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Faculty of Forestry and Wood Sciences

Drivers of tree growth, productivity and regeneration in traditional coppices

Doctoral Thesis

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Drivers of tree growth, productivity and regeneration in traditional coppices

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Objectives of thesis

Short-rotation coppicing was the main management system in forests across Europe for hundreds of years but was largely abandoned during the 19th and 20th centuries. It has recently regained popularity due to its rapid and sustainable woody biomass production and its positive effects on biodiversity. Traditional coppices have also been re-established as coppice or, more commonly, as coppice with standards in several, typically warmer areas of the Czech Republic. However, there is still limited knowledge about the main drivers and mechanisms of tree growth, productivity, and regeneration, both in coppices and coppices with standards. This knowledge gap hinders the optimisation of their management to maximise the benefits for which they have been established, mainly to support biodiversity and rapid biomass production. This thesis aims to enhance our knowledge of how forest structure, composition and climate influence woody biomass production, tree species diversity, and annual growth of the most common woody species in newly restored coppices and coppice-with-standards systems in the Czech Republic. Using data from long-term coppices restoration experiments, where high forest has been converted into coppice and coppice with standards, the study will analyse the impacts of different densities of standard trees and sprouting stumps on the occurrences and abundance of sprout and seed regeneration, sprout growth and woody biomass production for the main species of Central-European coppices. It will also aim to assess the contributions of seeding and sprout regeneration strategies to forest productivity and explore growth responses of different tree forms – sprouts, seedlings and high trees – to climate variation and drought. The findings will provide valuable insights into optimising forest management practices to promote biodiversity and productivity in coppice forests.

The aims of the thesis are:

1. To quantify the effects of the density of standards and sprouting stumps on sprout growth as well as woody biomass production of the most common tree species at the levels of individual trees and stands in newly restored coppices and coppices with standards.

2. To assess the contributions of seed regeneration and sprouts to above-ground biomass productivity and tree species diversity and examine the interactions between these regeneration strategies under varying densities of residual trees.

3. To investigate the influence of climatic factors, particularly drought, on the radial growth of vegetative and generative regeneration, as well as standard trees, and determine species-specific responses to predict future changes in coppice forest structure and composition.

Methodology

The research will be done mainly in two experimental plots, TARMAG Hády and Soběšice, located in the Training Forest Enterprise Křtiny of Mendel University in Brno, Czech Republic. In each of the two fenced 4-hectare plots (200x200 m, divided into 16 subplots), a high, oak-dominated forest was transformed into coppice and coppice with standards in 2008-2010. The transformation consisted of cutting all or most of the trees and leaving the stumps resprout. Varying numbers (per subplot) of healthy main-canopy trees were left uncut as standards. All trees in the plots were mapped and measured before the cutting, and then stumps were regularly revisited, and sprouts were measured in the following years.

In this thesis, new remeasurements and mapping (using Field-Map technology) of sprouts and standards will be done, in addition to analysing the existing data. Also, the regeneration from seed (not measured so far) will be mapped and measured. The resulting dataset will be used for the quantification of the contribution of sprout and seed regeneration to productivity and diversity in the early development stage of coppice forests. It will also be used to analyse the impact of standards on these two regeneration types. In addition, to asses long-term growth, the increment cores will be taken from standard trees, sprouting stumps and saplings of seed origin to evaluate the growth and growth reactions of these different regeneration types to climate variation and particularly drought. To assess and compare the abundances and productivity of the different regeneration types and species, the woody biomass will be calculated for each tree. To evaluate the effects on productivity and tree diversity on a stand level, total biomass (for all regenerating trees and separately for species and regeneration types) and diversity indices will be calculated for each subplot. Statistical analyses will be done in R using a proper set of models (mainly linear mixed effect models), in which growth, biomass and diversity will be modelled as a function of relevant explanatory variables such as standard and sprout density, regeneration type and species. The changes in species composition due to coppicing and the effects on it will be analysed using multivariate ordination methods.

The proposed extent of the thesis

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Keywords

natural regeneration, traditional coppice, coppice with standards, forest structure, above-ground biomass

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Recommended information sources

Bond WJ, Midgley JJ (2003) The Evolutionary Ecology of Sprouting in Woody Plants Author (s): William J . Bond and Jeremy J . Midgley Source : International Journal of Plant Sciences , Vol . 164 , No . S3 , Evolution of Functional Traits in Plants (May 2003), pp . S103-S114 Publ. Int J Plant Sci 164

Del Tredici P (2001) Sprouting in temperate trees: A morphological and ecological review. Botanical Review 67:121–140

Frelich LE (2002) Forest Dynamics and Disturbance Regimes: Studies from TemperateEvergreen-Deciduous Forests. Cambridge University Press.

Matula R, Damborská L, Nečasová M, et al (2015) Measuring biomass and carbon stock in resprouting woody plants. PLoS One 10:12–15. https://doi.org/10.1371/journal.pone.0118388

Pietras J, Stojanović M, Knott R, Pokorný R (2016) Oak sprouts grow better than seedlings under drought stress. http://iforest.sisef.org/ 9:529. https://doi.org/10.3832/IFOR1823-009

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I hereby confirm that this PhD. thesis “Drivers of tree growth, productivity and regeneration in traditional coppices” was elaborated independently with the usage of quoted literature and based on consultations and the recommendations of my supervisor.

I agree with publishing this PhD. thesis according to Czech law n. 111/1998 Sb. about the universities in its current valid wording. This agreement is independent from the results of defense.

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Abstract

Traditional coppices and coppice-with-standards were widely used throughout Europe and Asia for centuries but were largely abandoned in the second half of the 19th century, particularly in central and northwestern Europe. In the last decades, there has been renewed interest in traditional coppicing, mainly for nature conservation and rapid woody biomass production. However, there is little empirical knowledge regarding the main drivers affecting tree growth, biomass production, and natural regeneration in coppices, especially in the context of changing environmental conditions. This thesis seeks to fill this knowledge gap by investigating the interactions between tree growth, forest structure and climatic factors in newly restored coppices and coppice-with-standards in the Czech Republic. Specifically, we aimed to (1) to quantify the effects of stand density, standards, and tree species composition on sprout growth and biomass production; (2) to assess the contributions of seed and sprout regeneration to above-ground biomass (AGB) productivity and species diversity in early-stage forest development; and (3) to evaluate the growth responses of vegetative sprouts, seed regeneration, and standard trees to climatic factors, particularly drought. The research was conducted in two experimental forest plots, where a high, oak-dominated forest was transformed into coppice and coppice-with-standards. Trees were cut at varying intensities, leaving different densities of standing residual trees (standards) while allowing the stumps to resprout. Over time, we monitored the growth of all sprouting stumps, standards, and measured seed regeneration.

Main Findings of the thesis:

(1) Total sprout biomass decreased significantly with increasing density of standards for *Quercus petraea* and *Carpinus betulus*, while *Acer campestre* and *Tilia cordata* were not affected. The stand-level biomass productivity increased linearly with the density of sprouting stumps. A significant shift in species composition was observed due to

differential resprouting success and sprout growth after tree cutting, resulting in a large decline of *Quercus* in favor of *Carpinus* and *Tilia,* which, as very good resprouters, benefited substantially from coppice establishment (Section 5.1).

(2) Sprout regeneration contributed the majority of above-ground biomass and species diversity in early-stage forest development. Seed regeneration was significantly suppressed by residual trees, but despite low abundance, it introduced new species, enriching species pool and enhancing overall species diversity. This highlights the crucial but differential role of sprout and seed regeneration in post-disturbance forest dynamics (Section 5.2).

(3) *Quercus*, the predominant species at our study sites, consistently exhibits faster growth and maintains higher productivity in sprouts compared to seed regeneration, regardless of climatic conditions. While responses to relative air humidity and temperature showed no significant differences among regeneration types for *Quercus*, *Tilia*, or *Carpinus*, variations in precipitation response were observed in *Quercus* at different sites. *Tilia* and *Carpinus* exhibited no significant response to rising temperatures, unlike *Quercus*, which experienced a notable decrease in tree ring width (Section 5.3).

The findings of this thesis underscore the complex interactions between climate, forest structure, and tree growth in traditional coppice systems. The results suggest coppice restoration may enhance woody biomass production which is likely to be sustained under climate change as well as support woody plant diversity. Therefore, coppicing is a good forest management option particularly in warmer areas of Central Europe, which are most affected by increasing water limitation.

Key words: forest regeneration, traditional coppice, coppice with standards, forest structure, tree growth, above-ground biomass

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List of abbreviations

AGB – above-ground biomass

BA – basal area

CWS – coppice with standards

DBH – diameter at breasts height (1.3 m)

LAI – leaf area index

$\mathrm{SB}_{\mathrm{stand}}$ – total dry woody sprout biomass on stand level

$\mathrm{SB}_{\mathrm{stump}}$ – dry woody sprout biomass on stump level

SE – standard error

SR – species richness

TRW – tree-ring width

VPD – vapor pressure deficit

1. Introduction

Traditional coppices are short-rotation silvicultural system, which has been used throughout Europe and Asia for centuries mainly as a source of firewood (Buckley, 1992; Fujimori, 2001; Szabó, 2010; Müllerová, Szabó and Hédl, 2014). Coppicing has also often been combined with high forests in coppice-with-standards stands (CWS). CWSs consist of vegetative sprouts in the understory and overstory standards (residual trees) that grow from seed and usually have one high-quality straight trunk (Fujimori, 2001). Coppice management creates a dynamic mosaic of differently-aged forest patches, supporting high biodiversity by providing habitats for species with contrasting strategies, such as light and shade-tolerant plants, various invertebrates and fungi (Bartha *et al*., 2008; Hédl, Kopecký and Komárek, 2010; Fartmann, Müller and Poniatowski, 2013; Kopecký, Hédl and Szabó, 2013).

However, with the decreasing demand for coppice products, most coppices and CWSs in central and western Europe were either abandoned or transformed into high forests during the second half of the 19th century (Matthews, 1989; Mcgrath *et al.*, 2015). Due to a lack of regular interventions, the canopy of unmanaged coppices became significantly closed (Van Calster *et al.*, 2007; Müllerová, Hédl and Szabó, 2015), and abandoned coppices have faced various threats of degradation, such as changes in forest structures and decline in species diversity (Itô, Hino and Sakuma, 2012; Kopecký, Hédl and Szabó, 2013; Vild *et al*., 2013; Müllerová, Hédl and Szabó, 2015).

In the last decades, there has been a renewed interest in traditional coppicing, and coppices have been restored in many European countries due to biodiversity conservation (Kopecký, Hédl and Szabó, 2013; Vild *et al*., 2013; Müllerová, Hédl and Szabó, 2015), an improvement of ecological services (Imamura, Saito and Nakashizuka, 2017) and for rapid woody biomass production as a renewable source of energy (Jansen and Kuiper, 2004; Nestorovski *et al.*, 2009;

Fang *et al.*, 2011). This interest is further fueled by the increasing recognition that, in the context of climate change, forest management practices must adapt to more frequent and severe droughts (IPCC 2007). Rising temperatures, shifting precipitation patterns, and land-use changes have become major limiting factors to growth and productivity in temperate forests (Boisvenue and Running, 2006; Babst *et al.*, 2013). These factors have also been linked to a general lack of natural regeneration on a global scale (Annighöfer *et al.*, 2015). Many tree species are experiencing elevated mortality of seedlings (Engelbrecht, Kursar and Tyree, 2005; Engelbrecht *et al.*, 2006; Browne *et al.*, 2021) and forest managers, particularly in drought-prone regions, will need to adjust their practices and explore alternative ways of tree regeneration. One of the management options which seems to have a better adaptive strategy to drought is coppicing (Pietras *et al.*, 2016; Stojanović, Szatniewska, *et al.*, 2017). Especially at the sites under water-limiting conditions vegetative sprouts with already developed root system are more likely to survive than generative seedlings (Clark and Hallgren, 2003; Atwood, Fox and Loftis, 2011; Pietras *et al.*, 2016).

Despite the increasing popularity of traditional coppices and CWS, there is still very little empirical information on the drivers of biomass productivity, tree growth and natural regeneration patterns within these systems. Understanding the main drivers of tree growth, productivity and natural regeneration is essential for the successful restoration and sustainable management of traditional coppices.

This thesis aims to enhance our understanding of these drivers by examining the complex interactions between tree growth, climate variability, and forest structure in traditional coppices. By focusing on the specific responses of different tree species and regeneration types to both forest structure and climatic factors, this study provides valuable insights that can contribute to the development of more adaptive management strategies, aiding in the maintenance of productivity, biodiversity, and resilience within these forest ecosystems.

2. Literature review

2.1. Traditional coppice and coppice with standards

Traditional coppices are short-rotation silvicultural system, which has been used throughout Europe and Asia for centuries mainly as a source of firewood (Buckley, 1992; Fujimori, 2001; Szabó, 2010; Müllerová, Szabó and Hédl, 2014). This management involves cutting trees near ground level and allowing them to regrow from the stumps or root systems, a process that exploits the natural sprouting ability of many tree species (Bond and Midgley, 2001; Del Tredici, 2001). The rotation period of traditional coppices typically ranges from 7 to 40 years, depending on the species and the desired wood products such as firewood, posts, tool handles, and fencing materials (Buckley, 1992; Müllerová *et al.*, 2016).

Coppicing was particularly common in pre-industrial Europe, especially in densely populated European lowlands where the demand for firewood and construction timber was high (Müllerová, Szabó and Hédl, 2014); Rackham, 2006). The pressure on the remaining forests necessitated intensive management, making coppicing a prevalent practice for centuries.

Regular cutting of sprouts encourages rapid regrowth and biomass production (Peterken, 1996; Rackham, 2003). The cyclic nature of coppicing creates a dynamic mosaic of forest patches at different stages of growth, which support high levels of biodiversity by providing habitats for species with contrasting ecological strategies. The early stages of the coppicing cycle foster a functionally diverse mix of plants, including light-demanding, intermediate, and shade-tolerant species. Higher light levels following coppice cuts particularly favor heliophilous plants, both short-lived and perennial, which can thrive either by dispersing efficiently or by germinating from persistent seedbanks (Bartha *et al*., 2008; Hédl, Kopecký and Komárek, 2010; Kopecký, Hédl and Szabó, 2013). As the coppice stools regrow, light levels decline rapidly, sometimes dropping to only 1% of ambient light within five years (Mason and Macdonald, 2002; Broome *et al.*, 2011). However, many shade-tolerant species are resilient enough to survive these alternating periods of intense light and darkness. This diversity in microhabitat types created by this cycle benefits not only a variety of plant species but also various invertebrates (Freese *et al*., 2006; Spitzer *et al*., 2008; Broome *et al*., 2011; Vodka and Cizek, 2013), fungi, and other forest organisms (Diamandis and Perlerou, 2001; Fartmann, Müller and Poniatowski, 2013).

Coppice forests also provided additional resources, including leaf fodder, pasture (typically available 4–7 years after a coppice harvest to safeguard young shoots), and pannage, which involved feeding domestic pigs with acorns and beechmast during the autumn and winter months (Rackham, 2003; (Szabó and Hédl, 2013).

Coppicing has also been often combined with high-forests in coppice-with-standards stands (CWS). CWSs consist of vegetative sprouts in the understory and overstory standards (residual trees) that grow from seed and usually have one high-quality straight trunk (Fujimori, 2001), which is mostly used as building timber (Matthews, 1989; Buckley, 1992). This method combines the benefits of rapid coppice regrowth with the ecological and resource diversity provided by mature standard trees (Buckley, 1992; Peterken, 1996).

Coppicing was traditionally practiced on species that resprout easily, such as oak, lime, hazel, ash, hornbeam, maple, alder, willow, sweet chestnut, and beech (Peterken, 1996; Rackham, 2003; Matula *et al*., 2012). The underwood, consisting of coppice stools and shoots, was typically not directly influenced by humans, although the species composition could be enhanced by removing unwanted species or encouraging valuable ones through natural regeneration, layering, or planting (Peterken, 1993). In contrast, standard tree species were carefully selected, with oak often being the preferred choice due to its value as timber (Buckley, 1992).

The extent and importance of coppicing fluctuated over time, but it remained a vital practice until the second half of the 19th century. However, with widespread availability of fossil fuels and decreasing demand for coppice products, most coppices and CWSs in central and western

Europe were either abandoned or transformed into high forests during the second half of the 19th century (Matthews, 1989; Mcgrath *et al.*, 2015; Müllerová, Hédl and Szabó, 2015). The transition to high-forest management and modern forestry practices further contributed to the reduction in coppicing (Müllerová, Hédl and Szabó, 2015).

Due to a lack of regular interventions, the canopy of unmanaged coppices became significantly closed (Van Calster *et al.*, 2007; Müllerová, Hédl and Szabó, 2015), and abandoned coppices have faced various threats of degradation, such as changes in forest structures and decline in species diversity (Itô, Hino and Sakuma, 2012; Kopecký, Hédl and Szabó, 2013; Vild *et al.*, 2013; Müllerová, Hédl and Szabó, 2015). The homogeneous conditions in closed-canopy forests reduced opportunities for light-demanding and disturbance-adapted species, leading to a decrease in beta-diversity and the potential loss of some rare, red-listed species (Müllerová, Hédl and Szabó, 2015).

Despite its decline, coppicing remains relevant in certain regions, particularly in the Mediterranean and Balkan areas, where it continues to be used in significant portions of forest areas (Jansen and Kuiper, 2004). Countries such as Albania, Hungary, Portugal, Greece, Italy, Turkey, and France still retain coppice woodlands, with France having the largest reported area of over 6 million hectares (Buckley, 2020). The revival of interest in firewood, driven by rising fuel prices, has also sparked renewed appreciation for coppicing in both urban and rural areas (Kirby, Buckley and Mills, 2017).

2.1.1. Coppice restoration

In the last decades, there has been a renewed interest in traditional coppicing, and coppices have been restored in many European countries mostly due to biodiversity conservation (Kopecký, Hédl and Szabó, 2013; Vild *et al.*, 2013; Müllerová, Hédl and Szabó, 2015), an improvement of ecological services (Imamura, Saito and Nakashizuka, 2017) and for rapid woody biomass production as a renewable source of energy (Jansen and Kuiper, 2004; Nestorovski *et al.*, 2009; Fang *et al.*, 2011). Moreover, with ongoing climate change causing more frequent occurrences and higher severity of droughts (IPCC 2007), it will be necessary to adjust forest management practices, and coppicing represent a good silvicultural alternative to high forests in this respect (Pietras *et al.*, 2016; Stojanović, Szatniewska, *et al.*, 2017). Especially at the sites under water limiting conditions vegetative sprouts can survive more easily than generative seedlings. The reason for the better ability of coppices to cope with droughts is that, unlike seedlings or saplings, sprouts have large root systems of parent trees and thus better access to soil water (Clark and Hallgren, 2003; Atwood, Fox and Loftis, 2011; Xue *et al.*, 2014; Pietras *et al.*, 2016; Stojanović, Szatniewska, *et al.*, 2017).

As research has shown, the abandonment of coppicing practices has led to significant declines in species diversity, particularly among plants and insects dependent on the unique habitat structures created by regular coppicing cycles (Kopecký, Hédl and Szabó, 2013; Vild *et al.*, 2013; Müllerová, Hédl and Szabó, 2015). Coppiced woodlands provide a heterogeneous environment with varied light levels and a mosaic of different-aged stands, which are essential for maintaining diverse plant and animal communities (Freese *et al.*, 2006; Spitzer *et al.*, 2008; Müllerová, Hédl and Szabó, 2015). Re-coppicing experiments, such as those conducted in the Czech Republic, have demonstrated the potential of coppicing to restore lost biodiversity, particularly when heavy thinning treatments are applied, leading to significant increases in shrub, herb layers, and woody regeneration after 10 years (Vild *et al.*, 2013). However, the success of coppice restoration is not guaranteed in all cases, as reintroducing coppicing to long-neglected sites can sometimes enhance the spread of ruderal species and even lead to the invasion of alien species (Radtke *et al.*, 2013; Vild *et al.*, 2013). Additionally, while some of the diverse flora may be recovered with the reinstatement of traditional management, there is a risk that certain species linked to the light conditions of coppiced forests and tree regeneration could gradually disappear (Strubelt *et al.*, 2019; Longa *et al.*, 2020), including rare vascular species (Müllerová, Hédl and Szabó, 2015).

Coppicing has gained renewed attention also due to its ability to produce large quantities of low-quality wood at short intervals, aligning perfectly with the needs of the rapidly growing biomass economy (Jansen and Kuiper, 2004; Nestorovski *et al.*, 2009; Matula *et al.*, 2012; Ollikainen, 2014). As the demand for renewable energy sources continues to rise, traditional coppice systems are increasingly viewed as a more sustainable and practical solution compared to short-rotation coppice stands, which have faced financial and ethical challenges, particularly on ex-arable land (Glithero, Wilson and Ramsden, 2013). Existing coppice forests offer an abundant and consistent supply of raw material, making them ideal for meeting the large feedstock demands of the modern bio-economy (Ollikainen, 2014). This economic potential further underscores the importance of reviving and maintaining coppice management practices to support the expanding biomass industry (Matula *et al.*, 2012).

In addition, coppice forests also offer significant ecological benefits, including soil erosion control, enhanced nutrient cycling, and the maintenance of landscape heterogeneity, all of which are vital for supporting various wildlife species (Imamura, Saito and Nakashizuka, 2017). When thoughtfully planned and implemented, coppice management can maximize these ecological advantages while also achieving economic and conservation objectives (Götmark, 2013; Sjölund and Jump, 2013; Leonardsson and Götmark, 2015). As a result, the revival of coppicing practices is well-suited to modern environmental and economic goals, promoting sustainable forest management and biodiversity conservation (Miklín and Čížek, 2014).

Since coppicing entails cutting trees close to the ground and allowing them to regenerate, the crucial element in effective coppice restoration is ensuring the tree stumps can survive and resprout. This ability is influenced by numerous factors, such as the age and size of the parent tree (Del Tredici, 2001; Weigel and Joanne Peng, 2002; Matula *et al.*, 2012; Šplíchalová *et al.*, 2012), cutting height and season (Harrington, 1984; Xue *et al*., 2013), the density of living residual trees and neighboring stumps (Matula *et al*., 2012; Svátek and Matula, 2015), understory light availability (Ducrey and Boisserie, 1992; O'Hara and Berrill, 2010) and damage by deer browsing or pathogens (Joys, Fuller and Dolman, 2004; Pyttel *et al*., 2013; Mårell *et al*., 2018). For example, in a stand of sessile oak (*Quercus petraea*) in the Czech Republic, where trees were up to 97 years old, the likelihood of resprouting dropped to below 50% when the stem diameter at breast height exceeded 35 cm (Šplíchalová *et al*., 2012). A similar study in southwest Germany found higher stool survival in the same species, with only 16% of coppice stools (aged 80–100 years) dying within two years of felling, though mortality did slightly increase as stem diameters approached 25 cm (Pyttel *et al.*, 2013). Matula *et al*. (2012) observed a comparable pattern in sessile oaks that had been converted to high forest almost a century earlier, where the probability of successful resprouting was less than 40% for stumps with diameters over 70 cm. In contrast, in the same stand, nearly all lime (*Tilia cordata*) and most hornbeam (*Carpinus betulus*) stools successfully resprouted, with hornbeam showing improved sprouting likelihood as stem diameter increased.

Most of these factors can be managed by forest managers to optimize sprouting responses after thinning or partial cutting, although the outcomes are not always predictable due to the varying responses of different species.

Recently there have been many studies focusing on restoring of coppice forest (Vild *et al*., 2013; Strubelt *et al*., 2019), sprouting ability of different tree species (Matula *et al*., 2012) and measuring the biomass of resprouting trees (Spinelli, Ebone and Gianella, 2014; Matula *et al*., 2015; Mejstřík, Šrámek and Matula, 2022). However, there are only few studies evaluating the growth response of trees in coppices to changing microclimate conditions. (Stojanović, Sánchez-Salguero, *et al.*, 2017) analyzed dendrochronology samples to assess whether sessile oak trees from coppice and high stands experienced different long-term growth trends and if sessile oak trees from different origins exhibited contrasting growth responses to climate. Increasing knowledge about the response of tree growth to climate, especially during periods of drought, is an important step in the implementation of climate variables into real sustainable management plans for forest ecosystems (Martín-Benito *et al.*, 2008).

2.2. Natural regeneration

Post-disturbance natural regeneration is a critical initial stage of forest development (Frelich, 2002). It plays a pivotal role in shaping the trajectory of forest recovery and determining the composition and structure of future stands (Chazdon and Guariguata, 2016). As one of the most cost-effective methods for forest recovery (Chazdon and Guariguata, 2016; Chazdon *et al.*, 2016), it not only reestablishes forest cover but also enhances carbon sequestration and supports biodiversity conservation efforts (Holl, 2017). Understanding these natural processes is essential for informing forest management practices and restoring disturbed ecosystems.

As climate change and other global factors continue to drive widespread disturbances, the recovery of disturbed forests has become a key focus in forest ecology (Anderson-Teixeira *et al.*, 2013; Hérault and Piponiot, 2018; Senf and Seidl, 2022; Maurent *et al.*, 2023). Disturbances such as climate anomalies, pest infestations, diseases, and human activities are significantly altering forest dynamics worldwide (Seidl *et al.*, 2017). This increasing challenge highlights the need to understand forest recovery mechanisms more thoroughly to improve predictions and management of ecosystem responses to these disturbances (Anderson-Teixeira *et al.*, 2013; Hérault and Piponiot, 2018).

After the disturbance, trees that are severely damaged either die and regenerate from seed (non-sprouters) or recover through resprouting (sprouters) (Bond and Midgley, 2003). Sprouters can also produce seeds, but non-sprouters rely exclusively on seed production for regeneration

(Bond and Midgley, 2001; Premoli and Steinke, 2008). The ability to resprout is common among angiosperm tree species (Bond and Midgley, 2003; Matula *et al*., 2012; Clarke *et al*., 2013), and has been traditionally exploited in coppicing (Buckley, 2020).

Both regeneration strategies, sprouting and seeding, can be important for the persistence and continuity of tree populations (Li *et al.*, 2022). Because sprouters have the ability to regenerate from the existing root system or stem of the damaged tree, they quickly reoccupy the growing space previously occupied by disturbed trees and are less vulnerable to recruitment failure after severe disturbance compared to non-sprouters (Bond and Midgley, 2001). However, some disturbed trees may fail to resprout after a disturbance event (Matula *et al*., 2012). Also, sprouts are limited in their dispersal as they are spatially bound to the location of the original tree (root collar and stem sprouts) and can spread only within the reach of the root system (Matula *et al*., 2019). Therefore, the gaps between resprouting stumps can be colonized only by seed-origin regeneration (Howe and Smallwood, 1982; Brokaw and Busing, 2000). Moreover, non-sprouters are better suited to colonize gaps because their superior seed production, compared to sprouters, allows them to more efficiently disperse seeds into gaps (Bond and Midgley, 2003). Additionally, non-sprouters often form persistent seed banks, which can store viable seeds over extended periods (Shiferaw, Demissew and Bekele, 2018; Tiebel, Huth and Wagner, 2018).

