periods (Sohn et al. 2013). Reduced stand density of Norway spruce forests can also improve the growth resistance during drought periods (Laurent et al. 2003). The post-drought recovery of radial growth can be further improved by a higher-intensity thinning regime (Kohler et al. 2010). As the total tree density decreases in thinned stands, the total wood production will be lowered, but the remaining canopy layer trees provide larger economic value than wood from the understory layer (Cao et al. 2008; Ara et al. 2022). Higher-intensity thinning can reduce the total stand wood production compared to unthinned stands, but the difference decreases over time due to excessive tree mortality in high-density unthinned plots (Mäkinen, Isomäki 2004). It is pertinent to note that the older Norway spruce stands in this region are negatively affected by bark beetle infestation. Therefore, thinning alone can be ineffective if the trees cannot reach maturity (70–130 years); transformation of such forests to mixed/broadleaved forests is needed (Hillayová et al. 2022).

We observed no significant differences in tree water deficit between the treatments (Figure 7B). The high-intensity treatment experienced slightly greater *TWD* at the start of the vegetation season, and the low-intensity treatment experienced a greater *TWD* during the end of the vegetation season. It is possible the spring and autumn phenology were slightly altered, but we likely did not have a sample size large enough to recognise the shift. Norway spruce has a shallow root system; it is likely that all three treatments used the internal stem water storage similarly (Schäfer et al. 2019). The year of the measurements was colder and received more precipitation than the long-term average; therefore, the differences in *TWD* could be more pronounced if the trees experienced drought.

Comparison of sap flow and growth reaction to thinning. The low-intensity thinning showed

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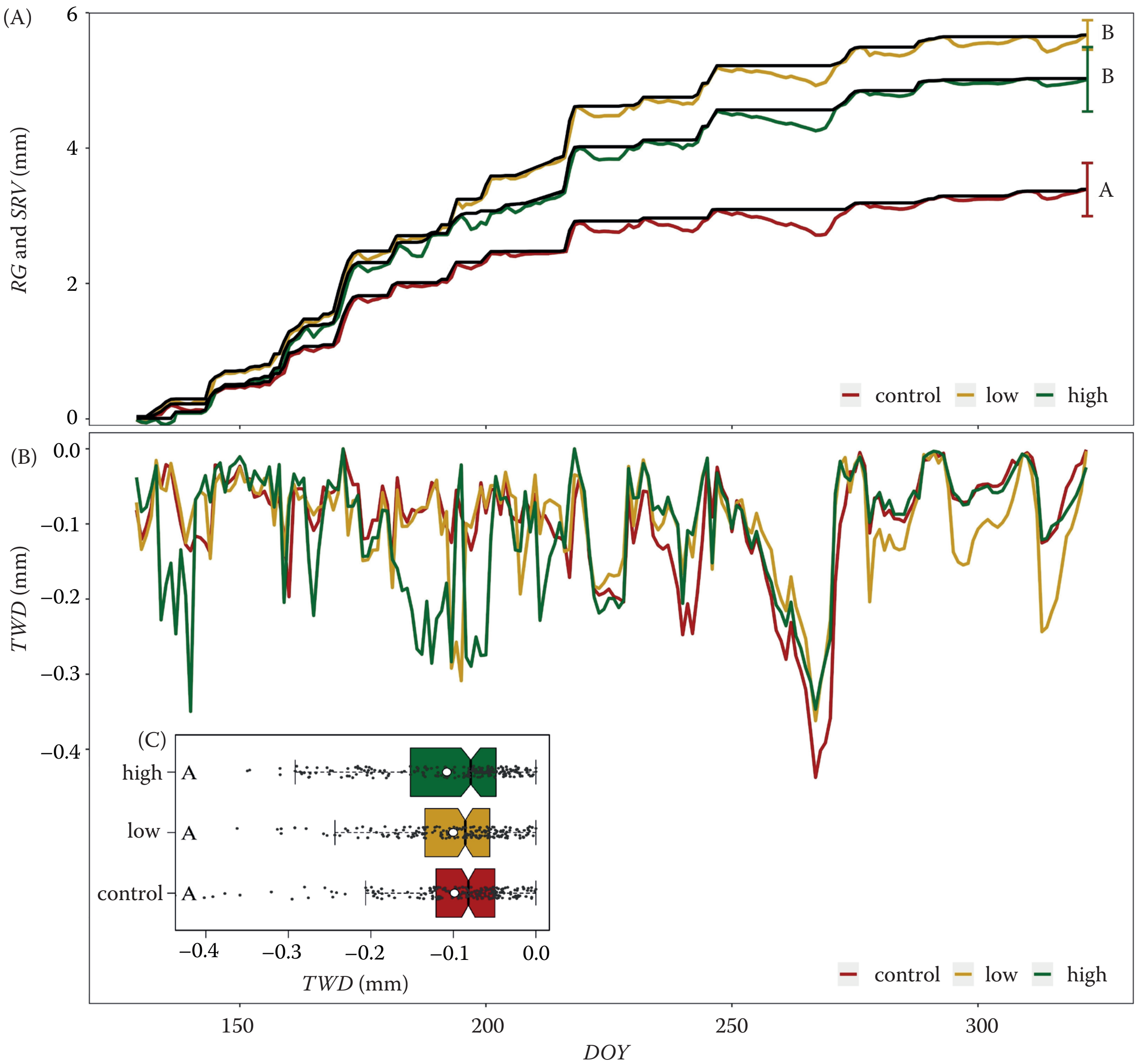

