Cent. Eur. For. J. 71 (2025) 3–13 sciendo DOI: 10.2478/forj-2024-0024

CENTRAL EUROPEAN Forestry Journal

ORIGINAL PAPER

Assessing crown reduction as a strategy to mitigate drought stress during initial development of sessile oak and Norway spruce saplings

Janko Arsić[1,2]*, Marko Stojanović[1], Petr Horáček[1,3], Sergei Mikhailov[1,3], Jan Krejza[1,2]

[1]*Global Change Research Institute of the Czech Academy of Sciences, Bělidla 986/4a, CZ - 603 00 Brno, Czech Republic*

[2]*Mendel University in Brno, Faculty of Forestry and Wood Technology, Department of Forest Ecology, Zemědělská 1665/1, CZ - 613 00 Brno, Czech Republic*

[3]*Mendel University in Brno, Faculty of Forestry and Wood Technology, Department of Wood Science and Wood Technology, Zemědělská 1665/1, CZ - 613 00 Brno, Czech Republic*

Abstract

Droughts, amplified by climate change, pose a significant threat to the success of both artificially and naturally regenerated forests. Understanding how these changes affect the initial stages of saplings development is crucial for forest establishment, particularly for ecologically and economically important species like Norway spruce and sessile oak in Central Europe. This study investigated the impact of crown reduction (CR) by 50% of crown length on saplings of each species. Automatic dendrometers were installed on 24 saplings per species to precisely monitor growth and water-related stem changes. The main objective was to investigate the potential ameliorative effect of CR on water-stressed saplings during their initial development. Our study hypothesized that CR, by decreasing leaf area and consequently water use, would improve water availability and facilitate sapling growth. The results indicate that CR may enhance soil water availability thereby supporting the growth of water-stressed Norway spruce saplings but not those of sessile oak. The tree water deficit – an indicator of tree water status – significantly improves in Norway spruce saplings subjected to CR ($p < 0.05$). Conversely, this treatment resulted in the depletion of stem water status in sessile oak saplings. The species-specific growth phenology revealed that CR led to an increase in the number of growing days for Norway spruce compared to sessile oak saplings. In summary, CR may be considered a beneficial method for alleviating stress in Norway spruce saplings, especially during drought. In addition, further testing in field conditions is necessary to confirm these results.

Key words: *Picea abies* [L.] Karst.; *Quercus petraea* [Matt.] Liebl.; stem radial variation; automatic dendrometers; water availability

Editor: Bohdan Konôpka

1. Introduction

Forests play an irreplaceable role in the landscape, and preserving these areas is crucial for numerous reasons: they stabilize soil, sequester and store carbon, regulate greenhouse gases, and provide a range of other ecosystem services (Bonan 2008). In recent decades, Europe has seen a significant increase in forest disturbances, largely due to past management practices such as the establishment of planted conifer monocultures, and the impacts of climate change (Hlásny et al. 2021; Patacca et al. 2023). In forests that have experienced large-scale disturbances, replanting with artificial plant material is not only an effective method for quickly establishing a new generation of forests, but also a crucial strategy for restoring these areas and preventing further degradation (Lázaro-González et al. 2023).

Current methods for reforesting large areas with numerous trees and shrubs predominantly rely on planting of nursery-grown seedlings due to their higher survival rates (Löf et al. 2004; Palma & Laurance 2015; Andivia et al. 2021). The successful development and growth of high-productivity forest stands are significantly dependent on the quality of these seedlings (Landis et al. 2010; Riikonen & Luoranen 2018; Mataruga et al. 2023). However, it is crucial to note that seedlings repre-

**Corresponding author. Janko Arsić, e-mail: arsic.j@czechglobe.cz*
© 2024 Authors. This is an open access article under the CC BY 4.0 license.

sent the most sensitive stage of a tree's life cycle, making them particularly vulnerable to water stress (Niinemets 2010; Grossnickle 2012; Hueso-González et al. 2016). This susceptibility partly arises from their lower capacity to absorb resources from deeper soil layers, primarily due to an underdeveloped root system (Savé et al. 1999; Lloret et al. 2004). Additionally, rising temperatures driven by climate change further complicate successful reforestation efforts by amplifying atmospheric evaporative demand, which increases aridity and drought conditions (Allen et al. 2010; Trnka et al. 2015). This effect is especially pronounced on bare land, where exposed topsoil heats up more quickly, significantly reducing the water availability in the topsoil, which is crucial for the establishment and survival of new saplings (Biehl et al. 2023). The most critical period during reforestation is when the saplings adjust their morphology and physiology to adapt to new environmental conditions (Close et al. 2005). Transplanted saplings are exposed to conditions that differ significantly from those in the nursery environment, which presents unique challenges for their initial adaptation and survival (Grossnickle 2005).

Given the high costs associated with reforesting large areas, it is crucial to ensure that seedlings are optimally prepared for transplantation into natural conditions. Several studies have investigated various methods aimed at increasing the survival and growth of seedlings initially after transplanting. Ensuring an adequate water supply post-planting is essential, and common measures include weed control, which reduces competition for water, and the selection of drought-tolerant genotypes and adapted planting times, which align seedling growth with favorable environmental conditions (Royo et al. 2001; Devine et al. 2007; Bakker et al. 2012; Gonçalves et al. 2013; Taïbi et al. 2016). In addition to these strategies, directly increasing water availability is also explored. Frequent irrigation can significantly aid in establishing seedlings by increasing their vigor, although it is often not feasible to implement on a large scale due to high costs and logistical challenges (Castro et al. 2005). Alternatively, soil amendments like hydrogels, which are designed to increase soil water holding capacity, have been tested. However, the results for hydrogels are mixed, ranging from positive to negative impacts on seedling survival and growth, suggesting that their effectiveness may vary depending on specific environmental conditions, soil types, and species-specific responses (Biehl et al. 2023 and references therein).

Low-cost and easily applicable techniques are essential in reforestation efforts. In this study, we examine the practice of crown reduction (hereafter CR) length and thereby leaf area (hereafter LA) which meets both of these criteria. Our assumption is based on the observation that trees typically possess more leaves than are necessary for their normal development (Fatichi et al. 2014). Many studies suggest that moderate defoliation hardly affects overall forest carbon uptake (Gough et al. 2013), tree growth (Hoogesteger & Karlsson 1992), or seedling growth (Volin et al. 2002). According to Fatichi et al. (2014), this excess of leaves is more of an evolutionary than a physiological trait, as trees need to shade competitors, protect themselves against defoliators, and store additional carbohydrates (particularly conifer needle-leaf trees). Additionally, an excessive foliar mass can increase a sapling's susceptibility to planting stress because a newly planted seedling's root system is often not developed enough to meet the evaporative water demands necessary to maintain a proper water balance (Grossnickle 2005).