The type of regeneration following disturbance has significant implications for tree species diversity in recovering forests. Sprout regeneration produces new shoots of the same genetic individual, maintaining the species composition of the preceding stand (Bond and Midgley, 2001; Del Tredici, 2001). In contrast, seed regeneration enables both the persistence of species from the original stand as well as the introduction of new species from external seed sources (Kammesheidt, 1998; Myers and Harms, 2009). As a result, seed regeneration has the potential to both maintain and increase tree community diversity.

Both sprout and seed regeneration often co-exist after disturbances, each substantially contributing to newly emerging tree regrowth (Matula *et al*., 2019). However, individuals originating from these two regeneration strategies play differential roles in forest development, due to their distinct physiology (Matoušková *et al.*, 2022), resource storage capacities (Bellingham and Sparrow, 2000; Bond and Midgley, 2001), and growth dynamics (Matula *et al*., 2019). Trees of seed origin are typically single-stemmed and have more stored carbon in their stems, allowing them to allocate more resources towards height growth (Midgley, 1996). Sprouters allocate considerable carbon belowground (Langley, Drake and Hungate, 2002), and have much higher starch levels than non-sprouters (Bond and Midgley, 2001), which allows them to persist through disturbances and quickly resprout when above-ground tissues are destroyed (Bond and Midgley, 2003). In addition, after a disturbance event, sprouters benefit from established large root systems, which provide better access to soil resources (Clark and Hallgren, 2003; Atwood, Fox and Loftis, 2011; Xue *et al.*, 2014; Pietras *et al.*, 2016; Stojanović, Szatniewska, *et al.*, 2017). Therefore, sprouters tend to dominate in less productive sites (Midgley, 1996; Ojeda', 1998; Bellingham and Sparrow, 2000), while in productive environments, they are often overtopped by single-stemmed seed regeneration (Midgley, 1996).

Tree seed ecology is a widely studied topic due to its significance in natural forest regeneration (Guariguata and A. Pinard, 1998; Kitajima and Fenner, 2009; Yan, Zhu and Yu, 2012; Kroschel, King and Keim, 2016). However, as a result of climate change leading to more frequent and more severe droughts (IPCC 2007), many tree species are experiencing elevated mortality of seedlings (Engelbrecht, Kursar and Tyree, 2005; Engelbrecht *et al.*, 2006; Browne *et al.*, 2021). On the other hand, the role of sprouting in early forest development, and its impact on biomass production, tree species composition, and diversity of regrowing stands is not well understood. Moreover, the majority of prior research on natural regeneration has predominantly focused on the initial few years after disturbance (Kennard *et al.*, 2002; Fang *et al.*, 2011; Knapp, Olson and Dey, 2017; Zhang *et al.*, 2018; Dinh *et al.*, 2019; Li *et al.*, 2022), a phase that can be significantly impacted by high turnover rates, whereas studies considering established regeneration more than a decade after disturbance are rare (Swaim *et al*., 2016). These short-term studies have shown that growth of sprouts can be affected by parent tree size (Matula *et al*., 2019), stump height (Fang *et al.*, 2011), number of sprouts per stump (Fang *et al.*, 2011; Dinh *et al.*, 2019), tree species identity (Knapp, Olson and Dey, 2017; Matula *et al*., 2019), gap size (Zhang *et al*., 2018) and light availability (Dinh *et al*., 2019; Matula *et al*., 2019).

While sprouting and seeding represent two distinct regeneration strategies, many tree species exhibit a mixed response, producing both sprouts and seeds following disturbance. The specific regeneration response often depends on the severity, frequency and type of disturbance (Bellingham and Sparrow, 2000; Kennard *et al*., 2002). For example, severe disturbances that destroy both the above- and below-ground tissues from which a tree could sprout (e.g., high-intensity fire), may decrease the prevalence of sprouts (Kennard *et al.*, 2002), thus often leaving regeneration from seed as the only option. In contrast, intense disturbances that preserve stumps, buds, and roots (e.g., coppicing and selective logging) may favour sprouting over seed regeneration (Kvasnica *et al.*, 2023) because many tree species have evolved vigorous sprouting abilities as an adaptation to severe disturbances.

The balance between sprout and seed regeneration after disturbances has been studied in various forest ecosystems (Bellingham and Sparrow, 2000; Bond and Midgley, 2001; Dietze and Clark, 2008; Mostacedo *et al*., 2009; Li *et al*., 2022), showing varying contribution of each regeneration strategy influenced by both environmental and anthropogenic factors. Resprouting is typically prevailing regeneration strategy in ecosystems with frequent and high severity disturbances (Bellingham and Sparrow, 2000; Bond and Midgley, 2001), but it is also common response to the least severe disturbance regimes (Bellingham and Sparrow, 2000) and rarely disturbed forests (Dietze and Clark, 2008; Matula *et al*., 2019). However, the contribution of sprout regeneration might decline with extended post-logging time (Xue *et al.*, 2014). On the other hand, seed regeneration is often dominant in unlogged stands (Xue *et al.*, 2014; Li *et al.*, 2022)and in stands with high logging intensity (Li *et al.*, 2022).

2.2.1. Effect of residual trees on natural regeneration

Silvicultural systems such as selective logging and coppicing rely on the natural regeneration of a disturbed stand. Both selective logging and coppice-with-standards systems can vary substantially in their intensity, leaving certain parts of the stand uncut. After such anthropogenic disturbances, the emerging sprouts and seedlings do not interact only with each other but also with the mature residual trees (standards). The initial growth of sprouts is much faster than that of seedlings (Bond and Midgley, 2001; Dietze and Clark, 2008; Pietras *et al.*, 2016). Therefore, sprouts are likely to be strong competitors for seed regeneration. However, mature residual trees have been shown to limit the sprout development (Mejstřík, Šrámek and Matula, 2022), primarily due to increased neighborhood competition for light (Matula *et al.*, 2019). This interaction potentially results in decreased competition between sprouts and seedlings, influencing the overall dynamics of forest regeneration.

Residual trees play a pivotal role in influencing the long-term recovery of degraded forests (N’Guessan *et al.*, 2019). They impact forest regeneration in two primary ways: by facilitating natural regeneration and enhancing overall forest ecosystem diversity. The presence of residual trees provides a critical source of seed for natural regeneration, contributing significantly to the composition and structure of the recovering stand (Norden *et al.*, 2009). Additionally, residual trees can increase species richness and diversity by creating a more heterogeneous environment, offering a variety of microhabitats and resources necessary for different species (Imai *et al.*, 2012). In a long-term perspective, the influence of residual trees can shape the forest community, as they can selectively favor species that are better adapted to local conditions and are more likely to withstand future disturbances (Bergeron *et al.*, 1999).

However, it is essential to balance these benefits against the potential negative impacts of high residual tree density on seed regeneration. An excessive density of residual trees can potentially reduce the overall success of forest recovery by obstructing seed regeneration. Because most seeds fall close to the parent tree (Clark *et al.*, 1999; McEuen and Curran, 2004), increasing the density of mature trees in an area typically leads to higher seedling density. Once the seeds reach the forest floor, two opposite but not mutually exclusive mechanisms—facilitation and competition—come into play (Holmgren, Scheffer and Huston, 1997). Facilitation promotes seedling growth and establishment by providing favorable conditions that helped the adult trees succeed, such as positive feedback related to mycorrhizal associations (Van Der Heijden and Horton, 2009). On the other hand, competition for resources between seedlings and older individuals, whether of the same or closely related species, as well as potential increased damage from herbivores and pathogens due to density-dependent effects (Janzen-Connell effects), may reduce survival and favor the success of other species (Craine and Dybzinski, 2013; Song *et al.*, 2020).

While it is accepted that facilitation and competition act simultaneously, the prevailing mechanism varies among species, habitats, and environmental conditions (Holmgren, Scheffer and Huston, 1997). Additionally, the relative strength of these interactions may shift over time from facilitation to competition (Valiente-Banuet and Verdú, 2008; Alba, Fahey and Flory, 2019). Species or individuals experiencing stronger facilitation during their transition from seedling to sapling are likely to suffer lower mortality compared to those under stronger competition. Consequently, we may expect a positive relationship between regeneration density and the density of neighboring trees for both seedlings and saplings. Conversely, when competition is stronger, higher mortality rates may result in a weaker relationship between regeneration density and the density of residual adult trees, particularly for saplings.

2.3. Drivers of tree growth, productivity and natural regeneration

2.3.1. Forest structure

Forest structure, encompassing the complex arrangement of physical components within a forest ecosystem, is a fundamental determinant of biodiversity, productivity, and a wide range of ecosystem services (Spies, 1998; McElhinny, Gibbons and Brack, 2006). It includes the spatial distribution and arrangement of trees, shrubs, and other vegetation, and serves as a key driver of forest growth and ecological processes. Forest structure is continuously shaped by forest dynamics and biophysical factors, directly influencing the provision of essential ecosystem goods and services such as carbon storage, nutrient cycling, and biodiversity (Pretzsch and Zenner, 2017). By impacting forest productivity, tree species diversity, and biological habitats, forest structure ultimately determines the quality of the ecosystem services that forests provide (Spies, 1998; Enquist, West and Brown, 2009; Gamfeldt *et al.*, 2013). The complexity of forest structure not only influences current forest functions but also dictates the forest's ability to respond to disturbances and environmental changes, making it a vital component of forest resilience (Franklin *et al.*, 2002).

Forest structure is typically characterized by individual structural elements and the spatial distribution patterns of these elements within the forest, both horizontally and vertically (Franklin *et al.*, 2002). These structural elements include features such as leaf area, life form (deciduous or evergreen) and branch configuration, all of which play crucial roles in basic tree functions and resource competition, influencing how trees grow, reproduce, and interact with their environment (Pan *et al.*, 2013). For instance, the vertical stratification of trees within a forest, from ground vegetation to the tallest emergent trees, regulates how light penetrates through the canopy layers. This variation in light availability strongly affects understory vegetation, influencing plant growth, seedling recruitment, and species composition (Kern *et al.*, 2013). Moreover, leaf area index (LAI), the total leaf surface area per unit ground area, is a crucial indicator of the forest's ability to capture light for photosynthesis and is directly linked to forest productivity (Bréda, 2003). The spatial arrangement of these elements, whether trees are evenly dispersed, clustered, or clumped, can significantly impact tree growth, resource competition, and forest dynamics (Franklin *et al*., 2002).

The spatial arrangement of forest structure also includes patterns of canopy layers, gaps, and the distribution of biomass, which are reflective of the forest's successional stage and disturbance history (Franklin *et al*., 2002). Canopy gaps, for example, are important features that create localized microenvironments, increasing light availability and promoting the regeneration of both shade-tolerant and shade-intolerant species (Chazdon, 2003). These gaps are typically formed by natural disturbances such as falling trees or windstorms, allowing light to penetrate the lower forest strata and supporting the establishment of new species (Brokaw, 1985). In turn, this dynamic influences forest diversity and resilience by fostering heterogeneity in species composition and stand structure (Chazdon, 2003). The presence of standing dead trees and fallen logs, often referred to as coarse woody debris, also contributes to the complexity of forest structure, providing critical habitat for a variety of organisms, including fungi, insects, and cavity-nesting birds (McEvoy, 1995).

In addition to the natural processes shaping forest structure, disturbances (both natural and anthropogenic) play a significant role in altering forest composition and complexity (Frelich, 2002). Natural disturbances such as fires, storms, and insect outbreaks serve as primary agents that modify structural attributes, creating a mosaic of patches at different stages of succession and facilitating species turnover (Swanson *et al.*, 2011). These disturbances promote structural diversity, which is important for maintaining ecosystem functions and supporting biodiversity. Anthropogenic disturbances, such as logging and land-use changes, also exert a considerable influence on forest structure, often reducing its complexity and negatively impacting ecosystem services (Lindenmayer and Laurance, 2012). When managed unsustainably, human interventions can lead to simplified forest stands with lower biodiversity and diminished ecological resilience, which is critical for forests' ability to withstand climate change and other stressors (Thompson *et al.*, 2009).

Forest structural development is often classified into various stages based on the age of the stand, with older stands generally displaying greater structural complexity due to processes like the formation of canopy gaps, horizontal diversification, and vertical stratification (Franklin *et al*., 2002). The structural complexity of older forests is associated with increased biodiversity, ecological stability, and resilience (Pan *et al*., 2013). For example, older forests often support a rich diversity of species due to the availability of a variety of habitats, such as large, old trees, snags, and fallen logs, all of which are essential for maintaining ecosystem function and services (Pan *et al*., 2013). Forests with high structural diversity are also more resilient to disturbances, as they can buffer the effects of environmental stressors, such as drought, pest outbreaks, and climate change (Frelich, 2002).

Complex forest structures, shaped by various natural and ecological processes over time, create diverse microclimates, niches, and habitats that are essential for sustaining biodiversity (Spies, 1998; Brown *et al.*, 2011; Pan *et al.*, 2013). Variations in stand structural attributes, such as individual tree size (both in diameter and height) within and among species, plays a significant role in forming these structures. This variation enhances canopy complexity, which improves light distribution and resource availability, supporting a wide range of plant and animal species

(Clark, 2010; Yuan *et al*., 2018; Zhang and Chen, 2015; Lindenmayer, Margules, and Botkin, 2000). It has been shown, that mature forest stands with a multi-layered structure consistently exhibited greater plant species diversity, especially when they included both broadleaved and coniferous trees and/or featured a semi-open canopy. Conversely, young, single-layered forest stands consistently showed low plant species diversity, particularly when they were composed of conifers and/or had a closed canopy (Gao *et al*., 2014).

Promoting structural complexity in forests is a key strategy for enhancing ecosystem biodiversity and resilience (Franklin *et al*., 2002; Valbuena *et al*., 2012; Fardusi *et al*., 2018). Such improvements represent effective strategies for elevating forest quality, a subject that has been at the forefront of forest management research for an extended period (Hui *et al*., 2019). By promoting varied and complex structural arrangements, forest managers can support robust and resilient ecosystems capable of providing essential services such as carbon sequestration, water regulation, and habitat provision while also fostering adaptability to changing environmental conditions.

2.3.1.1.Effects of forest structure on productivity

Understanding the factors that influence the productivity of forest ecosystems is essential not only for economic reasons, such as the valuation of forest wood, but also for broader ecological purposes, including carbon sequestration and biodiversity maintenance (Gamfeldt *et al*., 2013). Forest ecosystems play a fundamental role in mitigating climate change by absorbing atmospheric CO_2 and storing it as biomass (Bonan, 2008; Naeem *et al*., 2009), with trees acting as significant CO_2 sinks through the process of photosynthesis (Whitehead, 2011). This process of carbon capture is crucial for offsetting global greenhouse gas emissions, making forest productivity an essential component of climate regulation. Wood production, specifically, is one of the main contributors to carbon sequestration in the biosphere, as the biomass accumulated in trees serves as a long-term storage of carbon. However, wood production exhibits high spatial variation, influenced by an array of factors, including biotic interactions, environmental conditions, and forest management practices (Vayreda *et al.*, 2012). As such, understanding the productivity of woody biomass in forest stands is a key variable for assessing the sustainability and ecological health of these ecosystems (Chave *et al*., 2005; Matula *et al*., 2015). Moreover, understanding the factors that influence biomass production is of paramount importance for forest managers, ecologists, and policymakers alike, as it allows for more informed decision-making regarding conservation and sustainable use of forest resources.

Forest structure, which encompasses the composition, density, and spatial arrangement of trees, exerts a profound influence on forest productivity (Ishii, Tanabe and Hiura, 2004). The structural complexity of a forest determines how resources such as light, water, and nutrients are distributed among trees, which directly affects their growth and, consequently, the productivity of the forest as a whole. For instance, the microclimatic conditions within the understory, which are largely shaped by the forest's structural complexity, play a critical role in the regeneration and growth of trees (Parker, 1995). Factors such as light penetration, soil moisture, and wind conditions within the understory are heavily influenced by the vertical and horizontal structure of the forest canopy. In dense forests, where canopy cover is high, light availability in the understory may be limited, slowing down the growth rates of young trees and seedlings (Montgomery and Chazdon, 2001). However, in structurally complex forests with varying tree heights and canopy layers, light is distributed more efficiently, allowing for better resource utilization and promoting growth. This is particularly important for regenerating forests, where new cohorts of trees must compete for light and other resources in the understory. Therefore, the structural complexity of the forest plays a crucial role in shaping not only the immediate growth of individual trees but also the long-term productivity of the forest ecosystem (Parker, 1995).

Structural complexity, defined as the variability in the three-dimensional spatial arrangement of trees and other structural components within a forest, contributes to enhancing forest productivity by promoting efficient resource use. This complexity allows for complementary resource use among different plant species by creating a variety of niches and microhabitats that plants can exploit (Naeem *et al.*, 1994; Hooper and Vitousek, 1997). In forest ecosystems, where plants of various life forms coexist, the resulting complex three-dimensional structure further amplifies this effect, leading to higher overall ecosystem productivity (Ishii, Tanabe and Hiura, 2004). By promoting the efficient capture of sunlight, the uptake of nutrients, and the use of water, forests with complex structures are better able to sustain high levels of biomass production. The vertical stratification of trees, ranging from understory species to canopy-emergent giants, maximizes the use of available sunlight, particularly in forests with multiple canopy layers (Montgomery and Chazdon, 2001). This efficient utilization of resources results in a more productive ecosystem, as trees with different heights and light requirements occupy different vertical niches within the forest (Ishii, Tanabe and Hiura, 2004). Moreover, the increased structural complexity in these forests reduces competition for resources among trees, allowing for more harmonious coexistence and contributing to higher overall biomass production.

Research has shown that mixed-species forests are generally more productive than monocultures when species facilitation and vertical stratification are present (Cannell, Malcolm and Robertson, 1992; Kelty, 1992; Hartley, 2002; Ishii, Tanabe and Hiura, 2004). In mixed-species forests, the complementary nature of different species' resource use patterns allows for more efficient exploitation of available resources. For instance, species with deep root systems may access water and nutrients from lower soil layers, while species with shallow roots may take advantage of surface moisture and nutrients. Similarly, species that require high levels of sunlight for growth can occupy upper canopy positions, while shade-tolerant species thrive in the lower layers. This vertical and horizontal segregation of resources minimizes competition and maximizes productivity (Smith and Long, 1989). In natural stands with mixed species, trees exhibit various life forms and range in size from saplings to mature trees, spanning from understory and subcanopy species to those reaching the upper canopy. This variation in tree sizes creates a multi-layered foliage structure, adding to the structural complexity of the canopy and allowing for improved resource capture (Smith and Long, 1989; Hartley, 2002). As a result, mixed-species forests tend to have higher rates of biomass accumulation and are more productive than their monoculture counterparts. Additionally, these forests are often more resilient to disturbances such as pests, diseases, and extreme weather events due to the diversity of species present (Kelty, 1992).

The positive relationship between tree species richness and productivity has been demonstrated in multiple studies across different forest types, where natural mixed forests have been found to be more productive than monospecific ones (Cannell, Malcolm and Robertson, 1992; Kelty, 1992; Hartley, 2002; Vilà *et al.*, 2007; Piotto, 2008; Paquette and Messier, 2011; Zhang, Chen and Reich, 2012). The greater diversity of species in mixed forests allows for more efficient resource use, as different species specialize in utilizing various ecological niches. This diversity of functional traits, such as differences in leaf area, photosynthetic rates, and water use efficiency, enhances the overall productivity of the forest (Vilà *et al.*, 2007). Additionally, research has shown that diversity generally stabilizes aboveground wood production in forests across Europe, suggesting that mixed-species forests are better able to maintain consistent rates of productivity across a wider range of environmental conditions compared to monocultures (Jucker *et al.*, 2014). This stability is particularly important in the context of climate change, where increased variability in temperature and precipitation may disrupt the growth of trees in monoculture forests. Mixed-species forests, with their greater resilience, are more likely to continue growing and sequestering carbon under changing environmental conditions (Paquette and Messier, 2011).

Extensive simulations have also shown that tree species richness promotes productivity in European temperate forests across a large climatic gradient, primarily through strong complementarity between species (Morin *et al.*, 2011). This complementarity arises when species differ in their use of resources or when the presence of one species facilitates the growth of another. For example, nitrogen-fixing species can increase soil nitrogen levels, benefiting neighboring species that require nitrogen for growth. These interactions between species enhance overall forest productivity and contribute to the long-term sustainability of the ecosystem (Morin *et al.*, 2011). Moreover, the long-term productivity of natural forest ecosystems with high tree species diversity may exceed that of less diverse forests due to the increased resilience of these ecosystems to disturbances (Franklin, 1989). Diverse forests are better able to recover from events such as fires, storms, and pest outbreaks because they contain species that are adapted to different types of disturbances.

However, the relationship between species diversity and forest productivity can vary depending on factors such as site richness and forest type (Belote *et al.*, 2011; Paquette and Messier, 2011; Vilà *et al.*, 2013). In some cases, enhanced productivity has been found to be more influenced by species evenness (the relative abundance of different species) than by species richness alone (Zhang, Chen and Reich, 2012). For example, a forest with a few dominant species may exhibit lower productivity than one with a more balanced distribution of species, even if both have the same number of species. Furthermore, tree diversity may promote forest stand productivity primarily through an increase in tree density rather than through enhanced individual tree growth (Vilà *et al.*, 2013). This suggests that the relationship between diversity and productivity is complex and depends on a variety of ecological factors, including competition, resource availability, and environmental conditions.

Additionally, in some cases, increasing diversity could lead to a decrease in productivity, especially in temperate to boreal forests where tree species tend to occupy similar ecological niches and possess overlapping functional traits (Pretzsch, 2009). In these forests, the potential for complementarity between species is reduced, and competition for resources may outweigh the benefits of diversity. Therefore, the effect of diversity on productivity is context-dependent and may vary across different forest ecosystems and climatic regions.

Beyond species diversity, other critical factors influencing forest productivity include structural elements such as basal area and tree height heterogeneity. Studies analyzing large datasets from national forest inventories have underscored the substantial impact of these structural variables, often surpassing the influence of species diversity alone. For instance, Bohn and Huth (2017) analyzed approximately 300,000 forest stands and found that mean forest productivity does not increase with species diversity, but basal area and tree height heterogeneity are the dominant drivers of forest productivity. Basal area, which is the cross-sectional area of all the trees in a stand, is a key indicator of forest density and can have a direct impact on growth rates by influencing resource availability (Vilà *et al*., 2013). Similarly, tree height heterogeneity, which refers to the variation in tree heights within a stand, can enhance productivity by allowing for more efficient light capture and reducing competition for sunlight. Supporting these findings, Park *et al*. (2019) demonstrated that structural diversity had a stronger effect on forest productivity than species diversity, highlighting the importance of maintaining diverse forest structures to maximize biomass accumulation and sustain ecosystem services.

In addition to these structural elements, stand productivity can also be influenced by differences in the photosynthetic characteristics among species. Since trees are sessile organisms, the space occupied by their crowns and root systems directly affects the amount of resources they can acquire. Each tree species possesses a unique crown form, which is partially determined by genetic factors and ecological adaptations (Millet, Bouchard and Édelin, 1998). These photosynthetic characteristics vary among species depending on their successional status, crown form, and position within the canopy, further contributing to the overall productivity of the forest stand (Ishii, Tanabe and Hiura, 2004). Trees with more efficient photosynthetic rates and light capture strategies are able to grow more rapidly and contribute to higher levels of biomass production, ultimately enhancing the productivity of the entire forest ecosystem.

2.3.1.2.Effect of forest structure on tree regeneration

The regeneration of trees in a forest is crucial for the sustainability of the ecosystem, as it ensures the replacement of older trees and the continuation of vital forest functions such as carbon sequestration, biodiversity maintenance, and soil protection (Lindenmayer and Franklin, 2013). Natural regeneration plays an essential role in forest ecosystems, providing the means for forests to maintain their structure, composition, and resilience over time. Without consistent regeneration, forests would gradually lose their capacity to sequester carbon, support diverse species, and maintain the soil structure that prevents erosion. This process is particularly important in the context of global environmental changes, where forests are under increasing pressure from climate variability, human activities, and invasive species. Regeneration, in turn, is heavily influenced by forest structure, which includes the vertical and horizontal arrangement of trees, species composition, and the layering of canopy strata. This structural complexity serves as a critical determinant of tree regeneration, influencing every stage from seed production to seedling or sprout establishment (Franklin *et al.*, 2002; Frelich, 2002). The success of regeneration depends on how well these structural elements create favorable conditions for tree establishment, ensuring that forests can continue to thrive, provide ecosystem services, and support biodiversity.

Forest structure, including the composition, density, and spatial arrangement of trees within a stand, forms a microenvironment that has a direct impact on key factors that influence tree regeneration. These factors include light availability, soil moisture, temperature regulation, and competition for resources, all of which are crucial for the successful establishment and growth of new trees (Montgomery and Chazdon, 2001; Ashton and Kelty, 2018). A denser canopy structure, for example, can create shaded conditions that limit the amount of light reaching the forest floor, which is essential for seedling germination and early growth. The composition of species within the stand also plays an important role in regeneration success, as different species exhibit varying levels of shade tolerance, growth rates, and reproductive strategies. Some species may require gaps in the canopy to establish themselves, while others can thrive under the shaded conditions created by mature, taller trees. Understanding the intricate relationship between forest structure and tree regeneration is essential not only for maintaining biodiversity and ensuring long-term forest productivity but also for sustaining ecosystem services, such as carbon sequestration and nutrient cycling, that are critical for both local and global ecological balance.

One of the most critical factors influenced by forest structure during the regeneration process is light availability (Everham, Myster and Vandegenachte, 1996). The availability of light, particularly at the forest floor level, is heavily dependent on the density and composition of the canopy. The forest canopy cover, also referred to as canopy coverage or crown cover (Gill, Biging and Murphy, 2000), is defined as the percentage of the forest floor that is overlain by the vertical projection of tree crowns (Avery and Burkhart, 2015). Canopy cover is a key variable that influences numerous ecological processes within forest communities (Cook *et al.*, 1995) and plays a particularly important role in determining the light regime within a forest. Light availability is critical for the early stages of regeneration, as many tree species require specific light conditions for seed germination and seedling growth. Canopy cover also plays a role in estimating functional variables like the leaf area index (LAI), which provides crucial information for understanding biological and physical processes associated with vegetation (Colombo *et al.*, 2003). The arrangement and density of the canopy influence the amount of light that penetrates to the forest floor, directly affecting seedling growth and survival (Collet and Chenost, 2006). In forests with dense canopies, where light availability is limited, the regeneration of light-demanding species may be suppressed, while shade-tolerant species may thrive under these conditions. High canopy cover can limit regeneration by reducing the light available for seedling establishment, leading to the dominance of shade-tolerant species and the exclusion of species that require higher light levels to grow (Marchi and Paletto, 2010; Ashton and Kelty, 2018; Käber *et al.*, 2021). Consequently, the density of the canopy is a major driver in shaping the composition of the forest's next generation of trees.