Figure 7. Hourly dynamics of (A) radial growth (*RG*; black lines), stem radial variation (*SRV*), and (B) extracted tree water deficit (*TWD*) and (C) treatment level variability of *TWD* throughout the measurement period; the last value of radial growth includes a 95% confidence interval around it; capital letters represent significantly distinguishable groups based on the Fisher's LSD (parts A, B) and post-hoc test (part C); white dot in the boxplot refers to the mean value and the black line to the median

DOY – day of the year

greater radial growth but no significant change in sap flow compared to the control (Figure 3A, Figure 7A). This could suggest that the low-intensity treatment improved its water use efficiency for radial growth (Gebhardt et al. 2014; Niccoli et al. 2020). For example, Fernandes et al. (2016) found that thinning increased the water use efficiency of *Pinus halapensis*. On the other hand, the radial growth increased proportionally to sap flow in the high-intensity treatment. The treatments could have altered carbon allocation patterns; the high-intensity treatment might invest more carbon into crown expansion (higher light availability) or root growth (lower soil-zone competition), and the low-intensity treatment might retain carbon allocation patterns more similar to the control (Skovsgaard et al. 2006; Campbell et al. 2009). Low-intensity thinning can have an immediate effect on the wa-

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ter utilisation of Norway spruce trees for radial growth, but high-intensity thinning could alter the overall growth efficiency in the long term. Additional research focused on both water use efficiencies (carbon isotopes or eddy-covariance) and carbon allocation patterns of thinning intensity treatments could provide valuable information for adaptive forestry. The higher-intensity treatment might also improve the conditions for the regeneration and growth of understory seedlings (Lin et al. 2012). The best results for conversion of the Norway spruce stands would be achieved by their transformation to mixed forests with a heterogenous stand structure (Reventlow et al. 2021). Mixed heterogeneous forests are much more resilient under drought stress compared to Norway spruce monoculture stands (Pardos et al. 2021). Heavy thinning can improve the conditions in the forest for the establishment of other intermixed species.

CONCLUSION

Both low-intensity and high-intensity thinning had a positive impact on the radial growth of Norway spruce. Moreover, the high-intensity treatment showed greater tree-level sap flow due to the lower competition but reduced stand-level transpiration as a result of the lower leaf area index. The low-intensity treatment could be considered the most water-efficient management strategy at the individual tree level due to higher growth and unchanged transpiration compared to the control. On the other hand, the high-intensity thinning lowers stand-level transpiration, which could improve the overall soil water availability during a drought. Thinning practices should also be supported by actions that transform the pure Norway spruce forests into more resilient mixed forests. Further research, including an investigation into water use efficiency and soil water content, can be beneficial for adaptive forestry under climate change.

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