The most readily observed effects of dry conditions on seedlings are changes in their growth and survival (Grossnickle 2012; Fernández et al. 2014). Therefore, to explore how CR might alleviate drought effects in a controlled environment, we employed automatic dendrometers in an experiment on two contrasting tree species: broadleaf sessile oak (*Quercus petraea* [Matt.] Liebl.) and conifer Norway spruce (*Picea abies* [L.] Karst.), hereafter referred to as an oak and spruce. These devices allow for precise monitoring of growth dynamics, providing detailed insights into the trees' responses to modified growing conditions (e.g., Krejza et al. 2021; Szatniewska et al. 2022). Besides this, dendrometers provide a valuable tool for monitoring the water status of seedlings, including tree water deficit (TWD), which indicates reliance on stem water reserves (Zweifel et al. 2016). During prolonged droughts, trees increasingly depend on their stored water due to an imbalance between transpiration and root water uptake, leading to more pronounced TWD as these reserves are depleted (Salomón et al. 2022). Such depletion can result in reduced growth, hydraulic constraints, and, in extreme cases, death (Preisler et al. 2021). As our studied species exhibit distinct water-use strategies – with oak being anisohydric (Zang et al. 2012) and spruce isohydric (Zavadilová et al. 2023a) – one would expect these species to react differently to applied treatments. Therefore, our primary objective was to investigate how changes in LA through CR may positively affect soil water availability, thereby improving the water status of saplings and reducing their dependence on stored stem water.

Moreover, our study evaluated the following hypothesis:

(i) CR treatment is expected to enhance soil water availability by reducing the water use of saplings;

(ii) saplings subjected to CR will exhibit improved stem water status, consequently leading to a decrease in TWD;

(iii) under CR treatment, saplings growing in conditions with reduced water availability, will achieve growth rates comparable to those of saplings not receiving this treatment.

2. Materials and methods

2.1. Experimental location

The experiment was conducted on the campus of the Global Change Research Institute, CAS (Brno, Czech Republic, 49.1866°N, 16.5922°E). The experimental site is located at an elevation of 202 m above sea level. The climate is warm, characterized by a long-term average annual temperature of 10 °C and annual precipitation sum of 506 mm for the period 1990–2019.

2.2. Plant material and experimental design

The experiment involved 3-year-old saplings of oak and spruce with bare roots collected from the nursery of Mendel University Forest Enterprise, Masarykův les (Křtiny, Czech Republic), which represents the genetic profiles typically found in Drahanská vrchovina. This source is suitable for use in the lower and middle altitudes typical of Central European conditions. In June 2021, the day of the year (DOY 160) 144 saplings (72 saplings per each species) were transplanted in 20 L pots with substrate mixed with fertilizer (Klassman-Deilmann, Geeste, Germany). The substrate included a mixture of white peat, frozen black peat, and buffered coco coir. Additionally, lime fertilizer, NPK fertilizer, and micronutrients were incorporated into the mixture. The nutrient composition within the substrate included 90 mg L^{-1} of N, 100 mg L^{-1} of P_2O_5, 250 mg L^{-1} of K_2O, 100 mg L^{-1} of Mg, and 100 mg L^{-1} of S. The substrate displayed a pH of 5.5, a water capacity of 78–82% by volume, and an electrical conductivity of 25 mS m^{-1}. At planting, oak saplings had an average height of 79.5 ±10 cm and a diameter of 10.06 ±1.7 mm, while spruce saplings measured an average of 30.8 ±4.5 cm and a diameter of 6.7 ±1.3 mm. Pots were randomly distributed and placed into 6 large format plastic containers (24 pots in one container, 12 per species) with dimensions (1 × 2 m), equipped with drainage holes (Fig. 1). The containers with pots were placed under a 3-m high roof made of transparent, UV-permeable foil to provide natural light to the plants. The height of the shelter ensured proper ventilation and prevented excessive heating below the roof. In the initial year of the experiment (2021), the length of the crown of 36 saplings per species was reduced by 50% by clipping the branches from the bottom part of the crown upwards (Fig. 1). From June to the end of October 2021, all saplings were regularly watered with the same amount of water (i.e. 2 L) once per week with the primary objective of minimizing stress during their transplantation year. Starting in March 2022 the experiment was further divided into two groups (Fig. 1): well-watered saplings (wet) and water-stressed saplings (dry). This adjustment led to a total irrigation of 2 L and 0.5 L per saplings per week in the wet and dry treatments, respectively. This makes seasonal totals of approximately 800 mm for the wet treatment and approximately 200 mm for the dry

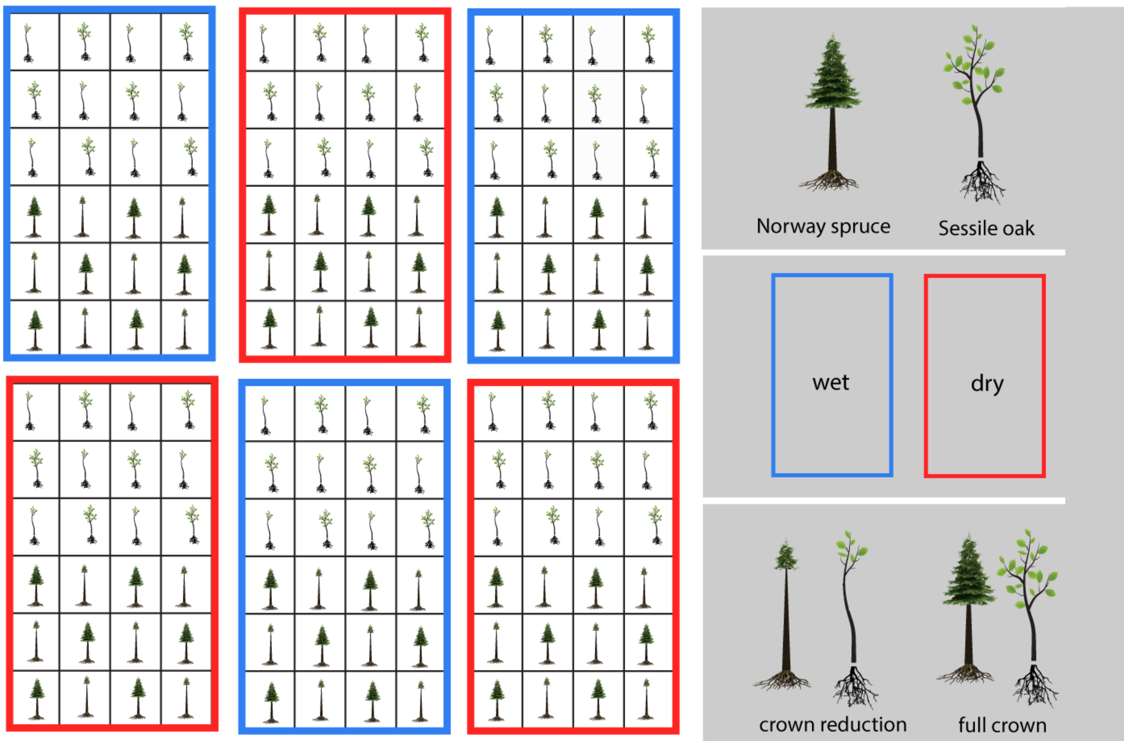

Fig. 1. Design of experiment. Blocks framed in blue and red indicate containers with pots of well-watered (wet) and water-stressed (dry) saplings, respectively.