The dynamics of light availability within a forest are also profoundly influenced by the presence of canopy gaps. Canopy gaps are created by natural or artificial disturbances, such as tree falls, logging, or windstorms, which temporarily open up spaces in the canopy and allow increased light to reach the forest floor. These gaps play an important role in regeneration by altering the microclimatic conditions, such as light intensity, air temperature, and humidity, that are essential for seedling establishment and growth (Dobrowolska, 2006). Larger canopy gaps provide opportunities for shade-intolerant species to establish themselves, as these species typically require more light than is available in the shaded conditions beneath a closed canopy. The increased light availability in canopy gaps often leads to enhanced seedling diversity and faster growth rates, as species that might otherwise be outcompeted under low-light conditions can take advantage of the additional resources (Duncan, 2002; Beckage *et al.*, 2008). On the other hand, smaller gaps may favor the growth of shade-tolerant species that are adapted to lower light conditions (Yamamoto, 2000; Montgomery and Chazdon, 2001; Beckage *et al.*, 2008; Díaz *et al.*, 2021). Thus, the size and frequency of canopy gaps are important factors that influence the diversity of tree species in a regenerating forest.

Forest structure and dynamics, particularly those related to canopy composition and light availability, are closely linked to stand attributes such as basal area, stem density, and the shade-casting ability of overstory species (Käber *et al.*, 2021). Basal area, which is a measure of the cross-sectional area of all trees in a stand, is an important indicator of forest density and canopy cover. A higher basal area often results in a denser canopy, which can significantly reduce the amount of light reaching the forest floor, thereby affecting the growth and establishment of new seedlings (Mina *et al.*, 2018). Similarly, stem density affects competition for both light and other resources such as water and nutrients. In stands with high stem density, competition for light can be intense, leading to slower growth rates for understory seedlings and potentially lower regeneration success (Klopcic, Poljanec and Boncina, 2012; Zell *et al.*, 2019). The shade-casting ability of the species present in the overstory is another critical factor in determining regeneration outcomes, as species with denser canopies create more shaded environments that can inhibit or favor the regeneration of different species depending on their light requirements. Species that cast heavy shade may prevent the establishment of light-demanding species, while favoring the regeneration of shade-tolerant species that are adapted to low-light conditions. These factors combined underscore the importance of basal area, stem density, and shade-casting ability in shaping the structure of the canopy and, consequently, the overall dynamics of forest regeneration (Klopcic, Poljanec and Boncina, 2012; Zell *et al.*, 2019).

The structural attributes of a forest, such as canopy cover, basal area, and stem density, are not only natural outcomes of forest growth and succession but can also be actively influenced by forest management practices. Forest management interventions, including thinning, selective logging, and the retention of specific tree species, can modify these structural attributes to promote desired regeneration outcomes. For instance, thinning practices that reduce stem density can increase light penetration to the forest floor, thereby enhancing the regeneration of light-demanding species (Ashton and Kelty, 2018). By carefully reducing the number of trees in a stand, managers can create a more open canopy structure that allows sunlight to reach the forest floor, promoting the growth of species that would otherwise be shaded out. Similarly, the strategic retention of certain species with lower shade-casting abilities can create microenvironments that support a broader range of species, fostering biodiversity (Montgomery and Chazdon, 2001). In some cases, management practices are specifically designed to create canopy gaps that encourage regeneration by increasing light availability and reducing competition for resources. These management strategies are crucial for maintaining the diversity and productivity of forest ecosystems, particularly in the face of environmental changes such as climate change and habitat fragmentation.

By carefully manipulating these structural attributes, forest managers can steer the regeneration process to maintain or enhance forest productivity, biodiversity, and resilience to environmental changes (Lindenmayer and Franklin, 2013). Such interventions are particularly important in managed forests, where natural disturbances that create canopy gaps may be less frequent. Through management practices that mimic natural processes, managers can promote regeneration patterns that support a diverse array of species and ensure the long-term sustainability of forest ecosystems.

2.3.2. Climatic factors

Climate change is increasingly recognized as a major factor influencing forest ecosystems, with significant implications for tree growth, productivity, and natural regeneration. Recent decades have seen episodes of forest mortality linked to droughts and heat waves, highlighting the vulnerability of these ecosystems to extreme climatic events (Allen *et al.*, 2010; Peng *et al.*, 2011; Vayreda *et al.*, 2012; Grimm *et al.*, 2013). One of the most critical climate-mediated challenges for natural regeneration is the survival of seedlings during their initial stages of growth (Calama *et al.,* 2017), particularly through the first summer when moisture conditions are crucial. During this period, mortality rates can exceed 90% for many tree species, underscoring the dependence of successful regeneration on adequate summer moisture (Castro *et al.*, 2004; Matías, Zamora and Castro, 2012).

As the world's climate continues to change, with projected increases in temperature ranging from 1.4 to 4.4 degrees Celsius by the end of the century (IPCC 2021), the impacts on forest ecosystems are expected to intensify (Kattenberg *et al*., 1996). These changes are likely to alter the growth, mortality, and reproduction of trees, thereby affecting the overall structure and composition of forests (Gebeyehu, 2019). Moreover, climate change is predicted to increase the frequency, duration, and severity of droughts, as well as other stressors such as insect outbreaks and invasive species, further compounding the challenges faced by forests (Allen *et al.,* 2010; Choat *et al.,* 2012; Thom and Seidl, 2016). The consequences of these changes are already observable in some regions, where increased tree mortality has been linked to climate-induced drought (Peng *et al*., 2011).

The temperate forests of Central Europe, characterized by long rotation periods of 80 to 200 years, are particularly susceptible to these changes. As these forests are likely to experience significant climatic shifts within their lifespans, there is an urgent need to develop adaptive management strategies to mitigate the impacts of climate change and ensure the sustainability of forest resources (Linder, 2000; Lasch *et al.*, 2002). Such strategies must consider the potential shifts in species composition and the resulting effects on forest productivity. While some species may tolerate projected climate scenarios, others may exhibit reduced biomass production, especially in drought-prone regions (Lasch *et al.*, 2002). Therefore, development of adaptive forest management should be guided by sensitivity and risk analyses to navigate the uncertainties associated with future climatic conditions (Lasch *et al.*, 2002).

Climatic factors are fundamental in determining the structure, function, and health of forest ecosystems. These factors, particularly temperature, precipitation, vapor pressure deficit and atmospheric carbon dioxide (CO_2) concentrations, serve as key regulators of tree growth, productivity, and the natural regeneration processes essential for sustaining forest biodiversity (Linder, 2000; Boisvenue and Running, 2006; Gebeyehu, 2019). Each of these variables exerts profound effects on trees at various stages of development, influencing physiological responses such as photosynthesis, respiration, and transpiration. However, their impacts are not uniform, rather, they fluctuate considerably across different forest biomes, depending on regional climatic conditions and local environmental factors (Paquette and Messier, 2011; Paquette *et al.*, 2018).

Importantly, the interaction between these climatic drivers is both intricate and dynamic, with each factor potentially amplifying or mitigating the effects of the others. For instance, elevated atmospheric CO_2 concentrations have been shown to enhance photosynthesis in certain tree species, potentially increasing biomass production and water-use efficiency in CO_2-enriched environments (Norby *et al.*, 2005). However, this CO_2 fertilization effect is highly dependent on adequate water and nutrient availability, which may be increasingly constrained by changes in precipitation regimes (Reyer *et al.*, 2014). In regions experiencing prolonged droughts, such as parts of the Mediterranean and western North America, increased atmospheric CO_2 levels may not be sufficient to offset the negative impacts of water shortages on tree productivity and forest regeneration (Linares *et al.*, 2009; Choat *et al.*, 2012). Therefore, understanding the complex interplay between temperature, precipitation, and atmospheric CO_2 is essential for predicting the resilience and adaptability of forest ecosystems under future climate scenarios.

These interdependencies also have significant implications for forest composition and ecosystem functioning. The responses of different forest types to climate change are expected to vary widely, as trees exhibit distinct physiological and ecological adaptations to local climate conditions. Tropical forests, for example, are likely to experience greater sensitivity to temperature increases due to the narrow thermal tolerances of many tropical tree species, while boreal forests, dominated by cold-adapted species, may initially benefit from warmer temperatures but face heightened risks from pest outbreaks and wildfire as the climate continues to warm (Paquette and Messier, 2011; Seidl *et al*., 2017). In temperate forests, such as those in Central Europe, the combination of longer growing seasons and more frequent droughts could lead to significant shifts in species composition, with drought-tolerant species potentially outcompeting others that are less adapted to changing moisture conditions (Linder, 2000; Lasch *et al.*, 2002). In contrast, forest ecosystems in arid and semi-arid regions, already at the margins of their climate tolerance, may see dramatic reductions in tree cover and biodiversity as higher temperatures exacerbate water scarcity (IPCC 2021; Reyer *et al*., 2013).

Further compounding these challenges is the fact that climate-induced changes in forests are often non-linear and can be influenced by interactions with other environmental stressors, such as invasive species, pathogens, and insect outbreaks. These biotic factors, in combination with climatic drivers, can create feedback loops that either enhance or undermine forest resilience (Allen *et al.*, 2010; Thom and Seidl, 2016). For example, increased temperatures and drought stress have been linked to heightened vulnerability to insect infestations, such as bark beetle outbreaks, which can cause extensive tree mortality across large areas of forest (Choat *et al*., 2012; Seidl *et al*., 2017). The cascading effects of such disturbances, combined with ongoing climate change, could lead to permanent shifts in forest composition, particularly in regions where regeneration is inhibited by unfavorable climatic conditions, such as prolonged droughts (Bonan, 2008; Peng *et al.*, 2011).

As the global climate continues to change, the vulnerability of forests to climatic extremes is anticipated to increase further (Dale *et al*., 2001; Seidl *et al*., 2017). This heightened vulnerability is not only a concern for biodiversity but also for the broader ecosystem services provided by forests, including carbon sequestration, water regulation, and habitat provision. As forests serve as critical carbon sinks, their ability to sequester carbon may be compromised under future climate conditions, particularly if increased tree mortality and slower regeneration rates reduce overall forest biomass (Pan *et al.*, 2011). Moreover, the adaptive capacity of different tree species and forest types to withstand these climatic changes will play a pivotal role in determining the long-term sustainability of forest ecosystems (Aitken *et al.*, 2008). The need for proactive management and conservation strategies has become increasingly urgent, as forest managers seek to balance short-term resilience with long-term adaptability in the face of growing climatic uncertainties (Lasch *et al.*, 2002).

2.3.2.1.Temperature

Temperature is one of the most critical environmental variables influencing tree growth, regeneration, and overall forest productivity. Its effects on trees are mediated through a range of physiological processes, most notably photosynthesis and respiration, which are key determinants of plant growth rates and metabolic functioning (Kirschbaum, 2000). Photosynthesis, the process through which trees convert sunlight into energy, is highly temperature dependent. Most biological metabolic activity of plants occurs within a temperature range of 0°C to 50°C, with optimal photosynthesis and growth typically observed between 15°C and 25°C (Hopkins, Hiiner and Wiley, 1995). Within this optimal range, trees maximize their carbon uptake, leading to higher growth rates and productivity. However, deviations from this temperature range, either below or above, significantly reduce photosynthetic efficiency. Lethal temperature levels, where biological activity ceases and irreversible damage occurs, range from 44°C to 52°C (Schulze, Beck and Müller-Hohenstein, 2005). In extreme cases, prolonged exposure to suboptimal temperatures can lead to tissue damage, reduced vitality, or even tree mortality, underscoring the sensitivity of forest ecosystems to temperature fluctuations.

The role of temperature in tree physiology is multifaceted, influencing not only individual tree growth but also the dynamics of forest regeneration. The effects of temperature on germination and early seedling establishment are particularly critical for determining forest composition and resilience. Temperature-induced germination vary across species, with many temperate tree species showing a strong positive response to warmer temperatures, which promote faster seed germination and improved seedling growth rates (Hobbie and Stuart Chapin, 1998; Munier *et al.*, 2010; Zurbriggen *et al.*, 2013). For instance, species in cooler temperate regions tend to exhibit enhanced germination under rising temperatures, potentially facilitating their expansion into higher latitudes or elevations, where conditions are becoming increasingly favorable due to climate warming (Fisichelli, Frelich and Reich, 2014). However, this temperature-driven expansion of temperate species may come at the expense of boreal conifers, which are less tolerant of elevated temperatures and may experience reduced survival and recruitment in warmer conditions (Fisichelli, Frelich and Reich, 2014). Thus, the temperature sensitivity of different tree species can lead to significant shifts in forest composition, with some species thriving while others struggle under the changing climate.

The impacts of temperature are not limited to temperate regions. In tropical montane wet forests, where temperature fluctuations are less pronounced than in temperate zones, warmer temperatures in canopy gaps can have notable effects on seed germination and seedling establishment. Studies have shown that increased temperatures in these forest gaps promote the recruitment of pioneer species by enhancing light availability and reducing competition from shade-tolerant species (Everham, Myster and Vandegenachte, 1996). In such ecosystems, even small increases in temperature can improve seedling survival and accelerate growth rates, thereby contributing to higher overall forest productivity. Conversely, in Mediterranean ecosystems, rising summer temperatures exacerbate drought stress, which can lead to lower seedling survival and reductions in forest productivity (Salamanca, 2022). This is particularly concerning in drought-prone regions, where trees are already operating near their physiological limits, and further temperature increases may push them beyond their tolerance thresholds (Grossiord *et al.*, 2020).

While the temperature effects on tree recruitment and growth are well documented, temperature also plays a critical role in shaping the species composition of forest stands. Warmer conditions may favor heat-tolerant species, leading to shifts in the competitive dynamics between species and altering the trajectory of forest succession (Zell *et al.*, 2019). For instance, warmer temperatures can create opportunities for fast-growing, drought-tolerant species to outcompete slower-growing species that are more vulnerable to heat and water stress. This shift in species composition has profound implications for forest structure and function, as it can alter key ecosystem processes such as carbon sequestration, nutrient cycling, and water regulation. Forests dominated by heat-tolerant species may exhibit different growth patterns, biomass accumulation, and ecological interactions compared to those dominated by species that thrive under cooler conditions (Scheller and Mladenoff, 2004).

The interaction between temperature and other environmental factors, such as soil moisture and nutrient availability, further complicates the temperature-tree growth relationship. Elevated temperatures can intensify drought conditions by increasing evaporation rates and reducing soil moisture levels, thereby exacerbating water stress in trees (Grossiord *et al.*, 2020). Under such conditions, trees may experience hydraulic failure, where the flow of water through the xylem becomes impaired, leading to carbon starvation and eventual mortality. This is particularly concerning in regions where rising temperatures are coupled with prolonged periods of low precipitation, such as in Mediterranean climates or semi-arid regions (Moreno-Fernández *et al.*, 2018; Salamanca, 2022). In contrast, in areas where water is not a limiting factor, warmer temperatures can stimulate faster decomposition of organic matter, leading to increased nutrient mineralization and availability for plant uptake (Gebeyehu, 2019). This enhanced nutrient cycling can promote forest productivity by providing trees with the essential nutrients they need for growth.

Moreover, temperature extremes, both high and low, can have lasting effects on forest ecosystems. Extreme heat events, such as heatwaves, can cause acute damage to tree physiology, particularly if they occur during critical periods of seedling establishment or in the peak growing season (Moreno-Fernández *et al.*, 2018). Similarly, cold temperature extremes, such as frost events, can damage newly germinated seedlings or cause frost cracking in mature trees, reducing their growth potential and increasing their vulnerability to pests and pathogens (Langvall and Nilsson, 2001). These temperature extremes are expected to become more frequent and severe as global temperatures continue to rise, adding significant complexity to forest management and conservation efforts in a warming world. The increasing intensity of heatwaves, cold spells, and other temperature fluctuations will further challenge the resilience of forest ecosystems. As global temperatures continue to rise, forest managers must consider these multifaceted effects, which will be critical in developing adaptive strategies to ensure the long-term sustainability and functionality of forest ecosystems in an increasingly unpredictable climate.

2.3.2.2. Precipitation

Water availability, closely linked to precipitation patterns, is a critical factor in determining tree growth, regeneration, and the overall health of forest ecosystems. Water is not only essential for photosynthesis, the process by which trees convert light energy into chemical energy, but also serves as the main component of plant cells, influencing cellular processes such as nutrient transport, tissue development, and metabolic functions (Mohr and Schopfer, 2012). In dry regions, where water is a limiting resource, there is a clear and direct correlation between increased water availability and higher net primary productivity (Loik *et al.*, 2004). This relationship underscores the importance of precipitation as a key driver of forest productivity. However, the effects of water availability on forest regeneration processes are far from straightforward. The germination, growth, and survival of seedlings, key stages in the regeneration cycle, can exhibit highly variable responses to changes in water availability, often dependent on species-specific traits, site conditions, and the timing of precipitation (Lett and Dorrepaal, 2018). This complexity highlights the need to consider both macroclimatic conditions, such as regional rainfall patterns, and microclimatic factors, such as soil moisture levels and humidity within forest stands, when assessing the impacts of water availability on forest dynamics.

In Mediterranean ecosystems, for instance, reduced precipitation is often accompanied by rising temperatures, which together lead to increased evapotranspiration rates and prolonged periods of drought stress. These conditions can significantly hinder seedling survival and compromise the overall health and productivity of forests (Peng *et al.*, 2011; Vayreda *et al.*, 2012). Drought-induced reductions in soil moisture availability, particularly during the critical summer months, limit the ability of seedlings and mature trees alike to maintain the water balance necessary for physiological processes. In such water-scarce environments, the combination of decreased precipitation and increased temperatures exacerbates water stress, often resulting in reduced growth rates and higher mortality risks, particularly for young trees and those species less adapted to drought conditions (Vayreda *et al.*, 2012). Over time, this can lead to shifts in species composition, favoring drought-tolerant species while diminishing the presence of more water-dependent ones. In some cases, entire forest stands may experience reduced productivity or even large-scale die-offs during prolonged droughts, with cascading effects on ecosystem services such as carbon sequestration, biodiversity support, and soil stabilization (Allen *et al.*, 2010).

In contrast, boreal forests, which typically receive abundant precipitation, often contend with the opposite problem: excessive water availability. These regions, characterized by poor drainage, limited evapotranspiration, and relatively short growing seasons, can experience waterlogging in soils, which restricts the oxygen availability necessary for root respiration and nutrient uptake (Paquette *et al.*, 2018). Boreal forests, therefore, face unique challenges where excess rainfall, rather than drought, can reduce tree growth and increase mortality risks. In areas with poorly drained soils, additional precipitation may exacerbate these problems, leading to heightened stress on trees, especially in low-lying areas where water accumulates (Paquette *et al.*, 2018). This highlights the fact that forest ecosystems, even those in high-rainfall areas, are highly sensitive to changes in precipitation patterns, whether in the form of deficits or surpluses. As global climate patterns continue to shift, these dynamics are expected to intensify, with some regions experiencing more frequent droughts while others face increased risks of flooding or waterlogging (IPCC 2021).

The role of water availability in forest ecosystems is also strongly influenced by the broader changes in water balance that accompany global climate warming. Warmer temperatures increase evaporative demand and transpiration rates, leading to heightened water stress even in regions that do not experience significant reductions in precipitation. A simulation study from Brandenburg (Germany) demonstrated primarily negative effects of climate warming on forest growth, primarily due to increased drought stress and reduced soil moisture availability (Lasch *et al.*, 2002). The findings from such simulations suggest that many temperate forests, which have historically benefited from a relatively stable water balance, may face increased challenges as warming continues to shift precipitation patterns and exacerbate evaporative losses. However, in northern European regions, where water limitations are less critical, the effects of climate warming on forest productivity may differ. In these areas, warmer temperatures combined with ample precipitation could enhance forest growth by extending the growing season and improving conditions for photosynthesis (Kellomäki and Kolström, 1993). In fact, simulation studies suggest that temperate forests in some regions could experience positive growth responses if increased precipitation can offset the heightened evaporative demand brought on by elevated temperatures (Bugmann, 1997; Lindner *et al.*, 1997). This variability in forest responses underscores the fact that the effects of water availability on forest ecosystems are not uniform across biomes and are highly dependent on the regional and site-specific climatic context.

Water availability is not only a macroclimatic concern but also intimately linked to the microclimatic conditions within forest stands. Microclimate encompasses a range of factors, including soil moisture, local humidity, and temperature fluctuations at the forest floor, all of which can be more important than broad-scale climate patterns for determining tree recruitment success (Zellweger *et al*., 2020; De Frenne *et al*., 2013, 2019; Von Arx *et al*., 2013). For instance, even in regions where rainfall patterns remain relatively stable, the microclimatic conditions experienced by seedlings at the forest floor can vary significantly due to factors such as canopy cover, which influences light availability, temperature, and humidity. Studies have shown that local microclimatic conditions, particularly soil moisture and humidity levels, can be decisive for seedling survival, especially in the early stages of tree establishment when young trees are most vulnerable to water stress (Zellweger *et al.*, 2020). This highlights the importance of considering both macro- and micro-scale climatic influences when evaluating the impacts of water availability on forest regeneration and overall ecosystem health.

In light of the complex interactions between precipitation patterns, temperature, and forest productivity, developing adaptive forest management strategies that account for these dynamics is essential for maintaining forest resilience in a changing climate. As climate change continues to alter precipitation regimes across the globe, forests will likely face new and intensified challenges related to water availability. In some regions, increased drought frequency may necessitate the adoption of water-conservation measures, such as selective thinning or the planting of drought-resistant species, to reduce competition for limited water resources and improve forest resilience (Millar, Stephenson and Stephens, 2007). In other regions, managing the risks of waterlogging and excess moisture will require improved drainage systems and the selection of species better suited to wet conditions (Kellomäki and Kolström, 1993). Understanding these interactions between water availability, temperature, and forest health is crucial for predicting the future trajectories of forest ecosystems and for implementing adaptive management practices that can sustain forest productivity and biodiversity in the face of a rapidly changing climate (Lindner *et al.*, 2010).

2.3.2.3. Vapor pressure deficit

Vapor pressure deficit (VPD) is a key environmental factor affecting tree physiology, particularly in terms of growth, productivity, and natural regeneration. VPD represents the difference between the actual moisture content in the air and the maximum moisture the air can hold when fully saturated (Monteith and Unsworth, 2013). As a measure of atmospheric dryness, VPD plays a critical role in regulating tree water use, photosynthesis, and overall health. Changes in VPD, especially in response to rising temperatures and shifting precipitation patterns due to climate change, have significant implications for forest ecosystems (Lendzion and Leuschner, 2008).

VPD has a profound effect on tree growth primarily through its influence on stomatal conductance and transpiration rates. Elevated VPD generally increases transpiration, leading to a higher demand for water in trees. When soil moisture is insufficient to meet this demand, trees experience water stress, which can impede growth (Monteith and Unsworth, 2013). Research indicates that even when soil moisture is adequate, high VPD can restrict stem growth (Zweifel *et al.*, 2021). This is because the high atmospheric water demand can result in transpiration rates exceeding the tree's ability to absorb water from the soil, leading to reduced turgor pressure, which is essential for cell expansion and growth (Zweifel *et al.*, 2021). Thus, VPD acts as a limiting factor for tree growth, especially during periods of heightened atmospheric dryness.

The response of trees to VPD also varies according to their age and species. Younger trees are generally more sensitive to high VPD, and this heightened sensitivity can significantly hinder their growth compared to older, more established trees, whose physiological mechanisms adapt more effectively to cope with water stress as they mature (Mirabel *et al.*, 2023). This variation in sensitivity has crucial implications for forest regeneration and management, particularly as climate change intensifies atmospheric dryness in many regions. Additionally, the influence of VPD on tree growth is not uniform across species. For example, Kerhoulas, Kolb and Koch, (2017) found that ponderosa pine exhibits a sharp decline in leaf conductance and photosynthesis with increasing VPD, which helps explain its growth patterns. Similarly, black spruce has been shown to have a lower capacity to recover from drought than jack pine, likely due to stricter stomatal control under dry conditions, which further reduces carbon inputs and growth rates (Pau *et al.*, 2022). This variation underscores the importance of understanding species-specific responses to VPD when assessing forest dynamics and health.

The productivity of forests is also strongly influenced by VPD. High VPD often leads to stomatal closure in trees, a process that conserves water but simultaneously reduces photosynthesis and carbon assimilation. Cunningham (2005) found that high midday VPD values frequently result in stomatal closure among tropical rainforest species, limiting photosynthetic activity and, in turn, productivity. This trade-off between water conservation and carbon uptake highlights the delicate balance trees must maintain to survive in dry conditions. Furthermore, VPD interacts with other environmental variables, such as light intensity and soil moisture, which can complicate its impact on tree productivity. High VPD, particularly during dry periods, can lead to significant declines in photosynthesis, which negatively affects both growth and productivity, especially in regions experiencing prolonged droughts where rising temperatures are expected to exacerbate VPD (Antezana-Vera and Marenco, 2021). This decline in photosynthesis under high VPD is also closely linked to canopy-level stomatal conductance, as higher VPD leads to reduced gas exchange and lower overall productivity (Grossiord *et al.*, 2017). As VPD increases, trees become less efficient in their water use, which not only exacerbates the effects of drought but also further limits forest productivity. The reduced water-use efficiency, combined with decreased carbon assimilation, presents a significant challenge for maintaining forest biomass, particularly in the context of a warming climate where such conditions are expected to become more frequent and severe.

Natural regeneration is another critical process influenced by VPD, as it affects the survival and establishment of seedlings. High VPD contributes to increased water stress in young seedlings, which are generally more vulnerable to environmental fluctuations compared to mature trees. Elevated VPD during the dry season can significantly limit stem growth in seedlings, thereby constraining the regeneration potential of trees (Camargo and Marenco, 2023). Successful regeneration is essential for maintaining the structure and function of forest ecosystems, making the effects of VPD on young trees particularly significant.

Seedlings, due to their small size and limited root systems, are more prone to dehydration under high VPD, leading to higher mortality rates (Mirabel *et al.*, 2023). This increased vulnerability can cause shifts in forest composition and reduce the overall resilience of forests, particularly in regions where drought frequency and intensity are projected to rise. On the driest sites, even a small increase in water deficit due to high VPD can negatively influence tree regeneration (Stevens-Rumann *et al.*, 2018). Conversely, on colder and more mesic sites, changing climatic conditions may actually enhance regeneration in areas that were previously limited by cold temperatures or snow accumulation (Stevens-Rumann *et al.*, 2018). This duality illustrates the complex interplay between VPD and other climatic factors in determining regeneration success.

3. Aims and overview of the dissertation thesis

Understanding the drivers of tree growth, productivity, and regeneration is essential for the sustainable management of forest ecosystems. This thesis aims to enhance our knowledge of the factors that influence woody biomass production, tree species diversity, and the growth of the most common woody species in newly restored coppices and coppice-with-standards (CWS) systems in the Czech Republic. To achieve this, data from two large experimental plots were used to analyze the impacts of different densities of standards (residual mature trees) and sprouting stumps on biomass production, assesses the contributions of various regeneration strategies, and explore the response of tree growth to climatic variations, such as drought.

Particular aims of the thesis are:

1. Quantify the effects of standard density and sprouting stump density on woody biomass production in newly restored coppices and CWS.
    a. Determine the impact of standards and sprouting stumps on biomass production on both stump and stand level.
    b. Compare biomass production among the most common tree species in European coppices, including sessile oak, European hornbeam, small-leaved lime, and field maple, under varying densities of standards and sprouting stumps.
    c. Determine how changes in standard density influence the overall structure and composition of newly restored coppice and CWS systems.

2. Assessing the contributions of different regeneration strategies to productivity and diversity in newly restored coppices and CWS.

a. Analyze the relative contributions of seed regeneration and vegetative sprouts to above-ground biomass (AGB) productivity and tree species diversity in early-stage forest development.
b. Examine how varying densities of standards affect the balance and interactions between seed and sprout regeneration.
c. Investigate whether vegetative sprouts limit the development of seed regeneration or vice versa, and how these dynamics impact the long-term species composition and structure of the forest.

3. Investigate the influence of climatic factors on the growth of different regeneration types and standards.

a. Analyze the influence of climatic factors, particularly the intensity of drought and high temperatures, on the radial growth of vegetative and generative regeneration, as well as standard trees.
b. Determine species-specific responses to climatic factors, to assess potential future changes in the structure and composition of coppice forests.
c. Analyze how different regeneration strategies respond to climatic stressors and how these responses may influence forest resilience and adaptation strategies.

By addressing these aims, the thesis seeks to contribute valuable knowledge to the field of forest ecology, offering practical recommendations for forest management practices that enhance ecological stability, biodiversity, and the resilience of forest ecosystems in the face of changing climatic conditions.

4. Methods

4.1. Study sites

The study was carried out in two experimental plots, Hády and Soběšice, located in the Training Forest Enterprise Křtiny of Mendel University in Brno, in the south-eastern Czech Republic (49°13’30’’N, 16°40’55"E and 49°14’43"N, 16°35'59"E, respectively). Each plot was 4 ha (200 m x 200 m) and fenced due to high game pressure. The elevation is 401 m a.s.l. in Hády and 355 m a.s.l. in Soběšice. The average annual air temperature is 8.4 °C in both plots. The average temperature in January (the coldest month) is -2.1 °C and in July (the warmest month) is 18.4 °C, based on data from the nearest Brno weather station from 1960–2010 for both plots. The bedrock is formed by limestone in Hády and granodiorite in Soběšice. The soils are brown forest soils in Hády and cambisols in Soběšice, which are both highly productive for forestry. However, brown forest soils, characterized by their well-decomposed organic matter and rich nutrient content, often exhibit higher productivity compared to cambisols, which are younger, less developed soils with limited horizon differentiation (Weil and Brady, 2017).

Until the early 20th century, both plots were regularly managed coppices (Kadavý, Kneifl and Knott, 2011). However, coppicing was gradually abandoned and both forest stands were transformed into high forests. The dominant tree species in the Hády plot were sessile oak (*Quercus petraea* (Matt.) Liebl.), small-leaved lime (*Tilia cordata* Mill.), European hornbeam (*Carpinus betulus* L.), and field maple (*Acer campestre* L.), while the Soběšice plot was dominated by sessile oak (95% of all individuals). For detailed characteristics of both stands see Table 1.

Table 1: Basic characteristics of experimental stands Hády and Soběšice before and after the cutting.

		Hády	Soběšice
original stand before cutting	Age of trees	98	73
	Number of trees	2651	2872
	Total basal area per ha (m2)	33.2	27.I
	Mean density of trees per ha	689	716
	Density of stocking	fully-stocked	fully-stocked
	Vertical structure of the stand	single-storey	single-storey
	Species composition	*Quercus petraea* 48% *Carpinus betulus* 25% *Acer campestre* 8% *Tilia cordata* 7%	*Quercus petraea* 95%
stand after cutting	Number of residual trees	450	412
	Mean density of residual trees per ha	113	103
	Species composition of residual trees	*Quercus petraea* 73% *Sorbus torminalis* 21%	*Quercus petraea* 100%
	Number of sprouting stumps in 2020	2222	1860
	Number of dead stumps in 2020	628	714
	Number of seed regeneration (dbh>5cm) in 2020	709	168

4.2. Experimental plot establishment

In both plots, all trees with a DBH ≥ 7 cm were identified to the species, and their exact positions were recorded using the Field-Map technology (IFER, Ltd., Jílové u Prahy, Czech Republic).

In 2009-2010, most of the trees in both plots were cut approximately 10 cm above the ground (2236 trees in Hády and 2453 in Soběšice) to restore a short rotation coppice forest. Some trees were left uncut as standards (450 trees in Hády and 412 in Soběšice) in densities from 0 to 275 trees per hectare. The standards averaged 25.6 cm in diameter at 1.3 m (DBH) and 18.0 m in height. The experimental plots were divided into 16 regular subsquares (50 x 50 m) with four different densities of standards. Each density was replicated in four subsquares, which were systematically distributed across the plots so that there were no adjacent subsquares with the same density (Figure 1). The four densities used were:

- clearcut (0 standards per plot; 100% of the volume was removed)
- very high felling intensity (20 standards per plot, 1.1 m2 BA; 77% of the volume was removed)
- high felling intensity (35 standards per plot, 1.8 m2 BA; 63% of the volume was felled on average)
- medium heigh felling intensity (50 standards per plot, 2.5 m2 BA; 54% of the volume was removed.

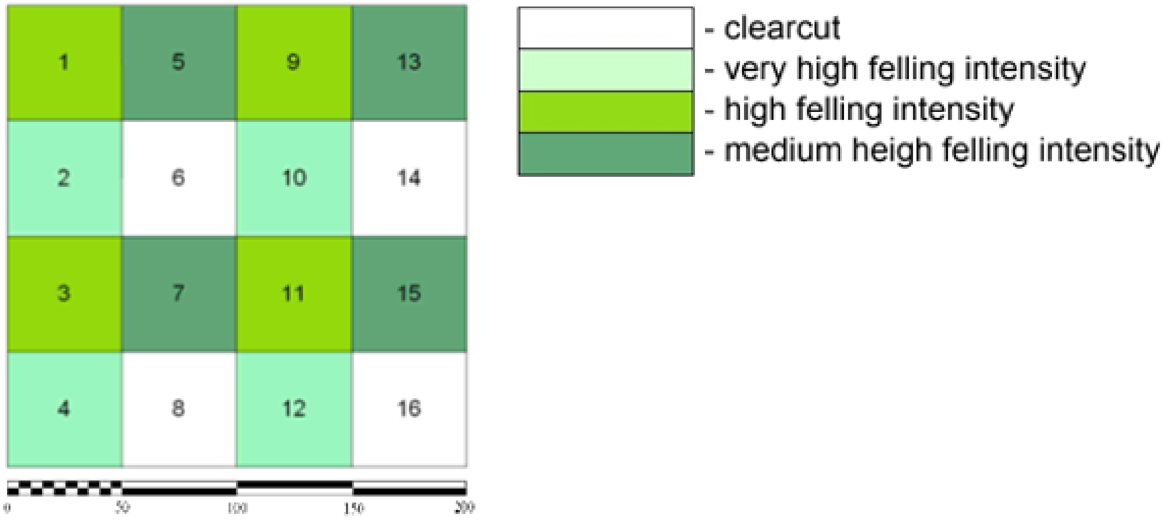

Figure 1: Design of the research plot (Kadavý, Kneifl and Knott, 2011).

For statistical analysis, each subsquare (50 x 50 m) was further divided into 4 smaller subplots (20 x 20 m). To minimize pseudoreplication, a 5 m belt was left between the individual subplots (Figure 2.)

Figure 2: Example of plot structure. Green dots represent positions of individual trees or resprouting stumps in 16 subsquares 50x50 m, further divided into 64 subplots 20x20 m with different densities of standards.

4.3. The effects of stand density, standards and species composition on biomass production in traditional coppices

4.3.1. Data collection

All stumps on both experimental study plots were regularly checked and in 2016-2017, seven complete growing seasons after harvesting, the basal diameter of five thickest sprouts on each resprouting stump was measured. This proved to be accurate estimator for the total sprout biomass of the individual resprouters and the populations of resprouters, respectively (Matula *et al*., 2015; Šrámek *et al*., 2020).

4.3.2. Data analysis

We calculated dry woody sprout biomass per each stump (SB_{stump}) using allometric equation developed for resprouting trees in the experimental plots (Matula *et al.*, 2015) using average basal diameter of five thickest sprouts per stump. In total, we evaluated sprout biomass from 115 stumps of *Acer*, 393 stumps of *Carpinus*, 381 stumps of *Quercus*, 124 stumps of *Tilia*, 20 stumps of *Sorbus torminalis* and 9 stumps of other tree species in Hády and 27 stumps of *Carpinus*, 1007 stumps of *Quercus*, 11 stumps of *Tilia* and 11 stumps of other tree species in Soběšice.

To evaluate the effect of standards and sprouting stumps on sprout biomass on stand level, for each subplot (20 x 20m), we calculated density of standards, density of sprouting stumps, and total biomass of sprouts (SB_{stand}) by summing sprout biomasses of individual stumps. To quantify the effect of standards and sprouting stumps on SB_{stump} on a stump level, we also computed mean SB_{stump} for each subplot, both for all species together and for the main 4 studied species separately, to evaluate interspecific differences in biomass production. To estimate the shift in tree species composition 7 years after the harvest, we also calculated the relative abundance of most common tree species for all subplots before the harvest by summing the basal area of cut trees of each species divided by basal area of all species. The post-harvest relative abundance was calculated as total sprout biomass of each species divided by SB_{stand} of all species. All the analyses were performed in R version 3.2.4 (R Core Team, 2016).

4.3.3. Model evaluation

To study the effect of varying density of standards and sprouting stumps density on both SB_{stand} and SB_{stump} we carried out a regression analysis. Since 4 subplots were nested within the subsquares, to remove the effect of potential autocorrelation, we used linear mixed effects models that included random effect of square identity. Firstly, we run the models with SB_{stand}

and SB_{stump} as response variables and density of standards, density of sprouting stumps and density of all stumps as explanatory variables. Insignificant variables ($p > 0.05$) were excluded from the models. The R formula of the starting model was:

Sprout biomass ~ Standard density + Sprouting stumps density + (1|Subsquare ID),

where Sprout biomass was either total biomass of sprouts in subplot (SB_{stand}) or mean biomass of sprouts per stump (SB_{stump}) and Standard density and Sprouting stump density were explanatory variables. In Hády, we also run the analysis separately for the four most common species: *Quercus*, *Tilia*, *Carpinus* and *Acer*. The sum of sprout biomass from each species in subplots was used as a response variable, and density of standards and density of sprouting stumps were used as explanatory variables. To test the interspecific differences in SB_{stump}, we used an ANOVA with a Tukey's honest significance post hoc test. The "lme4" (Bates *et al.*, 2015) and "lmerTest" package (Kuznetsova, Brockhoff and Christensen, 2017) were used to analyze the results, and the "visreg" package (Breheny and Burchett, 2013) was used to visualise the results.

4.4. Differential roles of seed and sprout regeneration in forest diversity and productivity after disturbance

4.4.1. Data collection

In 2020–2021, 11 complete growing seasons after harvesting, all stumps of the cut trees were checked for live sprouts. For stumps with sprouts, the DBH of three thickest sprouts on each resprouting stump was measured. This method proved to be an accurate indicator for estimating the total sprout AGB of individual sprouters as well as the populations of sprouters (Matula *et al.*, 2015; Šrámek *et al.*, 2020). Moreover, all individuals of seed regeneration with DBH ≥ 5 cm and all new sprouting stumps (with pre-logging DBH < 7 cm) with at least one sprout with

DBH ≥ 5 cm were also measured, identified to the species level, and their positions were mapped using the Field-Map technology. For new trees, we set the DBH threshold at 5 cm because it was the minimum size of individuals reaching the newly established, dense canopy typical of this stage of forest development. Individuals with DBH less than 5 cm were much less abundant and suppressed under the dense crowns and were not expected to significantly contribute to the newly formed canopy.

4.4.2. Data analysis

4.4.2.1. AGB estimations

To assess productivity and abundance of regrowth of sprout and seed origin, we estimated AGB for each sapling and resprouting tree. Because resprouting trees (stumps) were multi-stemmed while saplings of seed origin were mostly single-stemmed, we used different methods for the AGB estimation. AGB of sprouts from each resprouting tree was estimated using allometric equations previously developed for this purpose at the same study sites (Matula *et al*., 2015). As a predictor variable in allometric equations, we used mean DBH of the three thickest sprouts per stump, which has previously proved to be an accurate predictor of total AGB of sprouts per stump (Matula *et al*., 2015; Šrámek *et al*., 2020, 2023). To estimate AGB of individuals of seed origin, we used species-specific allometric equations from (Forrester *et al.*, 2017) (2017), using DBH of each individual as predictor variable. In total, AGB (stem and branches) was estimated for 1496 resprouting trees of 16 species in Hády and 1188 resprouting trees of 9 species in Soběšice, and for 502 seed-originated individuals of 14 species in Hády and 118 seed-originated individuals of 8 species in Soběšice (Table 6.). To account for spatial variability and irregularities in the distribution of residual trees, each of the 50 x 50 meter subsquares were uniformly divided into four smaller subplots (20 x 20 m) with a five-meter belt around each subplot to ensure spatial separation. For each subplot, we determined several variables: the density of residual trees, the density of sprouting stumps, and the density of seed regeneration.

Additionally, we calculated the total AGB of sprouts and the total AGB of seed regeneration. This was done by summing the AGBs of sprouts and seed origin individuals, respectively.

To find out how residual trees affect sprout and seed regeneration, we modelled AGB and density of sprouts and AGB and density of seed regeneration as a function of density of residual trees. To test the effect of sprout regeneration on seed regeneration, we also created models with either AGB or density or occurrence of seed regeneration as response variable and AGB of sprout regeneration as explanatory variable. We also ran another set of models with either AGB or density or occurrence of sprouts used as a response variable and AGB of seed regeneration as explanatory variable. We also used the density of stumps with live sprouts as a predictor for sprout AGB, because it was previously shown to have a positive effect on total sprout AGB (Mejstřík, Šrámek and Matula, 2022). Since plots have different environmental conditions, cutting history, structure and species composition, we conducted all analysis separately for each plot. To account for autocorrelation among subplots nested in subsquares, we used mixed-effects models in which the explanatory variables were defined as fixed-effect variables and subsquare identity as random effect with varying intercepts. Linear mixed-effects models were utilized for testing the effects on AGB of sprouts and AGB of seed origin individuals (i.e. response variables). We used generalized mixed-effects models with Poisson error distribution for testing the effects on density of regeneration of sprout and seed origin. To model the occurrence of sprout and seed regeneration, we used generalized mixed-effect models with binomial error distribution, in which either sprout or seed regeneration occurrence in subsquare (1 - present/0 - absent) was modelled as a function of the density of residual trees and sprout AGB. Because of multicollinearity detected in the models including both density of residual trees and AGB of sprouts and density of residual trees and AGB of seed regeneration, we did not use these variables together in one model but created separate models with each of the explanatory and response variables. The explanatory variables in the models with occurrence and density were standardized to zero mean and unit variance to make their model estimates directly comparable. All analyses were performed in R software (R Core Team, 2022) using the “lme4” package (Bates *et al.*, 2015) for linear mixed-effects models.

4.4.2.2. Diversity

We calculated the number of species (richness) and Shannon H’ index (diversity) for all woody regeneration together (total richness) and separately for sprout regeneration and seed regeneration in each subplot. Shannon H’ index was calculated based on the number of individuals of each woody species using the ‘diversity’ function of the ‘vegan’ package (Oksanen *et al*. 2016).

We also calculated beta diversity, which is a measure of the variability in species composition among sampling units for a given area. Beta diversity was computed for each regeneration strategy as well as for the original pre-logging stand by calculating the average distance from each individual subplot to the group centroid defined in the principal coordinate space of the dissimilarity measure (Anderson, 2006; Anderson, Ellingsen and McArdle, 2006). The calculation was performed with the Bray-Curtis index as the measure of dissimilarity using the ‘betadisper’ function of the ‘vegan’ package (Oksanen *et al*. 2016). To test for differences between different strategies of regeneration, a pairwise permutation test provided by ‘betadisper’ was performed.

To explore how residual trees and regeneration abundance affect the diversity of each of the regeneration strategies, we modelled richness and diversity as a function of the density of residual trees, sprout AGB (for seed regeneration only), and seed regeneration AGB (for sprout regeneration only). For diversity as the response variable, we used linear mixed-effect models. For richness, generalized mixed-effect models with Poisson error distribution were performed. Subsquare identity was used as random intercept effect in the models. Because of multicollinearity, we ran models separately for each combination of explanatory and response variables (i.e. only models with one fixed-effect variable). We also calculated the ratio of seed-origin richness to total richness and sprout richness to total richness to explore the trend of relative contribution of each regeneration strategy to total regeneration with changing density of residual trees. To demonstrate this relationship, we used locally estimated scatterplot smoothing (LOESS).

4.4.2.3. Species composition and beta diversity

To test for differences between species composition of original stand and regrowth of sprout and seed origin, we used non-metric multidimensional scaling ordination (NMDS) with the Bray-Curtis index as the measure of dissimilarity using the ‘vegan’ package (Oksanen *et al.*, 2016). To estimated difference in the species composition of different regeneration type as well as to compare it to original species composition before tree cutting, we fitted seed origin (as a categorical variable) into the results of NMDS using the function “ennvfit”, which also calculated statistical significant using permutation test. To compare species composition between regeneration categories, we used permutational multivariate analysis of variance using the Bray-Curtis index (function “adonis2). Multivariate homogeneity of group dispersions as measure of beta diversity (Anderson, Ellingsen and McArdle, 2006; Anderson-Teixeira *et al.*, 2013) was calculated for each of the regrowth strategy and original stand and the difference between the groups were tested using Tukey’s HSD post-hoc test.

4.5. Growth response of vegetative sprouts, generative regeneration and standards to climate and drought in oak dominated traditional coppice forests

4.5.1. Data collection

After the growing season in 2021 in Hády and 2022 in Soběšice, twelve years after the harvesting, the stumps of the cut trees were inspected for live sprouts and all seed-regenerated individuals with a DBH ≥ 5 cm were measured, identified by species, and their exact locations were mapped using Field-Map technology. Furthermore, we randomly selected residual mature trees (standards) and trees from both vegetative and generative regeneration for the most common species on both plots and collected increment cores. The tree species were sessile oak (*Quercus petraea* (Matt.) Liebl.), small-leaved lime (*Tilia cordata* Mill.), European hornbeam (*Carpinus betulus* L.). For each selected standard and individual of generative regeneration, one increment core was extracted, while three cores were taken from the three thickest sprouts for each selected sprouting stump. Given that all standing trees, resprouting stumps, and generative regeneration were fully mapped, it was possible to select individuals regularly distributed across the entire 4-hectare study plots. Sampled individuals were chosen in subplots with and without standing residual trees to create variability in light conditions and forest structure. On both study plots, we did not find a sufficient number of generative sessile oak individuals within the study plot to core, so we additionally cored randomly selected generative oaks in nearby forest stands with similar DBH to the vegetative sprouts. Standards were cored at a height of 1.3 meters using a Pressler increment borer. To extract samples from sprouts and seed regeneration, which often have small diameters and could be damaged by a Pressler increment borer, we used the Trephor tool. The Trephor is chisel-shaped for fast recovery of 2 mm diameter microcores. The cutting tube is inserted into the wood using a hammer, requiring no other accessories. Its simple technical characteristics allow high-quality samples to be collected from both softwood and hardwood species with minimal damage to the sampled trees (Rossi, Anfodillo and Menardi, 2006).

The cores were first left to get dry, glued on wooden boards and sanded with sandpaper of a progressively finer grain until the tree rings became clearly visible. The tree-ring widths (TRW) were then measured to the nearest 0.01 mm using the Lintab™ sliding-stage measuring device and TsapWin software (RINNTECH, http://www.rinntech.com). Cross-dating was verified using the CDendro 7.1 software (Larsson, 2003). To ensure the accuracy of the dating process, any cores that could not be confidently cross-dated were excluded from further analysis to minimize potential errors. In total, we evaluated 12 sprouting stumps, 15 individuals of generative regeneration, and 19 standards of sessile oak in Hády, along with 16 sprouting stumps, 14 saplings of seed origin, and 15 standards of sessile oak in Soběšice. Additionally, in Hády, we analyzed 13 sprouting stumps and 17 seed regeneration individuals of European hornbeam, as well as 14 sprouting stumps and 15 individuals of seed origin of small-leaved lime.

Climate data was obtained from the nearest weather station in Brno, Žabovřesky (accessible online at https://www.chmi.cz/). We utilized data on average daily temperatures (°C), average daily rainfall (mm) and average daily relative air humidity (%).

4.5.2. Data analyses

To compare the growth of standards and both types of regeneration for the three most common tree species in Central European coppices (Matula *et al.*, 2012), bar plots were constructed to visualize mean annual growth (TRW) across different years from 2013 to 2021. Error bars indicate the standard error for each year, providing a measure of variability within the growth data.

To analyze the effects of climatic variables on the tree-ring widths (TRW) of standard trees, generative regeneration, and vegetative regeneration, we calculated the average temperature, total rainfall and average relative air humidity for each month, year, as well as for the growing season (from May to August) for the study period (2013 - 2021). For TRW of vegetative regeneration, we also calculated mean growth, as an average of three measured sprouts per stump.

To find out how climatic variables affect radial growth of each regeneration type and standards, we used linear mixed-effect models with TRW as a response variable and annual, seasonal and monthly averages of temperature, relative air humidity and total rainfall as explanatory variables. The random effect of tree ID was included to account for the repeated measures on the same trees, capturing the within-tree correlation. We ran a set of models separately for each species and study plot. Given the high correlation among many climatic variables, especially between relative humidity and precipitation, each model included two parameters, carefully avoiding the inclusion of highly correlated explanatory variables within the same model to prevent multicollinearity. Additionally, marginal (R^2m) and conditional (R^2c) coefficients of determination were calculated for each model to measure the variance explained by the fixed effects, by the combination of fixed and random effects, and by the random effects, respectively (Nakagawa, Johnson and Schielzeth, 2017).

To refine the models, we used a backward variable elimination process, ultimately selecting the final models based on the lowest p-values and Akaike's Information Criterion (AIC).

For the final analysis, we selected models with mean annual temperature and total precipitation in June (month with the fastest tree growth) and models with mean annual temperature and relative air humidity in June, which fitted best the data (i.e. had lowest AICs). To address the non-normality of the growth data, we applied a base-10 logarithmic transformation. The R formula of the final model for each species was:

Log (TRW) ~ (Temperature + Precipitation/Humidity) * Regeneration type + (1 | Tree_ID),

where TRW represents either the annual increment of standards and generative individuals or the average increment of 3 thickest sprouts per stump, temperature and precipitation or relative air humidity represent temperature and precipitation or humidity, respectively, for selected periods (month, year, growing season, used separately due to correlation), regeneration type stands for the origin of the trees (vegetative/generative regeneration, standards).

To assess the differences between standards and both types of regeneration in response to climatic variables, we utilized a linear mixed-effects model followed by pairwise comparisons of estimated marginal trends. Specifically, we applied the emtrends function from the “emmeans” package (Lenth *et al*., 2024) to our model, which calculated the differences between regeneration types with respect to June precipitation, June relative air humidity and mean annual temperature. The same analytical approach was used to compare the growth of different species, ensuring consistency in the evaluation of species-specific responses to environmental factors. This analysis provided a rigorous statistical framework, employing the Kenward-Roger method for adjusting degrees of freedom, crucial for obtaining reliable and accurate inferences in mixed-effects modelling contexts.

All analyses were performed in R software (R Core Team, 2022) using the “lme4” package (Bates *et al.*, 2015) for linear mixed-effects models. The “sjPlot” package (Lüdecke *et al*., 2024) and “ggplot2” package (Wickham, 2009) were utilized to visualize the results.

5. Results

5.1. The effects of stand density, standards and species composition on biomass production in traditional coppices

Mean SB_{stand} after 7 growing seasons was 636.84 ± 33.9 kg ha^{-1} in Hády and 754.05 ± 54.6 kg ha^{-1} in Soběšice. Mean SB_{stump} was 1564.6 ± 33.9 g in Hády and 1830.18 ± 45.5 g in Soběšice and differ significantly between all 4 studied species ($p < 0.001$; Table 2). *Tilia* had the greatest mean SB_{stump} while *Acer* had the lowest (Table 2).

Also, in Hády we found a significant shift in tree species composition after tree harvesting (Table 2). While the relative abundance of *Tilia*, *Acer* and *Carpinus* increased significantly, it declined steeply in *Quercus* (Table 2). *Quercus* was clearly the most dominant tree species before the harvest, but its relative abundance after the harvest did not significantly differ from *Carpinus* and *Tilia*.

Table 2. The mean sprout biomass per stump for 4 studied species in Hády and Quercus in Soběšice (S), the relative abundance of studied species in Hády before (calculated from basal area of trees before the harvest) and 7 years after (calculated from biomass of sprouts) the tree harvesting.

Species	Biomass per stump (g)		Relative abundance before harvest (%)	Relative abundance after harvest (%)
	Mean (±SE)	Max	Mean (±SE)	Mean (±SE)
Acer	939.8 (± 59.4)a	3262.9	7.5 (± 1.1)a	13.3 ± (1.6)a
Carpinus	1420.0 (± 39.8)b	4703.0	18.2 (± 2.1)b	37.3 (± 3.2)b
Quercus	1784.9 (±70.8)c	8110.7	73.5 (± 2.1)c	41.9 ± (2.8)b
Tilia	2115.9 (±74.2)d	4815.9	10.6 (± 1.4)a	30.6 (± 4.3)b
Quercus (S)	1814.1 (± 47.1)	12487.0		

Letters signify differences among species means (α=0.05) based on Tukey's HSD test.

5.1.1. Effect of standards and sprouting stumps density on sprout biomass on stand level

We found significant effect of standards and density of sprouting stumps on both in Hády and Soběšice (Table 3). Increasing density of standards reduced SB_{stand} both in Hády (Table 3; Figure 3a) and Soběšice (Table 3; Figure 3b). With each standard, SB_{stand} decreased by 1040 ± 266 g in Hády and 2623 ± 522 g in Soběšice.