treatment, covering the period from March until October. Volumetric water content (VWC; %) in the top 30 cm of the pots was periodically (varying 1 to 4 times per month) measured using the CS616 water content reflectometer (Campbell Sci. Inc., Logan, UT). Measurements were taken in three different positions within each pot, and the mean value of these three measurements was used for further analysis (Fig. 2). Given our interest in capturing the initiation of growth and its phenology, while also aiming to minimize the effect of plant transplantation, we excluded the year 2021 from our analyses. We focused on the 2022 growing season as it allowed us to accurately capture the onset of growth and its dynamics.

2.3. Automatic dendrometers measurements

Immediately after planting, the saplings were equipped with automatic dendrometers (PDS40P, EMS Brno, Czech Republic) to monitor continuous stem diameter variations. These variations were monitored at a resolution of 0.62 µm, with measurements taken and stored at 1-hour intervals. We installed dendrometers on 24 saplings per species (48 in total), six per treatment, on the stem, 5–10 cm above the ground level. The measured data obtained from the dendrometers were converted into stem radius variations (SRV; µm) and partitioned into growth (GRO) and water-related processes using the "zero growth concept" (Zweifel et al. 2016). This method assumes that GRO occurs only when the stem radius exceeds the previous maximum radius value. The difference between the GRO and observed SRV values was considered a measure of TWD (µm). This approach provides information about stem growth and changes in tree water status by considering both growth and reversible changes in tree water balance due to de-rehydration of elastic tissues. Furthermore, we calculated the daily growth rate (µm day^{-1}) and established two distinct growth rate thresholds, ≥ 1 µm day^{-1} and 5 µm day^{-1}, to analyse the growth phenology and calculate the number of days each sapling spent in these specific categories. The start and end of the growing season were defined as the days when 5% and 95% of total growth was achieved. Additionally, we measured tree ring widths (TRW) from stem cross-sections obtained at the end of 2022, with five saplings per treatment, to complement the dendrometer data. We verified whether the annual growth patterns observed in dendrometer data correlate with those from TRW measurements. Upon confirming this correlation, we merged the datasets for each treatment to increase the sample size for our statistical analyses. These combined analyses, utilizing both dendrometer and TRW data, provided additional insights into the growth patterns of the saplings. Regarding TWD, we considered only the daily values during the growing season (1st May – 31st October) and excluded those likely affected by winter temperatures (Turcotte et al. 2009).

2.4. Statistical analyses

To assess the influence of drought and CR on VWC, GRO and TWD of oak and spruce saplings, a split-plot experimental design was applied. After examining the data's normality assumption and variance homogeneity, a one-way analysis of variance (ANOVA) was used to evaluate the effects of individual treatment on water balance (TWD) or stem growth. Significant differences between treatments were analysed using Tukey's HSD post-hoc test a commonly used method to assess the significance

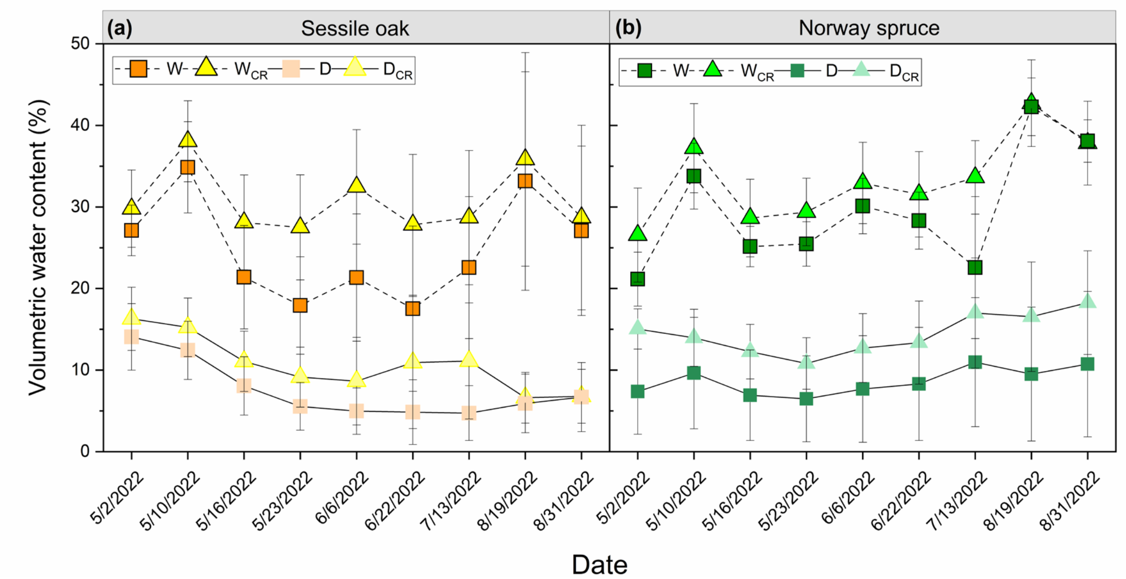

Fig. 2. Volumetric water content – (VWC; %) in the substrate of potted sessile oak **(a)** and Norway spruce **(b)** saplings treated with well-watered (W), well-watered and crown reduction (W$_{CR}$), water-stressed (D), water-stressed and crown reduction (D$_{CR}$).

of differences between pairs of group means. The data analyses and visualization were performed using OriginPro software (OriginLab Corporation, Massachusetts, USA), and statistical significance for all analyses was set at $p \leq 0.05$. The data presented in the figures are the mean values ± standard error of the mean value.

3. Results

3.1. Soil water availability

The saplings watering scheme significantly increased VWC in wet conditions compared to dry, with levels nearly four times higher ($p < 0.0001$; Fig. 2a and Fig. 2b). CR treatment consistently increased VWC in both wet and dry conditions for both species; in wet conditions, the increase ranged from 12–24%, while in dry conditions, the differences were even greater, ranging from 42–67%. Notably, in oak under wet conditions, CR led to a statistically significant increase in VWC ($p = 0.03$; Fig. 2a). The most pronounced difference was observed in oak saplings during summer months under wet conditions with CR, while in spruce, the VWC differences within the wet treatment were smaller. Under dry conditions, the differences in oak were less pronounced and not significant ($p = 0.428$), whereas in spruce, they were more pronounced and marginally significant ($p = 0.056$; Fig. 2b).

3.2. Annual radial growth and water status

In oak saplings, the highest GRO values were observed under wet treatment conditions, while significantly lower values were recorded under dry conditions ($p < 0.001$; Fig. 3a). Despite different moisture levels, CR treatment did not significantly affect oak GRO in either wet ($p = 0.379$) or dry conditions ($p = 0.983$). TWD in oak was significantly higher under dry conditions ($p < 0.001$; Fig. 3b). Furthermore, CR treatment led to a significant increase in TWD, regardless of whether conditions were wet or dry ($p < 0.001$). Finally, the lowest TWD values were observed under wet conditions without CR, while the highest were in dry conditions with CR (Fig. 3b).

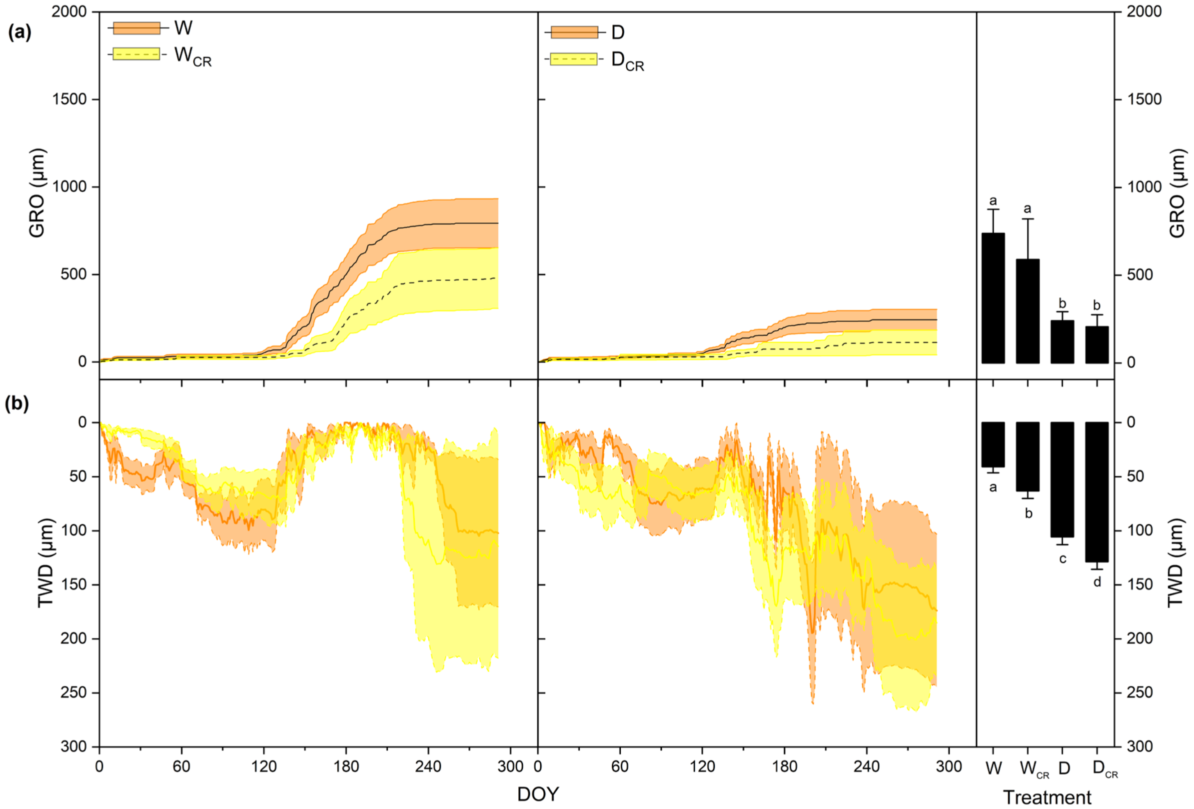

Fig. 3. Seasonal growth dynamics of sessile oak saplings during the 2022 growing season. **(a)** The growth line (GRO) and **(b)** tree water deficit (TWD) are represented by a solid line for the well-watered (W) and water-stressed (D) treatments, and by a dashed line for the well-watered with crown reduction (W_{CR}) and water-stressed with crown reduction (D_{CR}) treatments. Shaded areas surrounding the GRO and TWD lines represent the standard error of means (SE). Column graphs show mean GRO and TWD, with whiskers indicating SE. Different letters indicate significant differences ($p < 0.05$) as estimated by the Tukey ANOVA post-hoc test. DOY – Day of the year.

On the other hand, spruce saplings exhibited comparable GRO across both wet and dry conditions, regardless of CR application (Fig. 4a). Notably, saplings in dry conditions without CR significantly underperformed compared to those in wet conditions, with or without CR ($p < 0.05$). Applying CR in dry conditions resulted in GRO that was not statistically different from those in wet conditions, regardless of CR ($p < 0.05$). Concerning TWD, only dry conditions resulted in a significant increase for saplings without CR ($p < 0.001$), while CR-treated saplings showed TWD levels comparable to those in wet conditions ($p < 0.05$).

3.3. Number of growing days

We found an earlier start of growth for the spruce saplings, on average the spruce started growing on DOY 107. In contrast oak stem growth commenced one month later on DOY 139 (mean for all treatments). Regarding the end of the growing season we did not find such differences, the difference was only 8 days with an earlier end of growth of oak. Comparing the different treatments, the earliest growth was noted in the dry variant, exhibiting an early cessation of growth.

Observation of saplings growth revealed that spruce saplings commenced growth earlier and sustained it for a longer duration compared to oak saplings (Fig. 5). Oak saplings exhibited 81 growing days in wet conditions and 58 days in dry conditions. Despite moisture levels, oak saplings subjected to CR consistently experienced 55 growing days. Contrary, spruce saplings consistently showed extended growth periods across all treatments, with CR lengthen the number of growing days to 110 in wet conditions and 122 in dry conditions. Notably, under CR, spruce saplings growing days were up to twice as long as those of oak (Fig. 5).