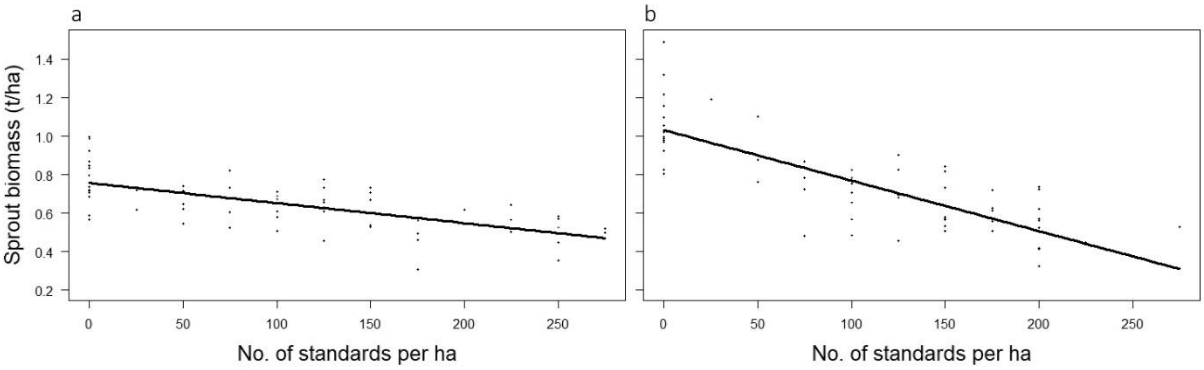

*Figure 3. Sprout biomass on stand level in **a** Hády and **b** Soběšice in relation to density of standards. Points represent observations, and the black lines represent partial effects of standard density obtained using linear mixed effect models with density of sprouting stumps set at the median value.*

Density of sprouting stumps had strong positive effect on SB_{stand} both in Hády (Table 3; Figure 4a) and in Soběšice (Table 3; Figure 4b). SB_{stand} linearly increased with each sprouting stump by (1318 ± 134 g and 1361 ± 190 g, respectively) and we observed no decline or levelling of total biomass production even in the highest densities (Figure 4).

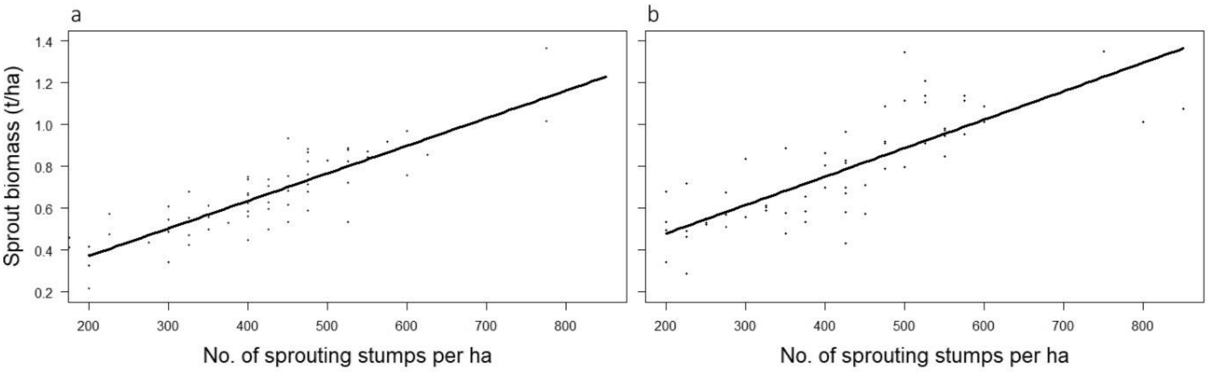

*Figure. 4. Sprout biomass on stand level in **a** Hády and **b** Soběšice in relation to density of sprouting stumps. Points represent observations, and the black lines represent partial effects of density of sprouting stumps obtained using linear mixed effect models with standards density at the median value.*

Table 3: Models of the effects of standards and sprouting stumps on sprout biomass on stand level (SBstand) and stump level (SBstump) in Hády and Soběšice, based on linear mixed-effects models.

Dependent variable	Explanatory variable	Hády		Soběšice	
		F	p	F	p
Sprout biomass$_{stand}$	Standard density	**15.35**	**0.0003**	**25.25**	**<0.0001**
	Sprouting stump density	**96.62**	**<0.0001**	**51.30**	**<0.0001**
		$R^2_m = 0.61$		**$R^2_m = 0.55$**	
Sprout biomass$_{stump}$	Standard density	**11.96**	**0.001**	**27.61**	**<0.0001**
	Sprouting stump density	3.58	0.06	1.65	0.21
		$R^2_m = 0.20$		**$R^2_m = 0.40$**	

Highlighted values indicate significant effects ($\alpha < 0.05$). R^2_m is marginal R^2 for the final models with significant variables.

5.1.2. Effect of standards and sprouting stumps density on sprout biomass on stump level

There was significant negative linear relationship between density of standards and SB$_{stump}$ in both Hády (Table 3; Figure 5a) and Soběšice (Table 3; Figure 5b). However, density of sprout ing stumps on both plots did not significantly affect SB$_{stump}$ (Table 3).

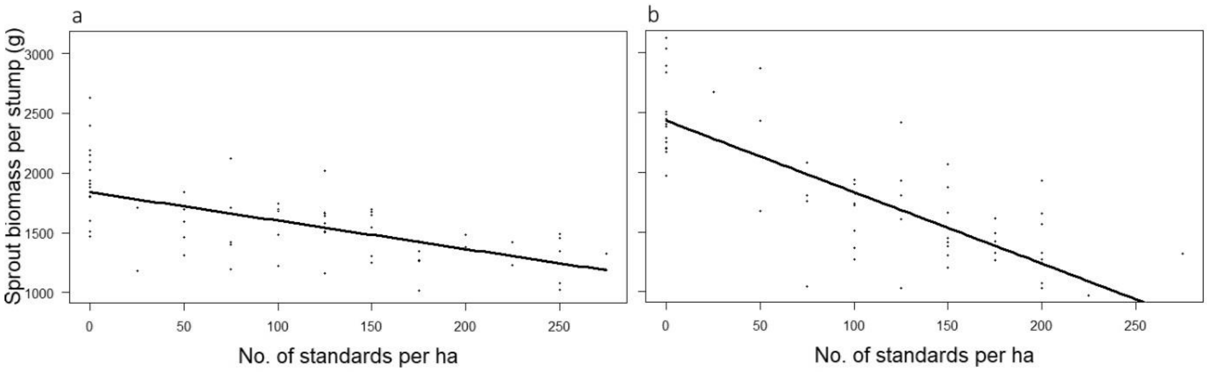

*Figure 5. Mean sprout biomass per stump in **a** Hády and **b** Soběšice in relation to density of standards.*

5.1.3. Effect of standards and sprouting stumps on sprout biomass – interspecific differences

Density of standards negatively affected SB_{stump} of *Carpinus* and *Quercus* in Hády and even more in Soběšice (Table 4). However, *Acer* and *Tilia* were not significantly affected by standards density (Table 4; Figure 6).

Table 4. Effect of standards on sprout biomass per stump (SB_{stump}) of 4 studied species in Hády and Quercus in Soběšice (S), based on linear mixed-effects models. The values are regression coefficients (Coef.) and their associated standard errors (SE), marginal and conditional R2, p-values (p) and F-values (F).

Species	Effect of standards on SB_{stump}					
	Coef.	SE	R2m	R2c	p	F
Acer	-0.957	1.048	0.022	0.634	0.370	0.835
Carpinus	-3.377	0.874	0.288	0.670	<0.001	14.932
Quercus	-4.283	1.353	0.169	0.305	0.004	10.025
Tilia	0.180	1.780	<0.001	0.351	0.920	0.010
Quercus (S)	-5.894	1.176	0.377	0.702	<0.001	25.110

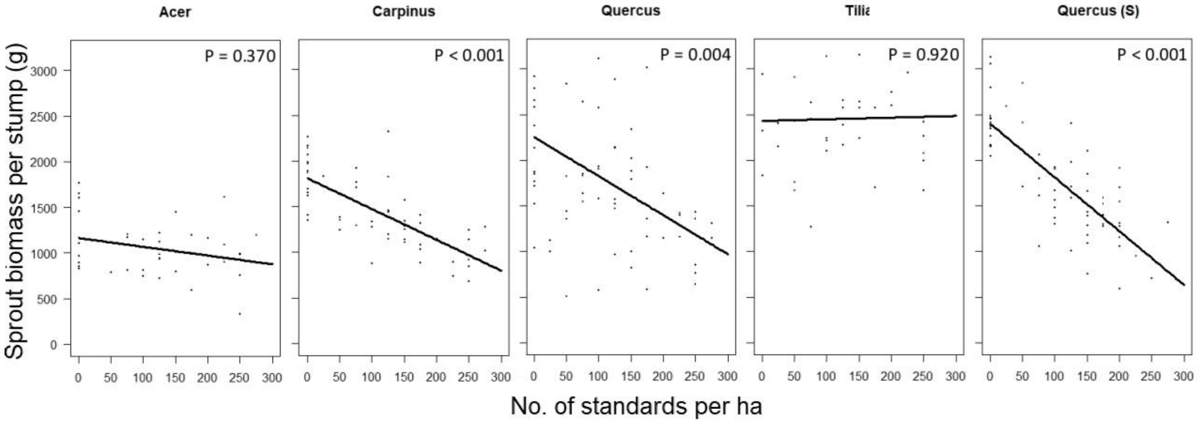

*Figure 6. Mean SB_{stump} 7 years after the harvest for 4 studied species in **a** Hády and for Quercus in **b** Soběšice (S) in relation to density of standards.*

There was no significant relationship between density of sprouting stumps and SB_{stump} for any of studied species ($p > 0.05$).

5.2. Differential roles of seed and sprout regeneration in forest diversity and productivity after disturbance

5.2.1. Above-ground biomass

Sprouts represented the predominant proportion of the total above-ground biomass (AGB) in natural tree regrowth, with an average of 97.1% in Hády and 98.6% in Soběšice. Seed-origin regeneration was much less abundant, contributing only 2.9% to the total AGB in Hády and 1.4% in Soběšice (Table 5).

Table 5: Mean (±SE) total above-ground biomass (AGB), the AGB of sprout and seed regeneration, and proportion of seed-origin AGB 11 years after logging. The values are shown for all plots as well as separately for plots without and with residual trees.

	Hády	Soběšice
Total AGB (t ha-1)	4.53 (±0.34)	3.60 (±0.25)
Total AGB (t ha-1) – plots without residual trees	7.11 (±0.58)	6.15 (±0.34)
Total AGB (t ha-1) – plots with residual trees	3.74 (±0.33)	2.68 (±0.18)
Sprout AGB (t ha-1)	4.35 (±0.32)	3.55 (±0.25)
Sprout AGB (t ha-1) – plots without residual trees	6.54 (±0.60)	6.07 (±0.34)
Sprout AGB (t ha-1) – plots with residual trees	3.68 (±0.32)	2.65 (±0.18)
Seed-origin AGB (t ha-1)	0.17 (±0.04)	0.05 (±0.01)
Seed-origin AGB (t ha-1) – plots without residual trees	0.56 (±0.12)	0.08 (±0.02)
Seed-origin AGB (t ha-1) – plots with residual trees	0.06 (±0.02)	0.03 (±0.01)
Proportion of seed-origin AGB (%)	2.92 (±0.77)	1.42 (±0.35)
Proportion of seed-origin AGB (%) – plots without residual trees	9.16 (±2.65)	1.28 (±0.21)
Proportion of seed-origin AGB (%) – plots with residual trees	1.00 (±0.23)	1.48 (±0.46)

Sprout AGB on both plots decreased as the density of residual trees increased (Hády: t = -5.28, P < 0.001; Soběšice: t = -5.57, P < 0.001; Figure 7). The density of residual trees affected negatively AGB of seed regeneration in Hády (t = -4.68, P < 0.001) but did not influence the AGB of seed regeneration in Soběšice significantly (t = -1.39, P = 0.135; Figure 7).

Sprouts were present in all subplots, while seed regeneration was absent in many subplots (41% and 47% of all subplots in Hády and Soběšice, respectively). The presence of seed regeneration was affected negatively by the density of residual trees (P < 0.001; Figure 8) but positively by increasing sprout AGB ($P < 0.010$, Figure 8). The density of seed regeneration declined with increasing density of residual trees in Hády ($P < 0.001$, Figure 8), but not in Soběšice ($P = 0.080$; Figure 8). Density of seed regeneration was positively affected by sprout AGB, but the effect was significant only in Hády ($P = 0.044$; Figure 8).

Sprout AGB increased with increasing density of sprouting stumps (Hády: regression coefficient = 0.039±0.003, $t = 11.48$, $P < 0.001$; Soběšice: regression coefficient = 0.064±0.011, $t = 5.84$, $P < 0.001$) but was not affected by the AGB or density of seed regeneration ($P > 0.059$).

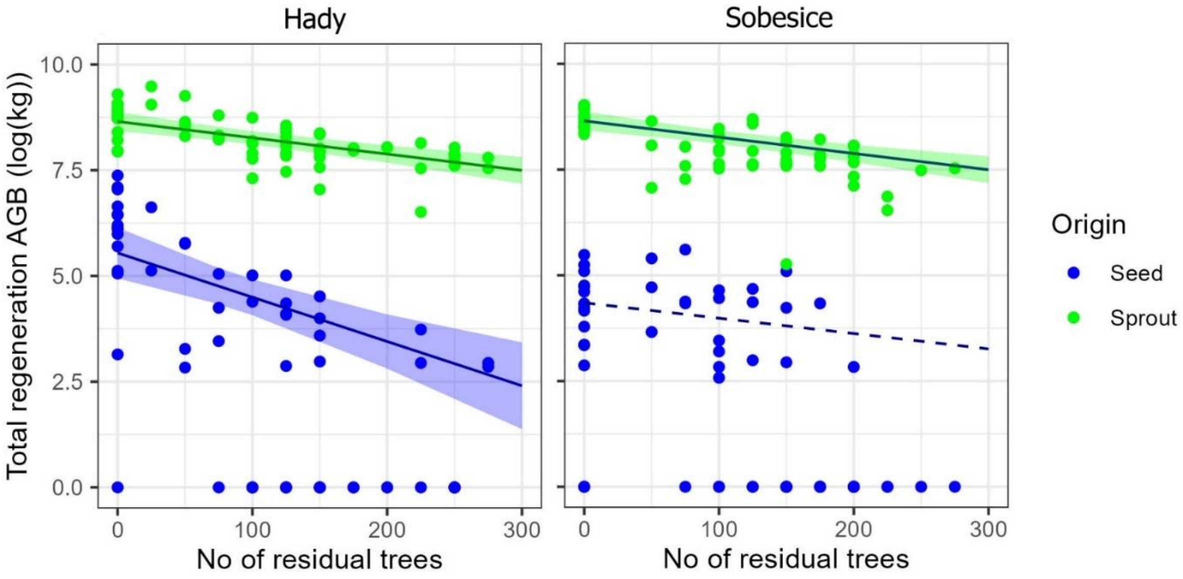

Figure 7: Total above-ground biomass (AGB) of sprouts and seed-origin regrowth 11 years after logging in Hády and Soběšice in relation to the density of residual trees. Points represent observations, solid lines represent fitted models with $P < 0.05$ while dashed lines indicate fitted models with $P > 0.05$. 95% confidence intervals are shown for models with $P < 0.05$.

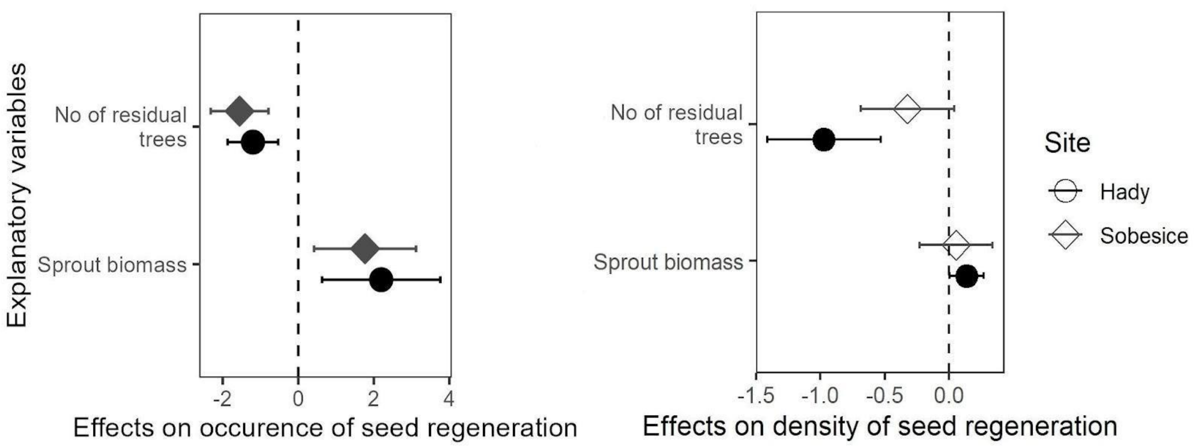

Figure 8: Model estimates (points) and confidence intervals (lines) of the effects of density of residual trees and sprout biomass on presence and density of seed-origin regrowth11 years after logging. Filled symbols indicate model estimates significantly different from zero.

5.2.2. Woody plant diversity

In total, we recorded 19 and 11 species of natural tree regeneration in Hády and in Soběšice, respectively. Sprouts accounted for 16 and 10 species, while 14 and 8 species originated from seed, in Hády and Soběšice, respectively (Table 6). The diversity and richness of sprout regeneration were higher than the diversity and richness of seed regeneration (P < 0.001; Table 7). The total diversity and richness of all regeneration were higher than that of the original pre-logging stand (P < 0.05; Table 7).

Table 6: Number of individuals of sprout and seed regeneration from 64 subplots in experimental stands Hády and Soběšice.

Tree species	Hády		Soběšice	
	seed origin	sprout origin	seed origin	sprout origin
Birch (*Betula pendula* Roth.)	82			
Black locust (*Robinia pseudoacacia* L.)			20	2
Blackthorn (*Prunus spinosa* L.)			11	5
Common hazel (*Corylus avellana* L.)		117		
Cornelian cherry (*Cornus mas* L.)		55		
European ash (*Fraxinus excelsior* L.)	17	2		3
European aspen (*Populus tremula* L.)	13		1	
European beech (*Fagus sylvatica* L.)		1		
European crab apple (*Malus sylvestris* Mill.)	2	1		
European hornbeam (*Carpinus betulus* L.)	82	458	27	40
European pear (*Pyrus communis* L.)		1		
European white elm (*Ulmus laevis* Pall.)	18	9		
Field maple (*Acer campestre* L.)	22	141	18	20
Hawthorn (*Crataegus* sp.)		1		
Norway maple (*Acer platanoides* L.)	43	9		1
Sessile oak (*Quercus petraea* (Matt.) Liebl.)	8	362	15	1017
Small-leaved lime (*Tilia cordata* Mill.)	45	325	2	94
Sweet Cherry (*Prunus avium* (L.) L.)	32	2	24	6
Sycamore maple (*Acer pseudoplatanus* L.)	7	2		
Wild Service Tree (*Sorbus torminalis* (L.) Crantz)	2	10		
Willow (*Salix caprea* L.)	129			

Table 7: Mean (±SE) Shannon H‘ diversity index and species richness (SR) of the original pre-logging stand, sprouts, seed regeneration, and both types of regeneration together 11 years after logging. The values are shown for all subplots and separately for subplots without and with residual trees.

	Hády	Soběšice
Shannon $H_{original}$	1.16 (±0.03)	0.74 (±0.02)
Shannon H_{sprout} - all subplots	1.15 (±0.03)	0.77 (±0.02)
Shannon H_{sprout} - subplots without residual trees	1.30 (±0.08)	0.89 (±0.04)
Shannon H_{sprout} - subplots with residual trees	1.10 (±0.03)	0.73 (±0.03)
Shannon H_{seed} - all subplots	0.69 (±0.09)	0.51 (±0.06)
Shannon H_{seed} - subplots without residual trees	1.14 (±0.17)	0.60 (±0.10)
Shannon H_{seed} - subplots with residual trees	0.53 (±0.08)	0.45 (±0.08)
Shannon $H_{sprout+seed}$ - all subplots	1.29 (±0.04)	0.87 (±0.03)
Shannon $H_{sprout+seed}$ - subplots without residual trees	1.56 (±0.09)	1.04 (±0.06)
Shannon $H_{sprout+seed}$ - subplots with residual trees	1.20 (±0.04)	0.80 (±0.04)
$SR_{original}$	4.59 (±0.13)	1.89 (±0.11)
SR_{sprout} - all subplots	4.70 (±0.18)	2.16 (±0.12)
SR_{sprout} - subplots without residual trees	5.13 (±0.38)	2.71 (±0.24)
SR_{sprout} - subplots with residual trees	4.57 (±0.21)	1.96 (±0.12)
SR_{seed} - all subplots	2.08 (±0.32)	1.06 (±0.16)
SR_{seed} - subplots without residual trees	5.07 (±0.67)	1.71 (±0.32)
SR_{seed} - subplots with residual trees	1.16 (±0.25)	0.83 (±0.17)
$SR_{sprout+seed}$ - all subplots	5.88 (±0.27)	2.70 (±0.17)
$SR_{sprout+seed}$ - subplots without residual trees	8.27 (±0.41)	3.59 (±0.34)
$SR_{sprout+seed}$ - subplots with residual trees	5.14 (±0.25)	2.38 (±0.17)

The diversity of sprouts was not significantly affected by residual trees ($P > 0.060$), while the diversity of seed regeneration declined steeply with increasing density of residual trees ($P < 0.001$; Figure 9). Sprout AGB had a positive effect on diversity of seed regeneration ($P < 0.001$; Figure 9).

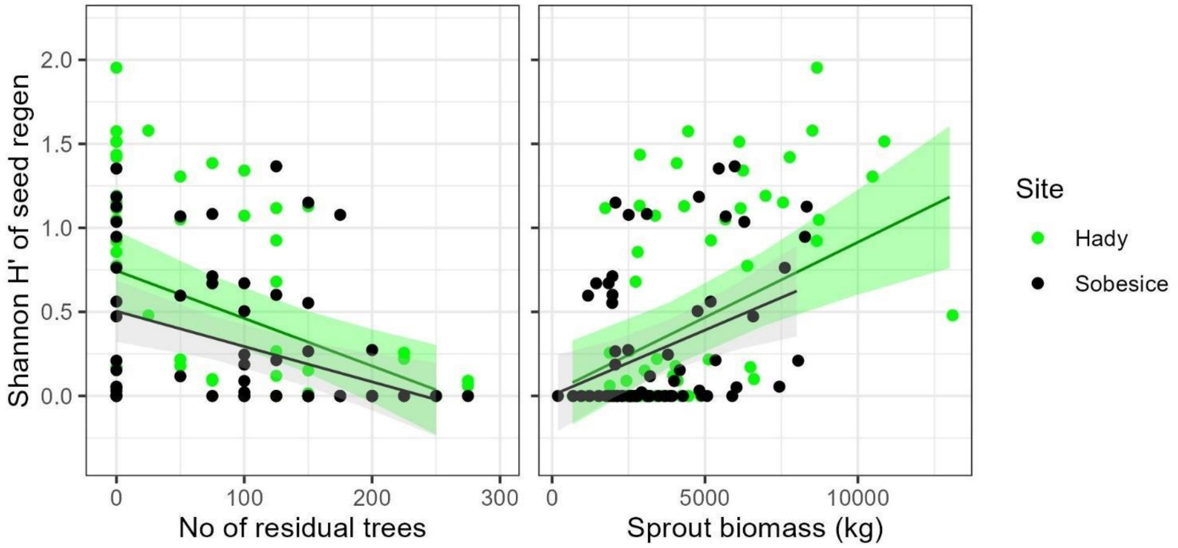

Figure 9: Mean Shannon H‘ diversity index of seed regeneration 11 years after logging in relation to the density of residual trees and sprout biomass. Points represent subplots, lines represent fitted linear mixed effect models ($P < 0.05$) with 95% confidence intervals.

Sprout regeneration accounted for the majority of total richness, and its proportion even increased with higher density of residual trees (Figure 10). The proportion of seed regeneration in total richness was approximately 50% in clearcuts but decreased significantly to near-zero values with increasing density of residual trees (Figure 10). The diversity of seed regeneration increased with increasing sprout AGB ($P < 0.006$; Figure 9). The diversity of sprouts was not affected by seed regeneration AGB ($P > 0.250$).

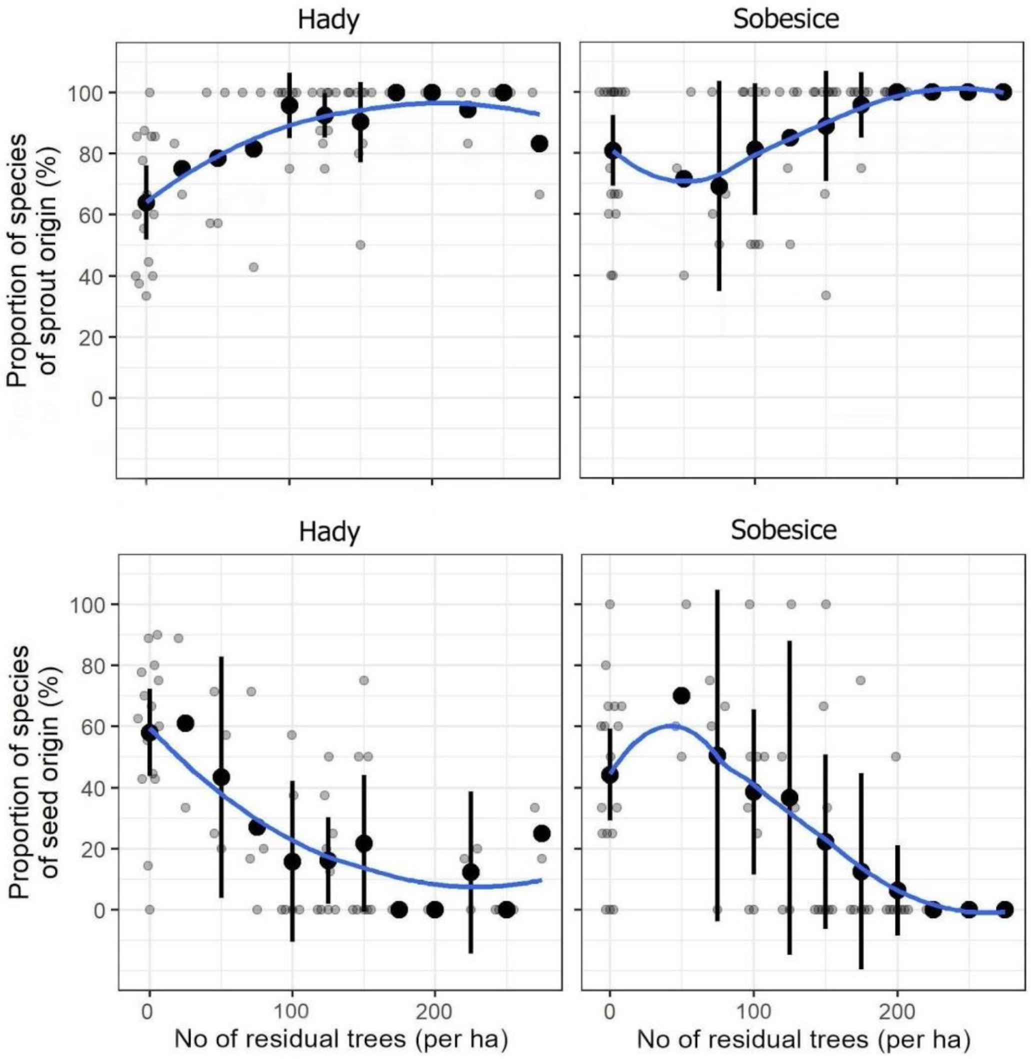

Figure 10: Proportion of species richness of sprouts and seed regrowth 11 years after logging in relation to the density of residual trees in Hády and Soběšice. Blue line represents the fitted LOESS model, dots indicate means for a given number of residual trees and the vertical lines represent 95% confidence intervals (omitted for means based on ≤ 2 data points).