4. Discussion

The study highlights significant differences in the responses of oak and spruce saplings to CR and varying soil water availability. While CR alleviated soil water availability, it did not support oak's GRO or tree water status (i.e. TWD; Fig. 3). In contrast, spruce responded positively to CR treatment, showing improved GRO and water status under wet and dry conditions (Fig. 4). The primary objective of CR is to reduce transpiration surface area, thereby decreasing the plant's water demand and delaying the onset of drought stress. The main advantage of CR mainly comes from improved soil moisture availability, which was demonstrated in our pot experiment

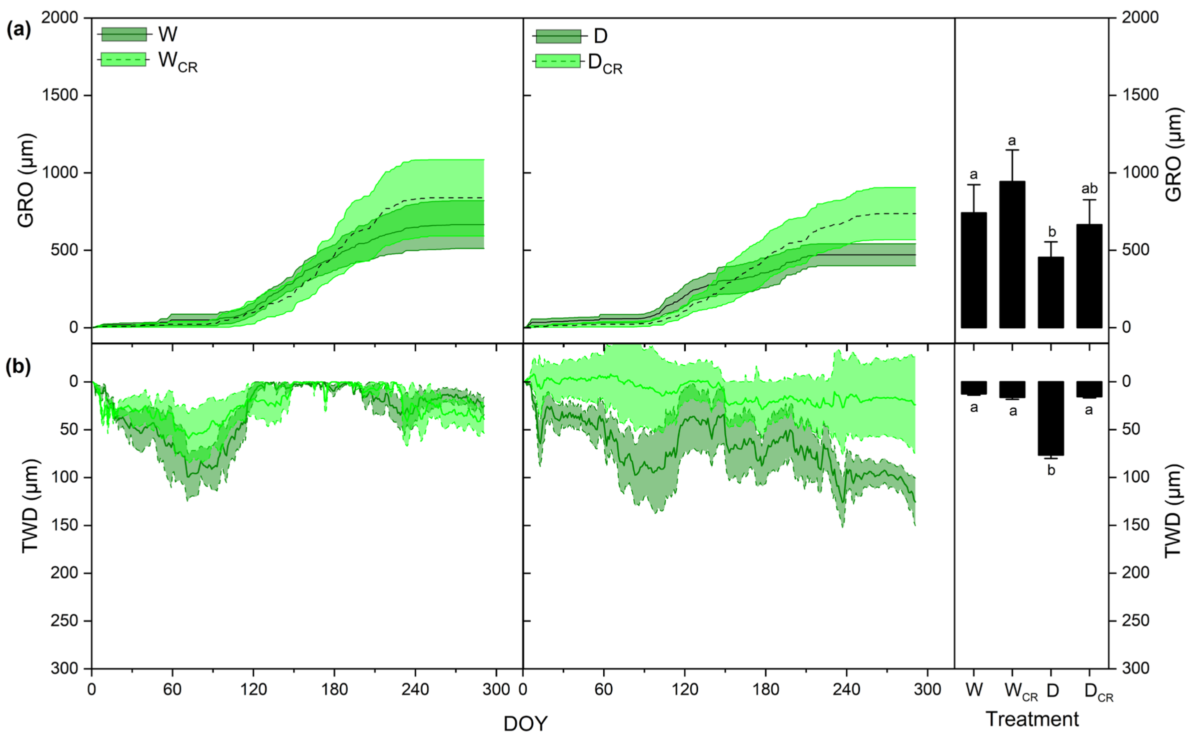

Fig. 4. Seasonal growth dynamics of Norway spruce saplings during the 2022 growing season. **(a)** The growth line (GRO) and **(b)** tree water deficit (TWD) are represented by a solid line for the well-watered (W) and water-stressed (D) treatments, and by a dashed line for the well-watered with crown reduction (W_{CR}) and water-stressed with crown reduction (D_{CR}) treatments. Shaded areas surrounding the GRO and TWD lines represent the standard error of means (SE). Column graphs show mean GRO and TWD, with whiskers indicating SE. Different letters indicate significant differences ($p < 0.05$) as estimated by the Tukey ANOVA post-hoc test. DOY – Day of the year.

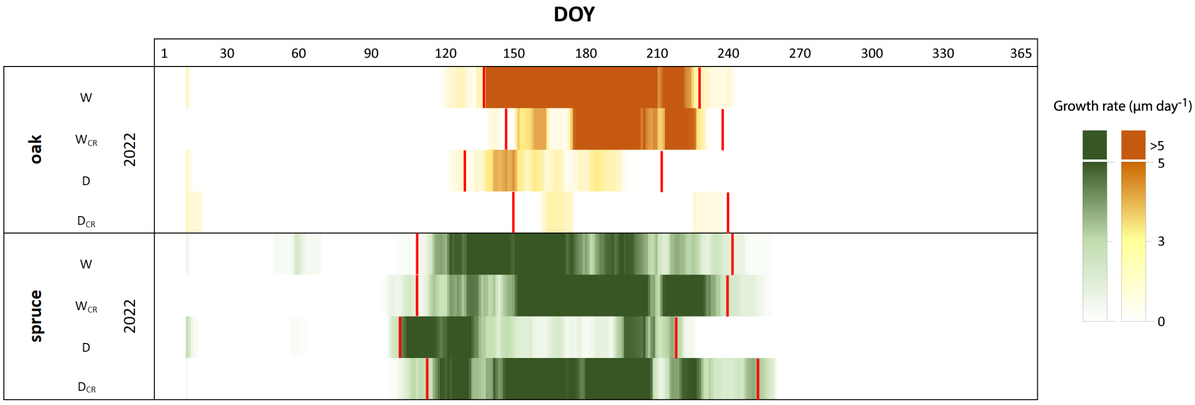

Fig. 5. Displays the annual growth phenology (number of growing days) for oak and spruce saplings within all different applied treatments during the growing season 2022. Treatments represented by (W) – well-watered, (W_{CR}) – well-watered and crown reduction, (D) – water-stressed, (D_{CR}) – water-stressed and crown reduction. The red vertical line indicates the beginning and the end of the growing season based on the growth rate (µm day^{-1}). DOY – Day of the year.

(Fig. 2). Lower LA can potentially decrease transpiration, consequently lowering water loss (Quentin et al. 2011). Although a high LA can be advantageous during periods of sufficient water availability, it may predispose trees to severe water stress when water availability declines due to the higher transpiration demand (Čater 2021).