Both sprout and seed regeneration had higher beta diversity than the original stand (P<0.001), but seed regeneration had significantly higher beta diversity than sprout regeneration (P<0.001; Figure 11).

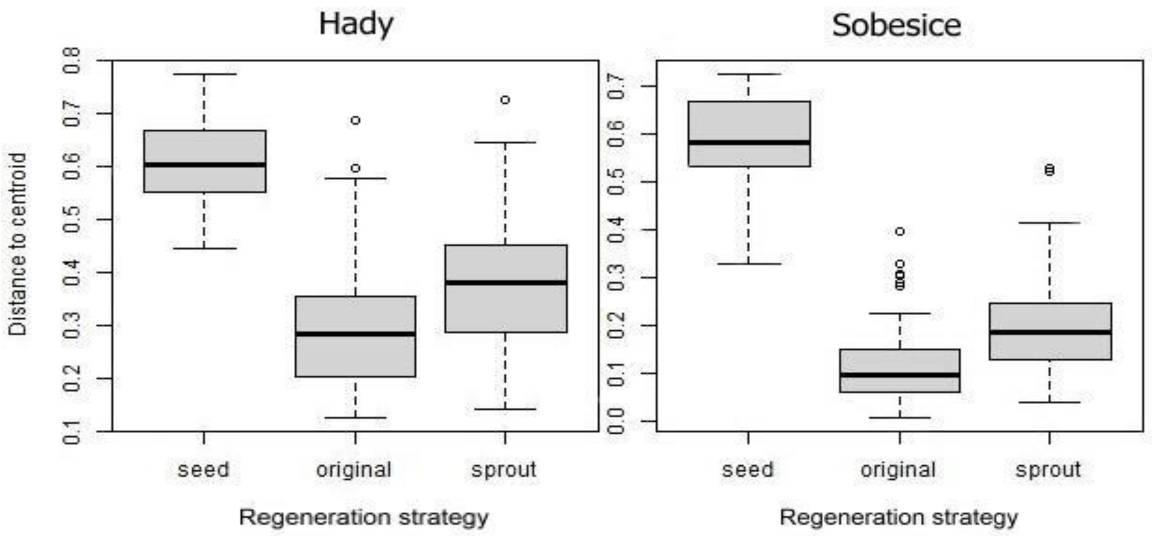

Figure 11: Beta diversity of tree community expressed as multivariate dispersion based on Bray-Curtis dissimilarities within the original pre-logging stand, sprout, and seed-origin regrowth 11 years after logging in Hády and Soběšice.

5.2.3. Species composition

The species composition of sprout and seed regeneration differed significantly (Hády R^2 = 0.22, $P < 0.001$; Soběšice: R^2= 0.38, $P < 0.001$), and both differed from the species composition of original pre-logging stand ($P < 0.001$; Figure 12). The difference between the composition of sprout regeneration and the original stand was smaller (Hády: R^2=0.18, $P < 0.001$; Soběšice: R^2=0.20, $P < 0.001$) than the difference between the composition of seed regeneration and the original stand (Hády: R^2=0.28, $P < 0.001$; Soběšice: R^2=0.42, $P < 0.001$; Figure 12).

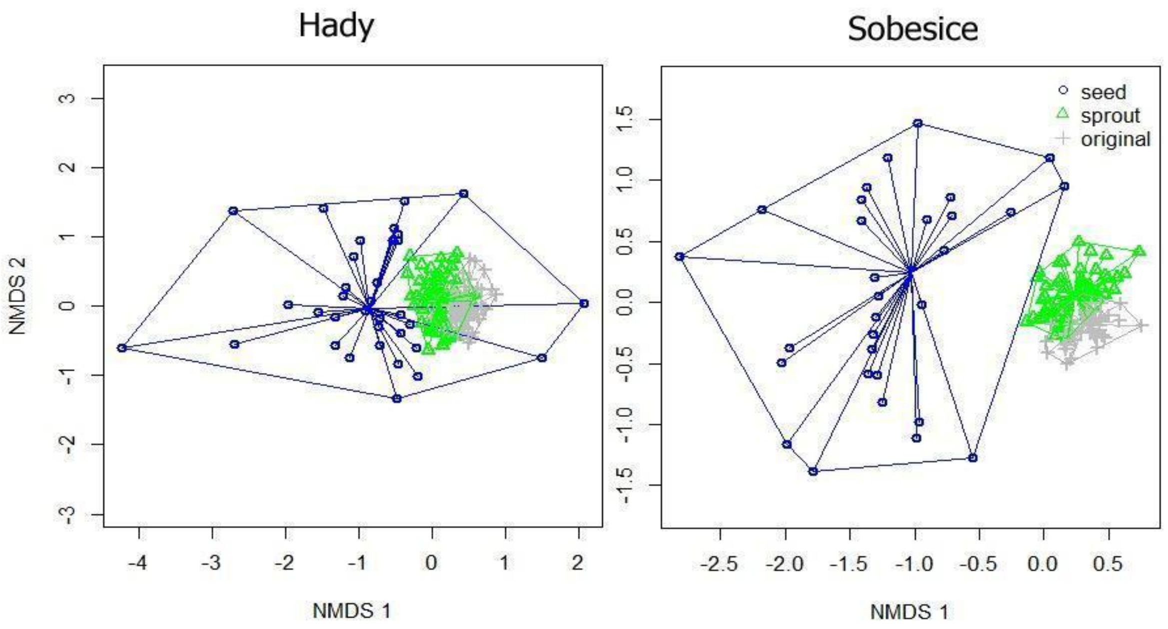

Figure 12: Nonmetric multidimensional scaling of the species composition of the original pre-logging stand, sprout, and seed-origin regrowth 11 years after logging in Hády and Soběšice. Points represent subplots for each type of regrowth and the point with they connect represent their centroids. The lines denote the boundaries of clusters of plots belonging to the same treatment.

5.3. Growth response of vegetative sprouts, generative regeneration and standards to climate and drought in oak dominated traditional coppice forests

Sprouts had, on average, the fastest growth in both Hády and Soběšice, followed by standards and seed regeneration (Figure 13), but the growth varied differentially among the plant groups and species with temperatures, precipitation and relative air humidity. *Quercus*, the predominant species at our study sites, demonstrated significantly faster growth of sprouts compared to seed regeneration (Table 8,9, Figure 13). In contrast, for *Carpinus* and *Tilia*, growth rates between sprouts and trees of seed origin showed no significant differences (Table 8,9, Figure 13). The model incorporating yearly mean temperatures and relative air humidity in June was the best one (i.e. with lowest AIC) in Hady, while in Soběšice, model with precipitation in June and mean temperature during season performed the best (Table 10).

Table 8: Estimated Mean Growth (± SE) of trees from different origin for 3 most common tree species in Hády and Quercus in Soběšice. The table presents the mean growth (in mm), degrees of freedom (df), and 95% confidence intervals (CI).

Plot	Species	Type	Mean Growth (mm)	df	CI
Hady	*Quercus*	Gen	1.09 (±0.12)	48.2	0.86 – 1.33
	Quercus	Veg	2.1 (±0.12)	48.3	1.87 – 2.34
	Quercus	Standard	1.71 (±0.12)	48.2	1.47 – 1.94
	Tilia	Gen	2.07 (±0.16)	31.2	1.75 – 2.40
	Tilia	Veg	2.2 (±0.17)	31.1	1.86 – 2.54
	Carpinus	Gen	1.68 (±0.14)	32.1	1.41 – 1.95
	Carpinus	Veg	1.86 (±0.15)	32.1	1.55 – 2.18
Sobesice	*Quercus*	Gen	0.53 (±0.16)	48.2	0.22 – 0.84
	Quercus	Veg	2.58 (±0.15)	49.1	2.29 – 2.88
	Quercus	Standard	1.99 (±0.15)	48.2	1.69 – 2.29

Table 9: Pairwise comparison of mean growth estimates among standards and both regeneration types for 3 most common tree species in Hády and Quercus in Soběšice. The table presents the estimated differences in mean growth (Estimate) between the regeneration types (generative and vegetative) and standards, the standard error (SE), degrees of freedom (df), t-ratio, and P-values for each comparison.

Plot	Species	Contrast	Estimate	SE	df	t-ratio	P-value
Hady	*Quercus*	Gen - Standard	-0.615	0.165	48.2	-3.72	**0.0015**
	Quercus	Gen - Veg	-1.012	0.165	48.2	-6.12	**<0.0001**
	Quercus	Standard - Veg	-0.397	0.165	48.2	-2.40	0.052
	Tilia	Gen - Veg	-0.127	0.229	31.2	-0.55	0.58
	Carpinus	Gen - Veg	-0.182	0.205	32.1	-0.89	0.38
Sobesice	*Quercus*	Gen - Standard	-1.46	0.215	48.2	-6.82	**<0.0001**
	Quercus	Gen - Veg	-2.05	0.212	48.6	-9.68	**<0.0001**
	Quercus	Standard - Veg	-0.59	0.208	48.6	-2.83	**0.018**

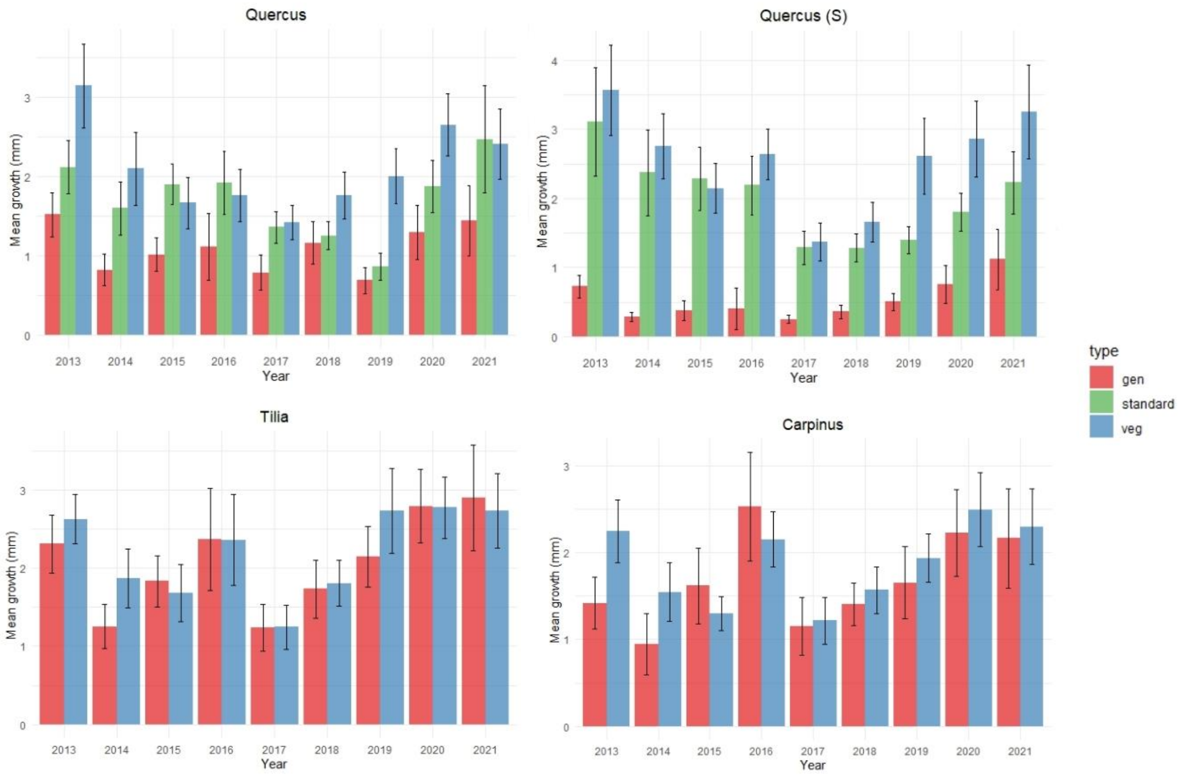

Figure 13: Comparison of mean annual tree growth (TRW) among standards, sprout regeneration (veg), and seed regeneration (gen) for the three most common tree species in Hády, and for Quercus in Soběšice (S). Error bars represent standard errors.

Table 10: Comparison of linear mixed effects models evaluating the impact of various climatic parameters on tree growth (TRW) in Hády and Soběšice. Each model includes tree ID as a random effect and assesses different combinations of climatic variables such as mean annual, seasonal and June relative air humidity (Hum), precipitation (Prec) and temperature (Temp). The values are Akaike Information Criterion (AIC), marginal R^2 (R^2m) and conditional R^2 (R^2c).

		Hady			Sobesice		
		AIC	R2m	R2c	AIC	R2m	R2c
model 9	Hum_June+Temp_year	**824.04**	0.23	0.64	422.06	0.74	0.85
model 10	Hum_June+Temp_season	837.81	0.23	0.63	410.71	0.75	0.86
model 6	Prec_June+Temp_year	902.51	0.20	0.60	432.64	0.74	0.85
model 5	Prec_June+Temp_season	919.37	0.19	0.60	**398.48**	0.75	0.86
model 8	Hum_season+Temp_season	925.31	0.19	0.59	434.01	0.74	0.85
model 7	Hum_season+Temp_year	948.44	0.18	0.58	425.33	0.74	0.85
model 1	Prec_year+Temp_year	970.27	0.17	0.57	455.93	0.73	0.84
model 3	Prec_season+Temp_year	976.68	0.17	0.57	439.13	0.73	0.85
model 2	Hum_year+Temp_year	987.70	0.16	0.56	465.12	0.72	0.83
model 4	Prec_season+Temp_season	1032.60	0.14	0.54	430.48	0.74	0.85

In Hády, TRW of seed regeneration for *Quercus* was significantly smaller than TRW of *Carpinus* and *Tilia* (Table 11). Conversely, TRW of vegetative sprouts for these species showed no significant differences (Table 11).

Table 11: Pairwise comparison of mean growth estimates among three most common tree species in Hády within generative and vegetative regeneration types. The table presents the estimated differences in mean growth (Estimate) between pairs of species within both regeneration types, the standard error (SE), degrees of freedom (df), t-ratio, and p-values for each comparison.

Regeneration Type	Contrast	Estimate	SE	df	t-ratio	p-value
Generative	*Quercus - Carpinus*	-0.59	0.21	50.2	-2.84	**0.02**
	Quercus - Tilia	-0.98	0.21	50.2	-4.61	**<0.0001**
	Carpinus - Tilia	-0.40	0.21	50.2	-1.92	0.14
Vegetative	*Quercus - Carpinus*	0.25	0.18	45.2	1.34	0.38
	Quercus - Tilia	-0.10	0.18	45.2	-0.53	0.86
	Carpinus - Tilia	-0.34	0.19	45.2	-1.83	0.17

Higher mean annual temperature negatively affected TRW of standard trees and seed regeneration of *Quercus* in both Hády and Soběšice. Vegetative sprouts of *Quercus* in Soběšice were also negatively impacted by the temperature increase, while in Hády, sprouts did not experience a significant negative effect (Table 12, Figure 14). Increasing temperature affected similarly standards, seed and sprout regeneration in Soběšice but in Hády its negative effect on standards was significantly greater than on both types of regeneration (Table 12). *Tilia* and *Carpinus* showed no significant response to temperature changes (Table 12, Figure 14).

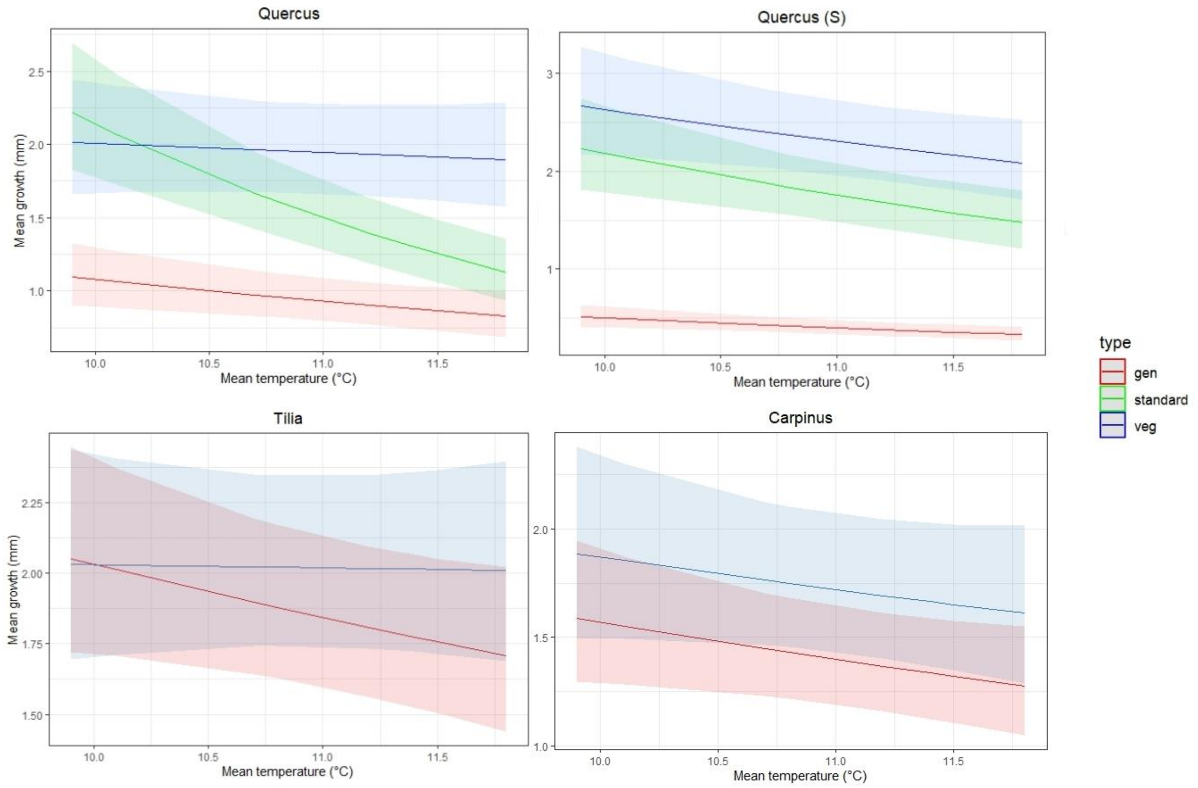

Figure 14: Mean growth (TRW) in 2013-2021 for sprout regeneration (veg), seed regeneration (gen) and standards of three most common tree species in Hády and Quercus in Soběšice (S) in relation to mean annual temperature. Lines represent fitted linear mixed effect models (P < 0.05) with 95% confidence intervals.

Seed and sprout regeneration of *Quercus* were positively influenced by increased June precipitation and higher relative air humidity at both study sites (Table 12, Figure 15,16). In Hády, *Quercus* sprouts exhibited the most positive response to increased June precipitation and relative air humidity, growing at a similar rate to standards and much faster than seed regeneration under drier conditions. As precipitation and relative air humidity increased, the growth rate of sprouts accelerated, further widening the difference between sprouts, standards, and seed regeneration of *Quercus* (Figure 15,16). Although the positive response of sprout regeneration to precipitation and relative air humidity was greater than that of seed regeneration, this difference was not statistically significant (Table 12).

In Soběšice, sprouts also grew the fastest overall, with standards showing no significant response to precipitation (Table 12). In contrast, seed regeneration responded most positively to increased precipitation, while sprout regeneration also showed a positive response, though to a lesser extent, with the difference between seed and sprout regeneration being statistically significant (Table 12). Additionally, increasing relative air humidity in June significantly enhanced growth across both regeneration types and standards in Soběšice, although the regeneration types experienced more pronounced benefits compared to the standards, with these differences being statistically significant (Table 12).

Standard *Quercus* trees in Hády exhibited a slight negative response to increased June precipitation, while response to increasing relative air humidity was not significant.

Both seed and sprout regeneration of *Tilia* and *Carpinus* responded positively to increased precipitation and relative air humidity, with no significant difference observed between the two types of regeneration for either species (Table 12, Figure 15,16).

Table 12: Models of the effects of mean annual temperature, June precipitation and mean June relative air humidity on growth of trees from different origin for 3 most common tree species in Hády and Quercus in Soběšice.

Site	Species	Type	Trend	SE	t.ratio	P value	
Mean annual temperature (°C)							
Hady	*Quercus*	gen	-0.147	0.0581	-2.53	**0.01**	A
		veg	-0.0311	0.0582	-0.54	0.59	A
		standard	-0.3559	0.0581	-6.13	**<0.0001**	B
	Tilia	gen	-0.097	0.0517	-1.88	0.06	A
		veg	-0.0054	0.0534	-0.1	0.92	A
	Carpinus	gen	-0.115	0.0633	-1.82	0.07	A
		veg	-0.0829	0.0724	-1.14	0.25	A
Sobesice	*Quercus*	gen	-0.224	0.0656	-3.41	**<0.001**	A
		veg	-0.131	0.062	-2.11	**0.04**	A
		standard	-0.216	0.0634	-3.41	**<0.001**	A
Precipitation in June (mm)							
Hady	*Quercus*	gen	0.0020	0.0009	2.1	**0.04**	A
		veg	0.0051	0.0009	5.41	**<0.0001**	A
		standard	-0.0019	0.0009	-2.04	**0.04**	B
	Tilia	gen	0.0051	0.0008	6.15	**<0.0001**	A
		veg	0.0056	0.0009	6.54	**<0.0001**	A
	Carpinus	gen	0.0027	0.001	2.64	**0.01**	A
		veg	0.0043	0.0012	3.74	**<0.001**	A
Sobesice	*Quercus*	gen	0.0077	0.0011	7.35	**<0.0001**	A
		veg	0.0035	0.001	3.49	**<0.001**	B
		standard	-0.0002	0.001	-0.16	0.87	C
Humidity in June (%)							
Hady	Quercus	gen	0.0184	0.0047	3.945	**0.0001**	AB
		veg	0.0258	0.0047	5.495	**<0.0001**	A
		standard	0.0038	0.0047	0.81	0.42	B
	Tilia	gen	0.0339	0.0038	8.824	**<0.0001**	A
		veg	0.0319	0.0040	8.055	**<0.0001**	A
	Carpinus	gen	0.0273	0.0048	5.665	**<0.0001**	A
		veg	0.0275	0.0055	4.982	**<0.0001**	A
Sobesice	Quercus	gen	0.0367	0.0053	6.979	**<0.0001**	A
		veg	0.0254	0.0050	5.079	**<0.0001**	AB
		standard	0.0105	0.0051	2.064	**0.04**	B

Letters signify differences among both types of regeneration and standards (α=0.05) based on Kenward-Roger Method.

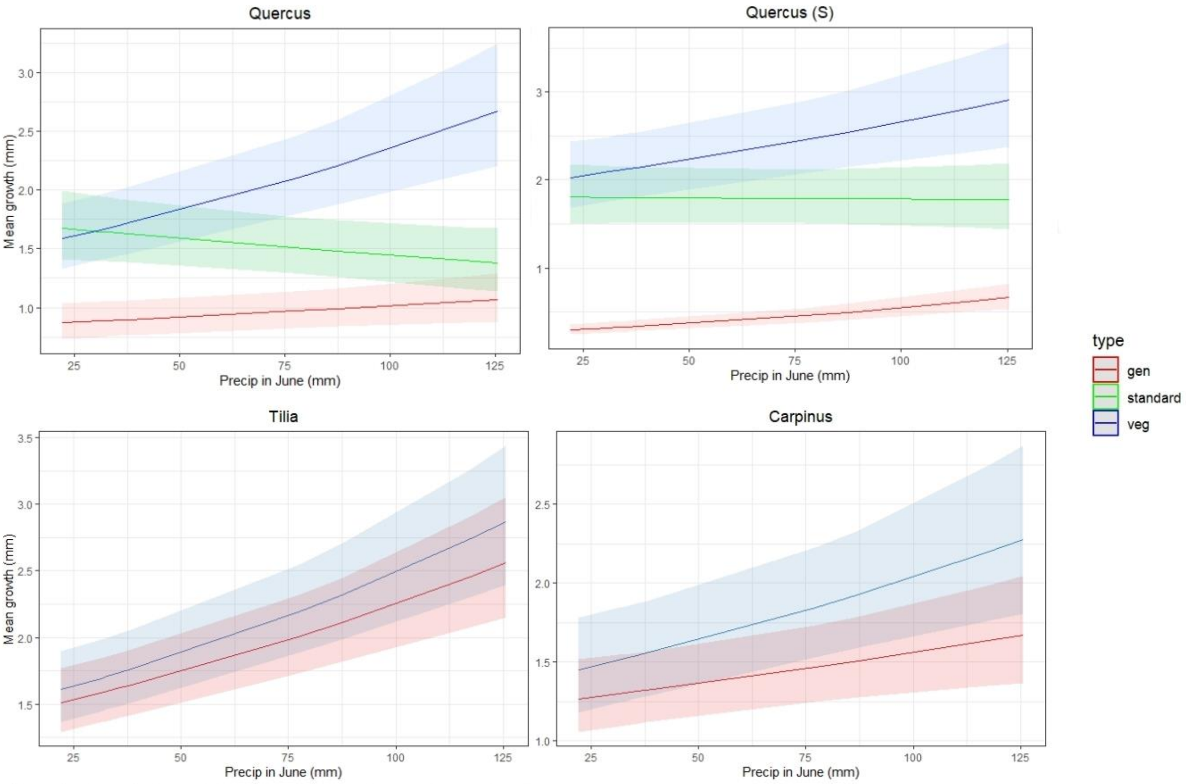

Figure 15: Mean growth (TRW) in 2013-2021 for sprout regeneration (veg), seed regeneration (gen) and standards of three most common tree species in Hády and Quercus in Soběšice (S) in relation to total June precipitation. Lines represent fitted linear mixed effect models (P < 0.05) with 95% confidence intervals.