The impact of reduced LA (mostly caused by defoliation) on plant growth varies depending on the intensity, tree development stage, species, and primarily on resource availability (Gieger & Thomas 2005; O'Hara et al. 2008; Pinkard et al. 2011; Matsushita et al. 2022) which is partly in agreement with our findings. Findings from Amateis & Burkhart (2011) suggest that during the initial stages of plants development, up to 50% of the live crown length can be pruned without significantly affecting diameter growth. Similarly, McGraw (1990), Eyles (2009), and Quentin (2012) found no significant impact of defoliation on tree growth across different water treatments. However, it remains uncertain whether defoliation might exacerbate or alleviate the effects of drought stress. Saplings can sustain higher leaf biomass and transpiration by improving their water absorption capacity through the allocation of resources to belowground structures (Padilla & Pugnaire 2007; Lloret et al. 2009). Unfortunately, our study focused only on aboveground (i.e. stem) parts, which limits our understanding of these belowground dynamics. Additionally, oak and spruce may have different priorities under stress, potentially leading to varied responses to CR and drought conditions (Gieger & Thomas 2005; Marchard et al. 2023). This is different for the contrasting conifer spruce and broadleaf oak tree species presented here. Spruce has functional needles ready to perform photosynthesis when environmental conditions allow, while oak must use stored non-structural carbohydrates (NSC) to create leaves at the beginning of the growing season (Michelot et al. 2012; Ramirez et al. 2024). This early-season allocation of resources to leaves to maximize carbon gain could compromise growth and survival under drought stress conditions (Wang et al. 2023), especially in young underdeveloped saplings.

Distinctions in their leaf morphological traits and NSC dynamics exert a more pronounced influence on growth phenology (Michelot et al. 2012; Van Der Maaten et al. 2018). Number of growing days and rates between oak and spruce reveals that spruce saplings commence growth much earlier than oak saplings (Fig. 5). The feedback to CR appears more pronounced in coniferous needles, resulting in sufficient leaf biomass for unhindered photosynthesis and, consequently, earlier initiation of stem growth compared to oak saplings. In our study, we observed that growth initiation in oak saplings occurs much later in the season (Fig. 5). This observation suggests that saplings in the early stages of development may not have accumulated sufficient reserves such as NSC to initiate growth before leaf formation, as mature trees do (Yan et al. 2022; Wang et al. 2023). Therefore, results from our experiment indicate that a reduction of 50% in crown length, decreases stem growth in oak saplings (Fig. 3). In contrast, the growth of spruce saplings is not reduced by the CR, moreover, the results indicate that spruce saplings can continue to grow without limitation, and even respond positively to CR (Fig. 4). One possible explanation is that the mobilization of NSC reserves can support tree survival and recovery during periods when photosynthesis is reduced, such as during drought or defoliation (Ramirez et al. 2024). Given that the highest NSC storage in conifers is found in their needles (Martínez-Vilalta et al. 2016), this may partly explain the better performance of spruce observed in our results (Fig. 3).

TWD is a proxy for plant water status that increases as transpiration exceeds root water uptake and stem water reserves progressively deplete (Salomón et al. 2022). In case of insufficient soil water supplies, water stress will cause TWD to increase and will likely result in growth suppression (Cabon et al. 2020). Trees may prevent TWD by stomatal closure, with a specific threshold for isohydric and anisohydric species (Ulrich & Grossiord 2023). Our studied tree species responded differently to limited water conditions, with spruce expressing lower TWD values than oak (Figs. 3 and 4). Typically, TWD is expected to be lower in conifers compared to broadleaf species, as conifers generally exhibit strong stomatal control and a conservative water-use strategy (Lin et al. 2015) which is in agreement with our results. As an anisohydric species, oak does not have strong control over its stomata, leading to higher water loss during drought conditions (Zang et al. 2012; Uhl et al. 2013). In contrast, spruce, an isohydric species, maintains tighter stomatal control to conserve water and prevent excessive water loss (Kurjak et al. 2012; Zavadilová et al. 2023b). This difference in stomatal regulation likely contributes to the observed variations in TWD between the two species, explaining why spruce performed better under limited water conditions (Figs. 3 and 4). Additionally, oak with CR treatment showed even more impoverished water status, while spruce with CR treatment exhibited a more favorable stem water status (lower TWD), further highlighting the contrasting responses of these species to CR and drought stress.

5. Conclusions

Our study investigated how CR and different water availability affect the growth and drought resistance of spruce and oak saplings, conducted in pot experiments. The results supported our initial hypothesis that CR would increase soil water availability, likely by reducing the sapling water use in both species. Likewise, the research outcomes indicated that saplings subjected to CR showed improved stem water status, with a corresponding decrease in TWD for spruce, but not for oak saplings, partially confirming the second hypothesis. We found that CR significantly enhances drought stress tolerance in spruce, increasing the number of growth days under both wet and dry conditions. Conversely, this treatment did not benefit the growth of oak saplings and adversely affected their growth within drought treatment again partly confirming our third hypothesis.

The results highlight the importance of selectively applying CR, suggesting its use should be limited to periods of anticipated drought to avoid potential negative impacts on growth. While the treatment shows promise, especially for spruce, field experiments are necessary to confirm these results and to test the efficacy of CR on different tree species. This research highlights the need for simple and cost-effective strategies to enhance sapling survival rates in times of ongoing climate change and large-scale disturbances that continue to challenge forest ecosystems (Grossnickle 2018). Understanding how saplings respond to environmental stressors is essential for developing effective management strategies and selecting suitable species for reforestation projects across Europe. These insights are essential for forest managers in mitigating abiotic stresses, and adapting forest ecosystem to changing climatic conditions.

Acknowledgements

This research was funded by IGRAČEK MENDELU project CZ.02.2.69/0.0/0.0/19_073/0016670, with registration number SGC-2021-013. J.A. benefited from the Internal Grant Agency of Mendel University in Brno under grant number 040/2021. The authors are sincerely grateful to Jan Světlík, Lucia Petrovičová, Emanuel Opoku, Hana Findurová, Martin Benz, and Lukáš Vlahovič for their invaluable help in establishing the experiment and watering campaigns. We thank Lorna MacPherson for proofreading the manuscript.

References

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M. et al. 2010: A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management, 259:660–684.

Amateis, R. L., Burkhart, H. E., 2011: Growth of young loblolly pine trees following pruning. Forest Ecology and Management, 262:2338–2343.

Andivia, E., Villar-Salvador, P., Oliet, J. A., Puértolas, J., Dumroese, R. K., Ivetić, V. et al., 2021: Climate and species stress resistance modulate the higher survival of large seedlings in forest restorations worldwide. Ecological Applications, 31:1–11.

Bakker, J. D., Colasurdo, L. B., Evans, J. R., 2012: Enhancing Garry oak seedling performance in a semiarid environment. Northwest Science, 86:300–309.

Biehl, J., Sandén, H., Rewald, B., 2023: Contrasting effects of two hydrogels on biomass allocation, needle loss, and root growth of *Picea abies* seedlings under drought. Forest Ecology and Management:538.

Bonan, G. B., 2008: Forests and Climate Change: Forcings, Feedbacks and the Climate Benefits of Forests. Science, 320:1444–1449.

Cabon, A., Fernández-de-Uña, L., Gea-Izquierdo, G., Meinzer, F. C., Woodruff, D. R., Martínez-Vilalta, J. et al., 2020: Water potential control of turgor-driven tracheid enlargement in Scots pine at its xeric distribution edge. New Phytologist, 225:209–221.

Castro, J., Zamora, R., Hódar, J. A., Gómez, J. M., 2005: Alleviation of summer drought boosts establishment success of *Pinus sylvestris* in a Mediterranean mountain: An experimental approach. Plant Ecology, 181:191–202.

Close, D. C., Beadle, C. L., Brown, P. H., 2005: The physiological basis of containerised tree seedling 'transplant shock': A review. Australian Forestry, 68:112–120.

Čater, M., 2021: Microsites influence the light response of young douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco). Forests:12:687.

Devine, W. D., Harrington, C. A., Leonard, L. P., 2007: Post-planting treatments increase growth of Oregon white oak (*Quercus garryana* Dougl. ex Hook.) seedlings. Restoration Ecology, 15:212–222.

Eyles, A., Pinkard, E. A., Mohammed. C., 2009: Shifts in biomass and resource allocation patterns following defoliation in *Eucalyptus globulus* growing with varying water and nutrient supplies. Tree Physiology, 29:753–764.

Fatichi, S., Leuzinger, S., Körner, C., 2014: Moving beyond photosynthesis: From carbon source to sink-driven vegetation modeling. New Phytologist, 201:1086–1095.

Fernández, M. E., Gyenge, J. E., Varela, S., de Urquiza, M., 2014: Effects of the time of drought occurrence within the growing season on growth and survival of Pinus ponderosa seedlings. Trees – Structure and Function, 28:745–756.

Gieger, T., Thomas, F. M., 2005: Differential response of two Central-European oak species to single and combined stress factors. Trees – Structure and Function, 19:607–618.

Gonçalves, J. L. de M., Alvares, C. A., Higa, A. R., Silva, L. D., Alfenas, A. C., Stahl, J. et al., 2013: Integrating genetic and silvicultural strategies to minimize abiotic and biotic constraints in Brazilian eucalypt plantations. Forest Ecology and Management, 301:6–27.

Gough, C. M., Hardiman, B. S., Nave, L. E., Bohrer, G., Maurer, K. D., Vogel, C. S. et al., 2013: Sustained carbon uptake and storage following moderate disturbance in a Great Lakes forest. Ecological Applications, 23:1202–1215.

Grossnickle, S. C., 2005: Importance of root growth in overcoming planting stress. New Forests, 30:273–294.

Grossnickle, S. C., 2012: Why seedlings survive: influence of plant attributes. New Forests, 3:711–738.

Grossnickle, S. C., 2018: Seedling establishment on a forest restoration site – An ecophysiological perspective. Reforesta, 6:110–139.

Hlásny, T., König, L., Krokene, P., Lindner, M., Montagné-huck, C., Müller, J. et al., 2021: Bark Beetle Outbreaks in Europe : State of Knowledge and Ways Forward for Management. Current Forestry Reports, 7:138–165.

Hoogesteger, J., Karlsson, P. S., 1992: Effects of Defoliation on Radial Stem Growth and Photosynthesis in the Mountain Birch (*Betula pubescens* ssp. *tortuosa*). Functional Ecology, 6:317–323.

Hueso-González, P., Francisco Martínez-Murillo, J., Damian Ruiz-Sinoga, J., 2016: Effects of topsoil treatments on afforestation in a dry Mediterranean climate (southern Spain). Solid Earth, 7:1479–1489.

Krejza, J., Cienciala, E., Světlík, J., Bellan, M., Noyer, E., Horáček, P. et al., 2021: Evidence of climate-induced stress of Norway spruce along elevation gradient preceding the current dieback in Central Europe. Trees – Structure and Function, 35:103–119.

Kurjak, D., Střelcová, K., Ditmarová, Ľ., Priwitzer, T., Kmeť, J., Homolák, M. et al., 2012: Physiological response of irrigated and non-irrigated Norway spruce trees as a consequence of drought in field conditions. European Journal of Forest Research, 131:1737–1746.

Landis, T. D., Dumroese, R. K., Haase, D. L., 2010: Seedling Processing, Storage, and Outplanting. The Container Tree Nursery Manual, 7:208.

Lázaro-González, A., Andivia, E., Hampe, A., Hasegawa, S., Marzano, R., Santos, A. M. C. et al., 2023: Revegetation through seeding or planting: A worldwide systematic map. Journal of Environmental Management, 337:117713.

Lin, Y. S., Medlyn, B. E., Duursma, R. A., Prentice, I. C., Wang, H., Baig, S. et al., 2015: Optimal stomatal behaviour around the world. Nature Climate Change, 5:459–464.

Lloret, F., Siscart, D., Dalmases, C., 2004: Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). Global Change Biology, 10:2092–2099.

Lloret, F., Peñuelas, J., Prieto, P., Llorens, L., Estiarte, M., 2009: Plant community changes induced by experimental climate change: Seedling and adult species composition. Perspectives in Plant Ecology, Evolution and Systematics, 11:53–63.

Löf, M., Thomsen, A., Madsen, P., 2004: Sowing and transplanting of broadleaves (*Fagus sylvatica* L., *Quercus robur* L., *Prunus avium* L. and *Crataegus monogyna* Jacq.) for afforestation of farmland. Forest Ecology and Management, 188:113–123.

Van Der Maaten, E., Pape, J., Van Der Maaten-Theunissen, M., Scharnweber, T., Smiljanić, M., Cruz-García, R. et al., 2018: Distinct growth phenology but similar daily stem dynamics in three co-occurring broadleaved tree species. Tree Physiology, 38:1820–1828.

Marchand, W., Buechling, A., Rydval, M., Čada, V., Stegehuis, A. I., Fruleux, A. et al., 2023: Accelerated growth rates of Norway spruce and European beech saplings from Europe's temperate primary forests are related to warmer conditions. Agricultural and Forest Meteorology, 329:109280.

Martínez-Vilalta, J., Sala, A., Asensio, D., Galiano, L., Hoch, G., Palacio, S. et al., 2016: Dynamics of non-structural carbohydrates in terrestrial plants: A global synthesis. Ecological Monographs, 86:495–516.

Mataruga, M., Cvjetković, B., De Cuyper, B., Aneva, I., Zhelev, P., Cudlín, P. et al., 2023: Monitoring and control of forest seedling quality in Europe. Forest Ecology and Management, 546:121308.

Matsushita, M., Nishikawa, H., Tamura, A., 2022: Effects of Girdling Intensity, Pruning Season and Thinning on Tree Growth, Crown Vigor and Wound Recovery in Japanese Larch. Forests, 13:449.