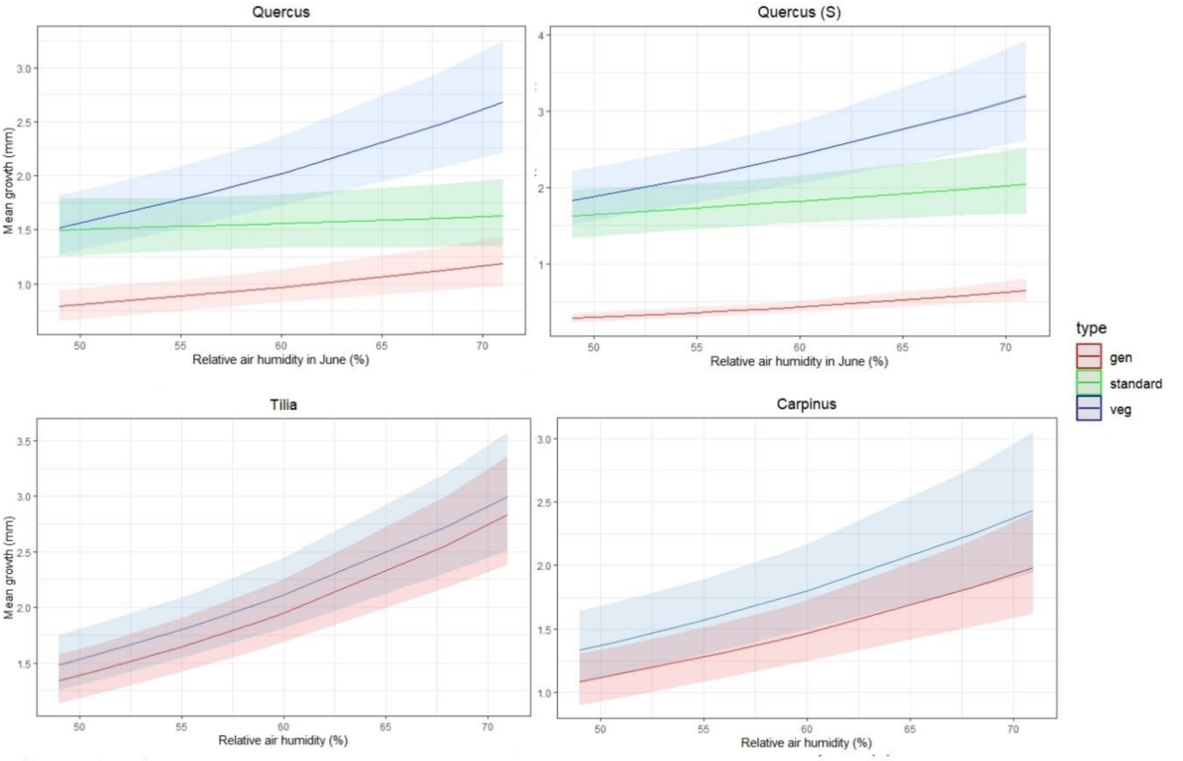

Figure 16: Mean growth (TRW) in 2013-2021 for sprout regeneration (veg), seed regeneration (gen) and standards of three most common tree species in Hády and Quercus in Soběšice (S) in relation to relative air humidity in June. Lines represent fitted linear mixed effect models (P < 0.05) with 95% confidence intervals.

6. Discussion

6.1. The effects of stand density, standards and species composition on biomass production in traditional coppices

Increasing interest in the restoration of coppice forests motivated by rapid woody biomass production brings out the necessity of understanding the effect of woody layer structure and tree species composition on the biomass productivity of coppiced trees. Such knowledge could help to optimize the management of coppices and increase their economic profitability. The results of this thesis help improve this understanding by unravelling the effects of standards, stand density, and tree species composition on sprout biomass in two coppice restoration experiments with different varying numbers of standards.

As expected, we found a significant negative relationship between density of standards and sprout biomass on stand level. This is consistent with (A.C. Joys, Fuller and Dolman, 2004), who demonstrated smaller amounts and less developed sprouts under high overstorey canopy cover than under low overstorey canopy cover. We also found a negative relationship between the density of standards and mean sprout biomass on stump level (SB_{stump}). However, this relationship varied significantly among studied species. Whereas SB_{stump} of *Carpinus* and *Quercus* decreased significantly with increasing density of standards, there was no significant effect for SB_{stump} of *Acer* and *Tilia*. These findings are consistent with Matula *et al.* (Matula *et al.*, 2012) who found decreasing diameter and height of *Carpinus* sprouts, whereas increasing amount and taller sprouts of *Tilia* under higher densities of standards one year after the harvest. Interspecific differences are probably result of different sensitivity of studied species to limited amount of light under standards and also effect of neighbourhood competition from standards for water and soil resources. Competition for light is the main determinant of forest structure and growth (Coomes, Lines and Allen, 2011) and density of trees and structure of the canopy determine light availability and moisture content for the understory layer (Barbier, Gosselin and Balandier, 2008). Light is generally considered as a limiting factor for tree growth (Wyckoff and Clark, 2005; Coomes and Allen, 2007), and whereas competition for nutrients affects trees of all sizes, competition for light affects mainly growth of small trees in understorey (Coomes and Allen, 2007). Also, (Matula *et al*., 2019) observed increased growth of sprouts with increasing distance from the closest standard, which might be the effect of both neighbourhood competition and reduced light availability by standards.

Tilia had the highest while *Acer* had the lowest SB_{stump} from all studied species, regardless of the density of standards. *Tilia* is therefore the most promising tree species in view of biomass production. This result is consistent with (Matula *et al*., 2012) who found higher sprout biomass of *Tilia* than *Quercus* and *Carpinus* one year after the harvest. No effect of standards on SB_{stump} of *Acer* and *Tilia* suggests that there are obviously different factors affecting SB_{stump} of these species such as parent tree size and age (Matula *et al*., 2012). On the other hand, *Quercus petraea* is a light-demanding species, which does not grow well under closed canopy. Decreasing SB_{stump} of *Quercus* due to increasing number of standards is therefore probably due to increasing light limitation. Surprisingly, we found also *Carpinus* to be similarly negatively affected by standards. It is rather shade- and drought-tolerant (Modrý, Hubený and Rejšek, 2004; Bredemeier M., Cohen S., Godbold D.L., Lode E., Pichler V., 2011); therefore, the light and water limitation seem unlikely to be the mechanism behind this relationship. However, it favours rather deep moist and fertile soils which suggests that neighborhood competition for nutrients with closest standards might be the main limiting factor of SB_{stump} production of *Carpinus*.

Interspecific differences in sprout growth together with differences in resprouting ability of studied species (Matula *et al*., 2019) resulted in significant shifts in tree species composition. We observed steep decline of *Quercus* and an increasing proportion of *Tilia*, *Acer* and *Carpinus*. Similar shifts were reported in coppice forests after abandonment (Hédl, Kopecký and

Komárek, 2010; Müllerová, Hédl and Szabó, 2015). Tree species composition is an important factor in view of economic rentability of coppice stands. Although *Tilia* has proven to have the highest sprout biomass production, quality of wood is much lower compared to other studied species and its increasing abundance over other, more valuable species might not be desirable for some forest owners. On the other hand, *Carpinus* and *Quercus* are very appreciated as firewood, especially for their high calorific value (Matula *et al.*, 2020). Therefore, foresters can to some extent influence tree species composition of newly restored coppices or CWS and support production of *Quercus* and *Carpinus* by decreasing density of standards, which are negatively affecting sprout biomass production of these species.

We also expected that increasing density of sprouting stumps will decrease SB_{stand} at some point, as competition between individual stumps will be too intense and will not be fully compensated by a higher number of sprouting stumps. However, up to the density of 775 sprouting stumps per hectare we did not find negative effect of competition of sprouting stumps on SB_{stand} nor SB_{stump}. It follows that even the highest stand density is not the limiting factor for sprout biomass, and therefore, it is not necessary to do the sprout thinning at this point of coppice development. Our results are in contrast with Matula *et al*. (Matula *et al*., 2019, 2020), who found significant growth-limiting neighborhood competition among resprouting trees. However, our results are based on density of sprouting stumps and we did not directly measure the amount of light and soil resources, neither stump parameters in our study. It suggests there might be different factors affecting neigbourhood competition of resprouting trees such as stump size, the size of root system or distance from closest resprouting tree.

6.2. Differential roles of seed and sprout regeneration in forest diversity and productivity after disturbance

Our study examined both sprout and seed regeneration 11 years after disturbance, a sufficient duration for established natural regeneration to develop (Harvey, Donato and Turner, 2016; Stevens-Rumann *et al.*, 2018b; Kuehne *et al.*, 2020; Demeter *et al.*, 2021). By evaluating regeneration in relation to forest structure, our findings provide new insights into the complex post-disturbance interactions between sprouting, seeding, and residual stand. As we hypothesized, sprouts contributed more to the early-stage stand biomass than seed-originated regeneration. Moreover, contrary to our expectations, sprouts were also the primary source of woody plant diversity, as seed regeneration was suppressed by residual trees even more than sprouts. On the other hand, seed regeneration introduced new species not present in the original stand, thereby enhancing beta diversity and genetic diversity of the emerging forest. Overall, the results reveal the complementary yet distinct contributions of sprouting and seeding to early forest development following logging disturbance.

Density of residual trees negatively affected sprout AGB, which is consistent with previous studies (Joys, Fuller and Dolman, 2004; Mejstřík, Šrámek and Matula, 2022). However, contrary to our expectations, seed regeneration did not increase with residual tree density. We predicted higher seedling abundance in subplots with more residual trees due to lower competition from sprouts (Mejstřík, Šrámek and Matula, 2022) and greater seed input, since most seeds fall near parent trees (Clark *et al.*, 1999; McEuen and Curran, 2004). Surprisingly, seed regeneration was suppressed by residual trees even more than sprouts, with most seed regeneration occurring in subplots lacking residual trees. Moreover, fast-growing pioneer species like birch (*Betula pendula* Roth.), European aspen (*Populus tremula* L.), willow (*Salix caprea* L.), and cherry (*Prunus avium* (L.) L.) dominated seed regeneration, while seedlings of of sessile oak (*Quercus petraea* (Matt.) Liebl.), the main residual tree species, were rare. This likely reflects the shade intolerance of oak seedlings (Leuschner and Meier, 2018), and their poor performance under closed canopies compared to sprouts and other faster-growing seedlings. Additionally, residual oak trees may negatively affect the survival of conspecific seedlings due to increased herbivory and pathogens (Janzen, 1970; J.H. Connell, 1971). Given that seedling growth is often limited by light availability (Wyckoff and Clark, 2005; Coomes and Allen, 2007), residual tree density was probably too high for oak seedling persistence in many subplots. Thus, for oak to regenerate after disturbance, sprouting was crucial. More shade-tolerant species like European hornbeam (*Carpinus betulus* L.), small-leaved lime (*Tilia cordata* Mill.) and field maple (*Acer campestre* L.) appeared in both sprout and seed regeneration but sprouting dominated. In summary, counter to expectations, seedlings did not benefit from residual trees and instead suffered from negative density-dependent effects, likely reflecting interactions between shade tolerance, growth rates and stand density.

The negative effect of residual tree density on AGB of seed regeneration was significant only in Hády. This can be possibly attributed to differences in species composition and diversity of the forest stands surrounding our study plots. In Soběšice, the surrounding stands are mostly monospecific sessile oak forests, whereas the forest stands around the Hády study plot are much more diverse. This greater diversity around Hády may have provided a richer seed source from various species not originally present, which could have more effectively occupied available niches in areas with lower densities of residual trees. In contrast, Soběšice, surrounded primarily by sessile oak stands, had a limited seed source from other species. This, together with suppression of oak seedlings, resulted in much less seed regeneration across the entire plot (168 seed-origin individuals in Soběšice, compared to 709 in Hády), regardless of the density of standards. Additionally, the differing microclimatic and soil conditions between Hády and Soběšice could play a role. The brown forest soils in Hády have more nutrients and support higher productivity than the cambisols in Soběšice, which can possibly lead to less competition for soil resources and greater potential for successful establishment of new seed regeneration.

As expected, seed regeneration did not affect sprout growth. Surprisingly, however, sprouts did not compete with seed regeneration either. In fact, sprouts had a positive effect on the occurrence of seed regeneration on both plots, and also increased the density of seed regeneration in Hády. This allowed both regeneration strategies to co-exist without significant competition, resulting in an overall increase in AGB production at the stand level. Seed regeneration could potentially benefit from the partial shading provided by the initially faster-growing sprouts, which served as an early canopy cover, thereby moderating microclimate temperatures and moisture levels after disturbance (Aussenac, 2003). Moreover, the initial rapid growth of sprouts enables them to quickly exploit available spaces, and seed regeneration may thus be more likely to occur in niches where sprouts have not yet established themselves or are unable to thrive. Another possible reason for this lack of competition is that sprouts have already established extensive root systems inherited from their parent trees, enabling access to deeper soil water and nutrients (Clark and Hallgren, 2003; Atwood, Fox and Loftis, 2011; Xue *et al.*, 2014; Pietras *et al.*, 2016; Stojanović, Szatniewska, *et al.*, 2017). This deeper resource acquisition potentially leaves the surface soil layers more available for the shallower, less-established root systems of seed regeneration. In addition, sprouting stumps may release water from deeper soil layers into the upper soil via hydraulic lift, providing access to this water source for shallow-rooted seedlings (Caldwell and Richards, 1989). While this mechanism has often been observed in arid or Mediterranean climates (Penuelas and Filella, 2003; Espeleta, West and Donovan, 2004), it is also documented for sessile oak in temperate forests (Zapater *et al.*, 2011). Furthermore, hydraulic lift facilitates favourable biogeochemical conditions near the surface by improving microbial activity, nutrient availability, and root nutrient uptake (Caldwell, Dawson and Richards, 1998). However, to fully understand these dynamics, additional studies on belowground interactions of sprout and seed regeneration with residual trees are needed.

The species diversity and richness of sprout regeneration was much higher than that of seed regeneration, making sprouts the major source of tree diversity on both plots (Appendix 4). This is likely tied to the resilience of mature trees, which can readily resprout after disturbance, thus maintaining the original stand's diversity (Bond and Midgley, 2001). Therefore, the composition of sprout regeneration more closely resembled the original stand compared to seed regeneration. Conversely, the composition of seed regeneration diverged more from the original stand possibly due to changing seed dispersal trends after disturbance (Calviño-Cancela, 2002). Interestingly, while residual trees had no significant impact on sprout occurrence and diversity, increased density of residual trees corresponded sharply with declining diversity of seed regeneration. This aligns with a study showing that high residual tree density can potentially restrict light availability and hinder seed regeneration (Gray, Spies and Easter, 2002). Overall, sprouting played a major role in maintaining stand species composition and diversity.

In contrast to sprouting, seed regeneration did not significantly contribute to the regeneration of original species but rather introduced new species (birch, European aspen and willow in Hády and European aspen in Soběšice, Appendix 2), increasing the overall species pool and beta diversity. The beta diversity of seed regeneration was much higher than that of sprout regeneration. However, the combined beta diversity of both regeneration strategies was higher than the original stand diversity, which is consistent with findings that disturbance often positively impacts beta diversity (Silva Pedro, Rammer and Seidl, 2016). Thus, while sprouting promotes high alpha diversity within communities, it limits opportunities for new species establishment, resulting in lower beta diversity between communities. In contrast, seed regeneration introduces genetically distinct individuals possibly representing species not present in the previous stand, thereby contributing to increased beta diversity (Török *et al.*, 2018). This disturbance-diversity relationship is modulated by multiple factors such as disturbance severity, life-history traits, and the available species pool (Miller *et al.*, 2012; Silva

Pedro, Rammer and Seidl, 2016). The positive effect of disturbance on tree species diversity tends to be greater in stands with larger species pools and higher disturbance intensities (Silva Pedro, Rammer and Seidl, 2016). Moreover, in early succession, incorporating pioneer species into stands containing primarily intermediate or late-successional species (e.g., sessile oak) can strongly facilitate diversity-driven gains in stand productivity (Silva Pedro, Rammer and Seidl, 2016).

6.3. Growth response of vegetative sprouts, generative regeneration and standards to climate and drought in oak-dominated traditional coppice forests

In a time of climate change, one major challenge is to determine how changes in environmental conditions will affect the structure and dynamics of ecosystems (Chapin, Sala and Huber-Sannwald, 2001). Rising temperatures, shifting precipitation patterns, and land-use changes have been reported as the main limiting factors to growth and productivity in temperate forests in recent decades (Boisvenue and Running, 2006; Babst *et al*., 2013). Given these challenges, coppicing has gained renewed attention as a management strategy with potential adaptive advantages, particularly under drought conditions (Pietras *et al.*, 2016; Stojanović, Szatniewska, *et al.*, 2017). However, despite the increasing popularity of this management, there remains a significant lack of empirical data on how tree growth and regeneration in these systems respond to climate variables. Our study addresses this gap by enhancing the understanding of how specific factors, such as rising temperatures, decreasing precipitation, and relative air humidity affect the growth of vegetative sprouts, generative seedlings, and mature standard trees in newly restored traditional coppices, providing valuable insights for sustainable forest management.

At both sites, *Quercus* sprouts exhibited significantly faster growth than seed regeneration, regardless of climatic conditions, which is consistent with previous studies indicating faster initial growth of sprouts compare to seedlings, mainly due to already developed root systems and better access to soil water (Bond and Midgley, 2001; Dietze and Clark, 2008; Pietras *et al.*, 2016). Conversely, for *Tilia* and *Carpinus*, there were no significant differences in growth rates between seed and sprout regeneration. The reason might be that water use efficiency of *Tilia* and *Carpinus* seedlings is highly effective (Pigott and Pigott, 1993). These species have economical water use, notably because of the great sensitivity of its stomata (Aasamaa *et al.*, 2004). Moreover, both *Tilia* and *Carpinus* are rather shade-tolerant species, which generally require significant biomass investment in foliage to maximize light capture in understory environments (Valladares and Niinemets, 2008). However, in the initial phase after cutting in our study plots, where light was more abundant due to the removal of many trees, seedlings of *Tilia* and *Carpinus* might allocated more resources towards developing their root systems. This strategic shift towards greater root system development, rather than immediate foliage expansion, is especially advantageous under the newly light-rich conditions post-clearing (Reich *et al.*, 1998). By focusing on root growth, these species enhance their capacity for water and nutrient uptake, crucial for supporting growth in environments with variable light availability (Poorter and Markesteijn, 2008). This strategy may explain the lack of significant differences in growth rates between the regeneration types for these species, as both are equipped to efficiently capitalize on the available resources, regardless of their type of regeneration.

Sessile oak is generally considered a species with higher resistance, particularly during summer droughts (Vanhellemont *et al.*, 2019; Toïgo *et al.*, 2020; Černý *et al.*, 2024). However, oak is still vulnerable to environmental changes such as drought and increased air temperatures (Černý *et al.*, 2024). In our study, we observed a negative impact of rising mean annual temperatures on the growth of standard trees and seed regeneration of *Quercus* in both Hády and Soběšice. Also sprouts of *Quercus* were negatively affected by rising temperatures, but this effect was significant only in Soběšice. Surprisingly, although there was no significant difference in the response to increasing annual temperatures between sprout and seed regeneration of *Quercus* on both plots, the standard *Quercus* trees in Hády exhibited a significantly greater negative growth response compared to both types of regeneration. The significant reduction in TRW of standard *Quercus* trees, particularly in Hády, suggests that mature trees may be less resilient to temperature increases than younger, regenerating individuals. This could be due to the higher water and nutrient demands of mature trees, which may not be met under conditions of elevated temperature and potential water scarcity (Bréda *et al.*, 2006). Additionally, the advanced age of standards (around 115 years in Hády and 90 years in Soběšice) likely contributes to their diminished capacity to adapt to worsening environmental conditions. Older trees might tend to respond less effectively to environmental stressors due to their age-related physiological limitations. Another factor impacting these mature trees is the low density of the forest stands, which leaves the crowns of these older trees fully exposed to the sun. This full exposure can exacerbate heat and drought stress, in contrast to the younger regeneration in the understory, which benefits from partial shading provided by neighboring trees and the canopy of the mature trees themselves.

In Hády, *Quercus* sprouts did not experience a significant negative effect from the temperature increase, unlike in Soběšice, where the effect was significant. This disparity between the two sites could be linked to local variations in microclimates, soil conditions, or stand structures, which might buffer the effects of temperature on sprout growth in Hády. In addition to climatic factors, soil nutrient availability is a critical factor influencing tree growth (Lévesque, Walthert and Weber, 2016). The brown forest soils in Hády often exhibit higher productivity compared to the cambisols in Soběšice (Weil and Brady, 2017). Furthermore, the Hády plot is more diverse compared to Soběšice, where the study plot is located in monospecific sessile oak forests with only a small proportion of other tree species. Previous studies have found that oak is more resistant and resilient to drought in mixed forests compared to monocultures (Pretzsch *et al.*, 2020; Steckel *et al.*, 2020; del Río *et al.*, 2022), which could also explain the differences in drought response of *Quercus* sprouts observed between the study sites.

Results of our study aligns with findings from other studies documenting temperature-induced stress in oak species. For instance, (Mészáros *et al.*, 2022) reported that high temperatures especially during the spring (May) and late summer (August) and low precipitation during the peak growing season negatively affect the radial growth of *Quercus*, resulting in reduced overall oak stand productivity. This reduction in growth is often linked to reduced photosynthetic capacity during critical periods of tree development. Furthermore, temperature-induced stress can lead to a decrease in carbon assimilation, which in turn affects the tree's ability to allocate resources for growth and defense mechanisms (Flexas and Medrano, 2002). Additionally, the impact of drought on *Quercus* regeneration can be influenced by factors such as age, height, and the protection provided by the mature stand canopy (Krstić, Kanjevac and Babić, 2018), but these factors were not included in our study.

Surprisingly, we did not observe significant temperature effects on either type of regeneration in *Tilia* and *Carpinus* in Hády, suggesting that these species may have a higher tolerance to temperature fluctuations compared to *Quercus*. This is consistent with findings by (Leuschner *et al.*, 2024), who reported that *Tilia* and *Carpinus* exhibit greater temperature and drought resistance than *Quercus* based on growth reactions and defoliation rates. For *Tilia*, critical maximum temperature is estimated to be 44 °C (Radoglou *et al.*, 2009), and generally, high temperatures do not pose a problem provided there is sufficient water supply (De Jaegere, Hein and Claessens, 2016). Therefore, *Tilia* and *Carpinus* appear to be more resilient under varying climatic conditions, potentially due to their more conservative water-use strategies and greater plasticity in physiological responses. These findings suggest that *Tilia* and *Carpinus* could play an increasingly important role in maintaining forest structure and function in the face of climate change.

June precipitation and relative air humidity had positive effect on growth of sprout and seed regeneration for all studied species at both study sites, which underscores the critical importance of water availability during the growing season. Although precipitation and humidity in other months were also important, the rapid growth of trees in June, coinciding with the longest days of the year, made precipitation and humidity during this period the most influential. This finding aligns with numerous studies that have demonstrated the strong reliance of tree growth, particularly in temperate regions, on adequate precipitation during key periods of the year (Boisvenue and Running, 2006; Michelot *et al.*, 2012; Lévesque, Walthert and Weber, 2016; Aldea *et al.*, 2017).

In Hády, the growth of *Quercus* sprouts accelerated more with increasing precipitation compared to seed regeneration, although this difference was not statistically significant. Conversely, in Soběšice, *Quercus* seedlings showed a significantly stronger response to increased precipitation than sprouts. This difference in response may be attributed to the seedlings' less developed root systems, making them more sensitive to water availability in the upper soil layers compared to sprouts, which benefit from the extensive root systems of their parent trees. These larger root systems allow sprouts to access water from deeper soil layers, making them better adapted to fluctuating moisture conditions (Pietras *et al.*, 2016; Stojanović *et al.*, 2016). Additionally, in Soběšice, the limited availability of *Quercus* seed regeneration within the study plot led us to sample generative individuals from nearby stands with similar DBH to the sprouts, many of which were suppressed under the canopy of mature trees. As (Trouvé *et al.*, 2014) found, stand growth in sessile oak is significantly reduced by high summer soil water deficits, with suppressed trees experiencing particularly severe growth reductions, suggesting asymmetric belowground competition for water in this species. This may explain why seed regeneration of *Quercus* in Soběšice responded more strongly to increased precipitation than sprouts.

The slight negative response of standard *Quercus* trees in Hády to increased June precipitation is somewhat unexpected, as increased moisture is generally considered beneficial for tree growth. However, this result may reflect a complex interplay between soil moisture and other factors such as nutrient availability, competition, and root distribution (Granier *et al.*, 2007). Additionally, relative air humidity in June showed no significant influence on these standards, suggesting that their growth may not be as sensitive to changes in atmospheric moisture as it is to other environmental variables.

In contrast, growth of *Quercus* standards in Soběšice was not affected by June precipitation, but positively affected by June relative air humidity, indicating a more pronounced response to atmospheric moisture than soil moisture. This suggests that while these trees may have ample access to groundwater through their well-established root systems, they still benefit from the ambient moisture which can alleviate the stress from higher temperatures. Moreover, higher relative air humidity can lower the vapor pressure deficit (VPD) and reduce the rate of transpiration, thereby conserving water within the plant. This conservation of water is critical during periods of heat stress when the risk of dehydration is higher (Novick *et al.*, 2016). Reduced transpiration demand not only helps in maintaining better hydration levels within the tree but also enables more consistent physiological processes, such as photosynthesis, which can otherwise be inhibited under water stress conditions (Grossiord *et al.*, 2017). In addition, the positive effect of relative humidity may also be linked to the indirect effects on stomatal conductance. Under higher humidity conditions, stomata can remain more open, allowing for better gas exchange, including the uptake of carbon dioxide necessary for photosynthesis

(Bartlett, Scoffoni and Sack, 2012). This improved gas exchange under favorable humidity conditions could lead to enhanced growth rates, as the tree can maintain higher levels of photosynthetic activity even during periods of heat.

Both *Tilia* and *Carpinus* exhibited a positive growth response to June precipitation and relative air humidity at the Hády site, with no significant difference observed between sprout and seed regeneration for these species. This uniform response across regeneration types suggests that *Tilia* and *Carpinus* are highly responsive to water availability during the growing season, regardless of their regeneration origin. The positive response to increased precipitation is indicative of these species' ability to efficiently utilize available water to support growth, even in environments where moisture availability may fluctuate. The lack of a significant difference between sprout and seed regeneration further suggests that both regeneration strategies are equally effective in capturing and using available water resources.