McGraw, J. B., Gottschalk, K. W., Vavrek, M. C., Chester, A. L., 1990: Interactive effects of resource availabilities and defoliation on photosynthesis, growth, and mortality of red oak seedlings. Tree Physiology, 7: 247–254.

Michelot, A., Simard, S., Rathgeber, C., Dufrêne, E., Damesin, C., 2012: Comparing the intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics. Tree Physiology, 32:1033–1045.

Niinemets, Ü., 2010: Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. Forest Ecology and Management, 260:1623–1639.

O'Hara, K. L., York, R. A., Heald, R. C., 2008: Effect of pruning severity and timing of treatment on epicormic sprout development in giant sequoia. Forestry, 81:103–110.

Padilla, F. M., Pugnaire, F. I., 2007: Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. Functional Ecology, 21:489–495.

Palma, A. C., Laurance, S. G. W., 2015: A review of the use of direct seeding and seedling plantings in restoration : what do we know and where should we go? Applied Vegetation Science, 18:561–568.

Patacca, M., Lindner, M., Esteban, M., Cordonnier, T., Fidej, G., Gardiner, B. et al., 2023: Significant increase in natural disturbance impacts on European forests since 1950. Global Change Biology, 29:1359–1376.

Pinkard, E. A., Battaglia, M., Roxburgh, S., O'Grady, A. P., 2011: Estimating forest net primary production under changing climate: Adding pests into the equation. Tree Physiology, 31:686–699.

Preisler, Y., Tatarinov, F., Grünzweig, J. M., Yakir, D., 2021: Seeking the "point of no return" in the sequence of events leading to mortality of mature trees. Plant Cell and Environment, 44:1315–1328.

Quentin, A. G., Beadle, C. L., O'Grady, A. P., Pinkard, E. A., 2011: Effects of partial defoliation on closed canopy *Eucalyptus globulus* Labilladière: Growth, biomass allocation and carbohydrates. Forest Ecology and Management, 261:695–702.

Quentin, A. G., O'Grady, A. P., Beadle, C. L., Mohammed, C., Pinkard, E. A., 2012: Interactive effects of water supply and defoliation on photosynthesis, plant water status and growth of *Eucalyptus globulus* Labill. Tree Physiology, 32:958–967.

Ramirez, J. A., Craven, D., Herrera, D., Posada, J. M., Reu, B., Sierra, C. A. et al., 2024:Non-structural carbohydrate concentrations in tree organs vary across biomes and leaf habits, but are independent of the fast-slow plant economic spectrum. Frontiers in Plant Science, 15:1–13.

Riikonen, J., Luoranen, J., 2018: Seedling production and the field performance of seedlings. Forests, 9:10–13.

Royo, A., Gil, L., Pardos, J. A., 2001: Effect of water stress conditioning on morphology, physiology and field performance of *Pinus halepensis* Mill. seedlings. New Forests, 21:127–140.

Salomón, R. L., Peters, R. L., Zweifel, R., Sass-Klaassen, U. G. W., Stegehuis, A. I., Smiljanic, M. et al., 2022: The 2018 European heatwave led to stem dehydration but not to consistent growth reductions in forests. Nature Communications, 13:1–11.

Savé, R., Castell, C., Terradas, J., 1999: Gas Exchange and Water Relations. In: Rodà, F., Retana, J., Gracia, C. A., Bellot, J. (eds.): Ecology of Mediterranean Evergreen Oak Forests. Berlin, Heidelberg, Springer, p. 135–147.

Szatniewska, J., Zavadilova, I., Nezval, O., Krejza, J., Petrik, P., Čater, M. et al., 2022:. Species-specific growth and transpiration response to changing environmental conditions in floodplain forest. Forest Ecology and Management, 516:120248.

Taïbi, K., del Campo, A. D., Aguado, A., Mulet, J. M., 2016: Early establishment response of different *Pinus nigra* ssp. *salzmanii* seed sources on contrasting environments: Implications for future reforestation programs and assisted population migration. Journal of Environmental Management, 171:184–194.

Trnka, M., Brázdil, R., Balek, J., Semerádová, D., Hlavinka, P., Možný, M. et al., 2015: Drivers of soil drying in the Czech Republic between 1961 and 2012. International Journal of Climatology, 35:2664–2675.

Turcotte, A., Morin, H., Krause, C., Deslauriers, A., Thibeault-Martel, M., 2009: The timing of spring rehydration and its relation with the onset of wood formation in black spruce. Agricultural and Forest Meteorology, 149:1403–1409.

Uhl, E., Pretzsch, H., Schu, G., 2013: Resistance of European tree species to drought stress in mixed versus pure forests : evidence of stress release by inter-specific facilitation. Plant Biology,15:483–495.

Ulrich, D. E. M., Grossiord, C., 2023: Faster drought recovery in anisohydric beech compared with isohydric spruce. Tree Physiology, 43:517–521.

Volin, J. C., Kruger, E. L., Lindroth, R. L., 2002: Responses of deciduous broadleaf trees to defoliation in a CO_2 enriched atmosphere. Tree Physiology, 22:435–448.

Wang, K., Jin, G., Liu, Z., 2023: Dynamic variation of non-structural carbohydrates in branches and leaves of temperate broad-leaved tree species over a complete life history. Frontiers in Forests and Global Change, 6:1130604.

Wang, Y., Han, X., Ai, W., Zhan, H., Ma, S., Lu, X., 2023: Non-Structural Carbohydrates and Growth Adaptation Strategies of *Quercus mongolica* Fisch. ex Ledeb. Seedlings under Drought Stress. Forests, 14:404.

Yan, L., Zhang, Z., Jin, G., Liu, Z., 2022: Variations of leaf nonstructural carbohydrates in an evergreen coniferous species : Needle age and phenology dominate over life history. Ecological Indicators, 136:108685.

Zang, C., Pretzsch, H., Rothe, A., 2012: Size-dependent responses to summer drought in Scots pine , Norway spruce and common oak. Trees, 26:557–569.

Zavadilová, I., Szatniewska, J., Stojanović, M., Fleischer, P., Vágner, L., Pavelka, M. et al., 2023a: The effect of thinning intensity on sap flow and growth of Norway spruce. Journal of Forest Science, 69:205–216.

Zavadilová, I., Szatniewska, J., Petrík, P., Mauer, O., Pokorný, R., Stojanović, M., 2023b: Sap flow and growth response of Norway spruce under long-term partial rainfall exclusion at low altitude. Frontiers in Plant Science, 14:1089706

Zweifel, R., Haeni, M., Buchmann, N., Eugster, W., 2016: Are trees able to grow in periods of stem shrinkage? New Phytologist, 211:839–849.