7. Conclusions

7.1. The effects of stand density, standards and species composition on biomass production in traditional coppices

Out of the tested species, *Tilia* proved to have the highest woody biomass production. The great biomass productivity and its superb resprouting ability (Matula *et al*., 2019) make this species ideal for growing in traditional coppices. Furthermore, due to high shade tolerance, coppiced trees of *Tilia* and *Acer* can be grown under standards without a significant adverse effect on their sprout biomass production. On the other hand, if forest managers aim to maximize woody biomass production in *Quercus* and *Carpinus* coppices, the density of standards needs to be minimized. However, high biomass production in sprouts is not always desirable. In contrast to standards, coppice sprouts can have a negative effect on understorey plant species diversity through their shading effect (Matula *et al.*, 2020). Therefore, if the goal of coppice management is biodiversity conservation, then maintaining a higher density of standards to supress sprout growth could be a good way to limit negative effects of sprouts on the understory biodiversity. In addition, standards may have many other important ecosystem functions such as providing nesting opportunities for birds, increasing habitat heterogenity, carbon storage, timber production or aesthetic value, and keeping them in the forest stand is therefore desirable. Our finding that the increasing density of sprouting stumps significantly increased stand-level biomass production but did not reduce the growth of sprouts on a stump level indicates that thinning is not necessary to support woody biomass productivity in young coppices as previously suggested by Matula *et al*. (Matula *et al*., 2019).

7.2. Differential roles of seed and sprout regeneration in forest diversity and productivity after disturbance

This study provides novel insights into the relative roles of sprout and seed regeneration in early forest development following logging disturbance. Sprout regeneration, although often overlooked compared to seed regeneration, can serve as the primary driver of AGB and within-community diversity across sites, maintaining it even under higher densities of residual trees, which limit seedlings' establishment. In contrast, seed regeneration introduces new species to the stand despite being less abundant. Moreover, both regeneration strategies seem to use different resources and coexist without significant competition, increasing overall AGB production and carbon storage of the whole forest stand. These results demonstrate the differential but important roles of both seed and sprout regeneration in the early stages of forest diversity recovery and post-disturbance development. The study's implications extend to forest management strategies, emphasizing the need for a balanced approach. While residual trees provide habitat heterogeneity, nesting opportunities, and aesthetic values, our results indicate a trade-off between residual tree retention and seed regeneration abundance and diversity. Low retention that favors seedlings may boost compositional diversity, while high retention, which favors sprouts, may accelerate biomass recovery but limit diversity. Sprouting appears important for retaining existing diversity from the pre-disturbance community. Seeding enables new species to colonize, but these opportunities decline sharply with residual tree retention. A mix of both regeneration strategies may be ideal for balancing continuity and change in species composition. Given the importance of forest recovery for climate change mitigation, optimizing natural regeneration offers a cost-effective approach to enhance carbon sequestration while conserving biodiversity.

7.2.1. Management implications

Our study underlines the importance of employing strategic tree retention levels to optimize the balance between sprout and seed regeneration in post-logging forest recovery. To enhance biomass productivity and maintain biodiversity, forest managers should aim for tree retention patterns that avoid both extremes of too high or too low densities. Specifically, low to intermediate residual tree densities facilitate sprout regeneration effectively, while still permitting enough light for seed regeneration. Additionally, the findings of this study suggest the value of promoting sprout-associated biomass as it positively impacts the diversity of seed-origin regrowth. However, although sprouts are a good source of woody biomass and help maintain woody plant diversity, in greater abundance, they suppress the development of the herbaceous layer, negatively affecting its diversity (Matula *et al.*, 2020). Therefore, maintaining higher densities of residual trees may be a convenient way to limit sprout growth in areas with high conservation value.

7.3. Growth response of vegetative sprouts, generative regeneration and standards to climate and drought in oak dominated traditional coppice forests

This study offers insightful observations on the growth dynamics of oak-dominated traditional coppice forests under changing climatic conditions. Our findings indicate that *Quercus* sprouts generally grow much faster than seed regeneration regardless of climatic conditions and there were no significant differences in growth responses (TRW) of these two regeneration types to climatic variables such as mean annual temperature, June precipitation and relative air humidity. This indicates that both regeneration types possess similar capacities to adapt to climatic fluctuations. *Quercus* exhibited a significant decrease in TRW with rising temperatures, affecting standard trees and seed regeneration at both study sites and sprouts in Soběšice. In contrast, *Tilia* and *Carpinus* demonstrated no significant response to increasing temperature, indicating their suitability for Central European coppice forests in a warmer, drier climate. Increasing June precipitation and relative air humidity positively affected both types of regeneration for all studied species and there was no difference between regeneration types and studied species. These findings underscore the importance of understanding the complex interactions between climate, forest structure, and tree growth in traditional coppice forests. By taking into account the specific responses of different tree species and regeneration types to climatic factors, forest managers can develop more effective strategies to bolster the resilience and productivity of these valuable ecosystems in the face of a changing climate.

7.3.1. Management implications

The findings of this study have significant implications for the management and restoration of traditional coppice forests. *Quercus* sprouts generally exhibit faster growth and maintain high productivity compared to seed regeneration even under warmer and dryer climatic conditions. Although responses to climatic variables such as temperature, precipitation, and relative air humidity do not significantly differ between regeneration types, the consistent high productivity of sprouts suggests that coppicing practices favoring sprout regeneration could be an ideal source of wood biomass in conditions of climate change. Furthermore, sprouts may increasingly assist in maintaining species diversity with the rising frequency of droughts, as demonstrated by (Mejstřík *et al.*, 2024). The absence of significant temperature effects on *Tilia* and *Carpinus* suggests that these species may be less susceptible to climate-induced stress compared to *Quercus*. Consequently, promoting a diverse mix of species within coppice systems could help buffer against the negative impacts of climate change, thereby ensuring the long-term sustainability of these forests (Pardos *et al.*, 2021). Moreover, mixed stands not only provide greater stand stability, but their varied ecological requirements allow for more efficient use of available resources (Pretzsch *et al.*, 2013; del Río *et al.*, 2022), further enhancing the productivity and stability of the entire stand.

7.4. General conclusions

This thesis provides comprehensive insights into the complex interactions between forest structure, regeneration strategies, and climatic factors in the traditional coppice forests. The research underscores the importance of understanding both the ecological and climatic drivers that influence tree growth, biomass production, and species diversity in coppice and coppice-with-standards, particularly in the context of ongoing climate change. Forest structure plays a pivotal role in shaping the productivity and species composition of traditional coppices. The arrangement and density of mature residual trees are key drivers of overall biomass production and forest dynamics. Managing these structural elements effectively can enhance both productivity and biodiversity of these forests. This thesis highlights the necessity of integrating structural considerations into forest management practices to optimize outcomes and maintain ecological balance within these valuable forest ecosystems. Moreover, the findings underscore the significant but differential role of sprout and seed regeneration in post-disturbance forest development in terms of both productivity and diversity. While sprout regeneration plays a dominant role in biomass production and the retention of pre-disturbance species, seed regeneration contributes significantly to species diversity by enriching the species pool of the forest stand. This combination of regeneration strategy within a stand increases the resilience of the forest ecosystem, enhancing its capacity to adapt to future environmental changes. The study also found that while climatic factors such as temperature and drought influence similarly the growth of sprout and seed regeneration, sprout regeneration generally exhibited consistently faster growth across various climatic conditions particularly for *Quercus*. This suggests that coppice systems, with predominantly sprout regeneration, are well-suited to maintaining forest productivity under challenging environmental conditions.

This thesis supports the view that traditional coppicing and coppice-with-standards are effective forest management strategies in the context of climate change. They can sustain high levels of biomass production and maintain species diversity, even as environmental conditions become warmer and drier as result of climate change. The insights gained from this research provide a foundation for developing adaptive management strategies that ensure the long-term sustainability and productivity of coppice forests.

8. References

Aasamaa, K. *et al.* (2004) 'Drought acclimation of two deciduous tree species of different layers in a temperate forest canopy', *Trees - Structure and Function*, 18(1), pp. 93–101. Available at: https://doi.org/10.1007/s00468-003-0285-8.

Aitken, S.N. *et al.* (2008) 'Adaptation, migration or extirpation: climate change outcomes for tree populations', *Evolutionary Applications*, 1(1), pp. 95–111. Available at: https://doi.org/10.1111/j.1752-4571.2007.00013.x.

Alba, C., Fahey, C. and Flory, S.L. (2019) 'Global change stressors alter resources and shift plant interactions from facilitation to competition over time', *Ecology*, 100(12), p. e02859. Available at: https://doi.org/10.1002/ecy.2859.

Aldea, J. *et al.* (2017) 'Thinning enhances the species-specific radial increment response to drought in Mediterranean pine-oak stands', *Agricultural and Forest Meteorology*, 237–238, pp. 371–383. Available at: https://doi.org/10.1016/j.agrformet.2017.02.009.

Allen, C.D. *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(4), pp. 660–684. Available at: https://doi.org/10.1016/j.foreco.2009.09.001.

Anderson, M.J. (2006) 'Distance-based tests for homogeneity of multivariate dispersions', *Biometrics*, 62(1), pp. 245–253. Available at: https://doi.org/10.1111/J.1541-0420.2005.00440.X.

Anderson, M.J., Ellingsen, K.E. and McArdle, B.H. (2006) 'Multivariate dispersion as a measure of beta diversity', *Ecology Letters*, 9(6), pp. 683–693. Available at: https://doi.org/10.1111/J.1461-0248.2006.00926.X.

Anderson-Teixeira, K.J. *et al.* (2013) 'Altered dynamics of forest recovery under a changing climate', *Global Change Biology*, 19(7), pp. 2001–2021. Available at: https://doi.org/10.1111/gcb.12194.

Antezana-Vera, S.A. and Marenco, R.A. (2021) 'Intra-annual tree growth responds to micrometeorological variability in the central amazon', *IForest*, 14(3), pp. 242–249. Available at: https://doi.org/10.3832/ifor3532-014.

Von Arx, G. *et al.* (2013) ‘Microclimate in forests with varying leaf area index and soil moisture: Potential implications for seedling establishment in a changing climate’, *Journal of Ecology*, 101(5), pp. 1201–1213. Available at: https://doi.org/10.1111/1365-2745.12121.

Ashton, M.S. and Kelty, M.J. (2018) *The practice of silviculture: applied forest ecology*. John Wiley & Sons.

Atwood, C.J., Fox, T.R. and Loftis, D.L. (2011) ‘Effects of Various Silvicultural Systems on Regeneration in Mixed Hardwood Stands of the Southern Appalachians’, *Journal of Sustainable Forestry*, 30(5), pp. 419–440. Available at: https://doi.org/10.1080/10549811.2011.541020.

Aussenac, G. (2003) ‘Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture’, *Annals of Forest Science*, 57(3), pp. 287–301. Available at: https://doi.org/10.1051/forest:2000119.

Avery, T.E. and Burkhart, H.E. (2015) *Forest measurements*. Waveland Press.

Babst, F. *et al.* (2013) ‘Site- and species-specific responses of forest growth to climate across the European continent’, *Global Ecology and Biogeography*, 22(6), pp. 706–717. Available at: https://doi.org/10.1111/geb.12023.

Barbier, S., Gosselin, F. and Balandier, P. (2008) ‘Influence of tree species on understory vegetation diversity and mechanisms involved-A critical review for temperate and boreal forests’, *Forest Ecology and Management*. Elsevier, pp. 1–15. Available at: https://doi.org/10.1016/j.foreco.2007.09.038.

Bartha, S. *et al.* (2008) ‘Changes of vascular plant diversity along a chronosequence of beech coppice stands, central Apennines, Italy’, *Plant Biosystems*, 142(3), pp. 572–583. Available at: https://doi.org/10.1080/11263500802410926.

Bartlett, M.K., Scoffoni, C. and Sack, L. (2012) ‘The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: A global meta-analysis’, *Ecology Letters*, 15(5), pp. 393–405. Available at: https://doi.org/10.1111/j.1461-0248.2012.01751.x.

Bates, D. *et al.* (2015) ‘Fitting linear mixed-effects models using lme4’, *Journal of Statistical Software*, 67(1). Available at: https://doi.org/10.18637/jss.v067.i01.

Beckage, B. *et al.* (2008) ‘Differential effects of understory and overstory gaps on tree regeneration’, *Journal of the Torrey Botanical Society*, 135(1), pp. 1–11. Available at: https://doi.org/10.3159/07-RA-034.1.

Bellingham, P.J. and Sparrow, A.D. (2000) ‘Resprouting as a life history strategy in woody plant communities’, *Oikos*. Blackwell Munksgaard, pp. 409–416. Available at: https://doi.org/10.1034/j.1600-0706.2000.890224.x.

Belote, R.T. *et al.* (2011) ‘Forest productivity and tree diversity relationships depend on ecological context within mid-Atlantic and Appalachian forests (USA)’, *Forest Ecology and Management*, 261(7), pp. 1315–1324. Available at: https://doi.org/10.1016/j.foreco.2011.01.010.

Bergeron, Y. *et al.* (1999) ‘Forest management guidelines based on natural disturbance dynamics: Stand- and forest-level considerations’, *Forestry Chronicle*, 75(1), pp. 49–54. Available at: https://doi.org/10.5558/tfc75049-1.

Bohn, F.J. and Huth, A. (2017) ‘The importance of forest structure to biodiversity-productivity relationships’, *Royal Society Open Science*, 4(1). Available at: https://doi.org/10.1098/rsos.160521.

Boisvenue, C. and Running, S.W. (2006) ‘Impacts of climate change on natural forest productivity - Evidence since the middle of the 20th century’, *Global Change Biology*, pp. 862–882. Available at: https://doi.org/10.1111/j.1365-2486.2006.01134.x.

Bonan, G.B. (2008) *Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests*. Available at: https://www.science.org.

Bond, W.J. and Midgley, J.J. (2001) ‘2001_Bond_Trend in Ecol and Evo_Ecology of sprouting in woody plants the persistence niche’, *Trends in Ecology & Evolution*, 16(1), pp. 45–51.

Bond, W.J. and Midgley, J.J. (2003) ‘The Evolutionary Ecology of Sprouting in Woody Plants Author (s): William J . Bond and Jeremy J . Midgley Source : International Journal of Plant Sciences , Vol . 164 , No . S3 , Evolution of Functional Traits in Plants (May 2003), pp . S103-S114 Publ’, *International Journal of Plant Sciences*, 164(May 2003).

Bréda, N. *et al.* (2006) ‘Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences’, *Annals of Forest Science*, 63, pp. 625–644.

Bréda, N.J.J. (2003) ‘Ground-based measurements of leaf area index: A review of methods, instruments and current controversies’, *Journal of Experimental Botany*, pp. 2403–2417. Available at: https://doi.org/10.1093/jxb/erg263.

Bredemeier M. S.P., Cohen S., Godbold D.L., Lode E., Pichler V., (2011) ‘Forest Management and the Water Cycle: An Ecosystem-Based Approach’. Springer Netherlands.
Breheny, P. and Burchett, W. (2013) *Visualization of Regression Models Using visreg*.

Breheny, P. and Burchett, W. (2013) *Visualization of Regression Models Using visreg*.

Brokaw, N. and Busing, R.T. (2000) ‘Niche versus chance and tree diversity in forest gaps’, *Trends in Ecology & Evolution*, 15(5), pp. 183–188. Available at: https://doi.org/10.1016/S0169-5347(00)01822-X.

Brokaw, N.V.L. (1985) ‘Gap-Phase Regeneration in a Tropical Forest’, *Ecology*, 66(3), pp. 682–687. Available at: https://doi.org/https://doi.org/10.2307/1940529.

Broome, A. *et al.* (2011) ‘The effect of coppice management on moth assemblages in an English woodland’, *Biodiversity and Conservation*, 20(4), pp. 729–749. Available at: https://doi.org/10.1007/s10531-010-9974-y.

Brown, C. *et al.* (2011) ‘Linking ecological processes with spatial and non-spatial patterns in plant communities’, *Journal of Ecology*, 99(6), pp. 1402–1414. Available at: https://doi.org/10.1111/j.1365-2745.2011.01877.x.

Browne, L. *et al.* (2021) ‘Increased mortality of tropical tree seedlings during the extreme 2015–16 El Niño’, *Global Change Biology*, 27(20), pp. 5043–5053. Available at: https://doi.org/10.1111/GCB.15809.

Buckley, G.P. (1992) *Ecology and Management of Coppice Woodlands, London, Chapman-Hall: 336.*

Buckley, P. (2020) ‘Coppice restoration and conservation: a European perspective’, *Journal of Forest Research*. Taylor and Francis Ltd., pp. 125–133. Available at: https://doi.org/10.1080/13416979.2020.1763554.

Bugmann, H. (1997) ‘Sensitivity of forests in the European Alps to future climatic change’, 8, pp. 35–44.

Calama, R. *et al.* (2017) ‘Natural regeneration in iberian pines: A review of dynamic processes and proposals for management’, *Forest Systems*. Ministerio de Agricultura Pesca y Alimentacion. Available at: https://doi.org/10.5424/fs/2017262-11255.

Caldwell, M.M., Dawson, T.E. and Richards, J.H. (1998) ‘Hydraulic lift: consequences of water efflux from the roots of plants’, *Oecologia 1998 113:2*, 113(2), pp. 151–161. Available at: https://doi.org/10.1007/S004420050363.

Caldwell, M.M. and Richards, J.H. (1989) ‘Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots’, *Oecologia 1989 79:1*, 79(1), pp. 1–5. Available at: https://doi.org/10.1007/BF00378231.

Van Calster, H. *et al.* (2007) ‘Management driven changes (1967-2005) in soil acidity and the understorey plant community following conversion of a coppice-with-standards forest’, *Forest Ecology and Management*, 241(1–3), pp. 258–271. Available at: https://doi.org/10.1016/j.foreco.2007.01.007.

Calviño-Cancela, M. (2002) ‘Spatial patterns of seed dispersal and seedling recruitment in Corema album (Empetraceae): The importance of unspecialized dispersers for regeneration’, *Journal of Ecology*, 90(5), pp. 775–784. Available at: https://doi.org/10.1046/j.1365-2745.2002.00711.x.

Camargo, M.A.B. and Marenco, R.A. (2023) ‘Stem growth of Amazonian species is driven by intra-annual variability in rainfall, vapor pressure and evapotranspiration’, *Acta Botanica Brasilica*, 37. Available at: https://doi.org/10.1590/1677-941X-ABB-2022-0219.

Cannell, M.G.R. (ed.), Malcolm, D.C. (ed.) and Robertson, P.A. (ed.) (1992) ‘The ecology of mixed-species stands of trees’. Oxford (UK) Blackwell Scientific Pub.

Castro, J. *et al.* (2004) ‘Seedling establishment of a boreal tree species (Pinus sylvestris) at its southernmost distribution limit: Consequences of being in a marginal Mediterranean habitat’, *Journal of Ecology*, 92(2), pp. 266–277. Available at: https://doi.org/10.1111/j.0022-0477.2004.00870.x.

Černý, J. *et al.* (2024) ‘Sessile oak (Quercus petraea [Matt.] Liebl.) and its adaptation strategies in the context of global climate change: a review’, *Central European Forestry Journal*, 70(2), pp. 77–94. Available at: https://doi.org/10.2478/forj-2024-0012.

Chapin, F., Sala, O. and Huber-Sannwald, E. (2001) *Global biodiversity in a changing environment: scenarios for the 21st century*.

Chave, J. *et al.* (2005) ‘Tree allometry and improved estimation of carbon stocks and balance in tropical forests’, *Oecologia*, 145(1), pp. 87–99. Available at: https://doi.org/10.1007/s00442-005-0100-x.

Chazdon, R.L. (2003) ‘Tropical forest recovery: legacies of human impact and natural disturbances’, *Perspectives in Plant Ecology, Evolution and Systematics*, 6(1,2), pp. 51–71. Available at: http://www.urbanfischer.de/journals/ppees.

Chazdon, R.L. *et al.* (2016) ‘Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics’, *Science Advances*, 2(5). Available at: https://doi.org/10.1126/sciadv.1501639.

Chazdon, R.L. and Guariguata, M.R. (2016) ‘Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges’, *Biotropica*, 48(6), pp. 716–730. Available at: https://doi.org/10.1111/btp.12381.

Choat, B. *et al.* (2012) ‘Global convergence in the vulnerability of forests to drought’, *Nature*, 491(7426), pp. 752–755.

Clark, J.S. *et al.* (1999) ‘Interpreting recruitment limitation in forests’, *American Journal of Botany*, 86(1), pp. 1–16. Available at: https://doi.org/10.2307/2656950.

Clark, J.S.C. *et al.* (1999) ‘Interpreting recruitment limitation in forests’, *American Journal Of Botany*, 86(1), pp. 1–16. Available at: https://doi.org/10.2307/2656950.

Clark, S.L. and Hallgren, S.W. (2003) ‘Dynamics of oak (Quercus marilandica and Q. stellata) reproduction in an old-growth cross timbers forest’, *Southeastern Naturalist*, 2(4), pp. 559–574. Available at: https://doi.org/10.1656/1528-7092(2003)002[0559:DOOQMA]2.0.CO;2.

Clarke, P.J. *et al.* (2013) ‘Resprouting as a key functional trait: How buds, protection and resources drive persistence after fire’, *New Phytologist*, 197(1), pp. 19–35. Available at: https://doi.org/10.1111/nph.12001.

Collet, C. and Chenost, C. (2006) ‘Using competition and light estimates to predict diameter and height growth of naturally regenerated beech seedlings growing under changing canopy conditions’, *Forestry*, 79(5), pp. 489–502. Available at: https://doi.org/10.1093/forestry/cpl033.

Colombo, R. *et al.* (2003) ‘Retrieval of leaf area index in different vegetation types using high resolution satellite data’, *Remote Sensing of Environment*, 86(1), pp. 120–131. Available at: https://doi.org/10.1016/S0034-4257(03)00094-4.

Connell, J.H. (1971) ‘On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees’, *Dynamics of Populations* [Preprint].

Cook, J.G. *et al.* (1995) ‘Spherical Densiometers Produce Biased Estimates of Forest Canopy Cover’, *Wildlife Society Bulletin (1973-2006)*, 23(4), pp. 711–717. Available at: http://www.jstor.org/stable/3783003.

Coomes, D.A. and Allen, R.B. (2007) ‘Effects of size, competition and altitude on tree growth’, *Journal of Ecology*, 95(5), pp. 1084–1097. Available at: https://doi.org/10.1111/j.1365-2745.2007.01280.x.

Coomes, D.A., Lines, E.R. and Allen, R.B. (2011) ‘Moving on from Metabolic Scaling Theory: hierarchical models of tree growth and asymmetric competition for light’, *Journal of Ecology*, 99(3), pp. 748–756. Available at: https://doi.org/10.1111/j.1365-2745.2011.01811.x.

Craine, J.M. and Dybzinski, R. (2013) ‘Mechanisms of plant competition for nutrients, water and light’, *Functional Ecology*. Edited by D. Robinson, 27(4), pp. 833–840. Available at: https://doi.org/10.1111/1365-2435.12081.

Cunningham, S.C. (2005) ‘Photosynthetic responses to vapour pressure deficit in temperate and tropical evergreen rainforest trees of Australia’, *Oecologia*, 142(4), pp. 521–528. Available at: https://doi.org/10.1007/s00442-004-1766-1.

Dale, V.H. *et al.* (2001) ‘Climate Change and Forest Disturbances: Climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides’, *BioScience*, 51(9), pp. 723–734. Available at: https://doi.org/10.1641/0006-3568(2001)051[0723:CCAFD]2.0.CO;2.

Demeter, L. *et al.* (2021) 'Rethinking the natural regeneration failure of pedunculate oak: The pathogen mildew hypothesis', *Biological Conservation*, 253. Available at: https://doi.org/10.1016/j.biocon.2020.108928.

Diamandis, S. and Perlerou, C. (2001) 'The mycoflora of the chestnut ecosystems in Greece', *Forest Research*, 504, pp. 499–504.

Díaz, I.A. *et al.* (2021) 'Advanced canopy regeneration: an unrecognized mechanism of forest dynamics', *Ecology*, 102(1). Available at: https://doi.org/10.1002/ecy.3222.

Dietze, M.C. and Clark, J.S. (2008) 'Changing the gap dynamics paradigm: Vegetative regeneration control on forest response tO disturbance', *Ecological Monographs*, 78(3), pp. 331–347. Available at: https://doi.org/10.1890/07-0271.1.

Dinh, T.T. *et al.* (2019) 'Stump sprout dynamics of Quercus serrata Thunb. and Q. acutissima Carruth. four years after cutting in an abandoned coppice forest in western Japan', *Forest Ecology and Management*, 435, pp. 45–56. Available at: https://doi.org/10.1016/j.foreco.2018.12.034.

Dobrowolska, D. (2006) 'Warunki mikroklimatyczne w lukach w drzewostanach mieszanych w rerwacie Jata', *Leśne Prace Badawcze*, 3, pp. 45–56.

Duncan, S. (2002) 'Canopy gaps and dead tree dynamics: poking holes in the forest', *Science Findings*, pp. 1–5. Available at: http://www.fs.fed.us/pnw.

Engelbrecht, B.M.J. *et al.* (2006) 'Short dry spells in the wet season increase mortality of tropical pioneer seedlings', *Oecologia*, 148(2), pp. 258–269. Available at: https://doi.org/10.1007/S00442-006-0368-5/TABLES/5.

Engelbrecht, B.M.J., Kursar, T.A. and Tyree, M.T. (2005) 'Drought effects on seedling survival in a tropical moist forest', *Trees - Structure and Function*, 19(3), pp. 312–321. Available at: https://doi.org/10.1007/S00468-004-0393-0/FIGURES/6.

Enquist, B.J., West, G.B. and Brown, J.H. (2009) 'Extensions and evaluations of a general quantitative theory of forest structure and dynamics', *Proceedings of the National Academy of Sciences of the United States of America*, 106(17), pp. 7046–7051. Available at: https://doi.org/10.1073/pnas.0812303106.

Espeleta, J.F., West, J.B. and Donovan, L.A. (2004) ‘Species-specific patterns of hydraulic lift in co-occurring adult trees and grasses in a sandhill community’, *Oecologia*, 138(3), pp. 341–349. Available at: https://doi.org/10.1007/s00442-003-1460-8.

Everham, E.M., Myster, R.W. and Vandegenachte, E. (1996) ‘Effects of light, moisture, temperature, and litter on the regeneration of five tree species in the tropical montane wet forest of Puerto Rico’, *American Journal of Botany*, 83(8), pp. 1063–1068. Available at: https://doi.org/10.1002/j.1537-2197.1996.tb12804.x.

Fang, S. *et al.* (2011) ‘Sprout development, biomass accumulation and fuelwood characteristics from coppiced plantations of Quercus acutissima’, *Biomass and Bioenergy*, 35(7), pp. 3104–3114. Available at: https://doi.org/10.1016/j.biombioe.2011.04.017.

Fardusi, M.J. *et al.* (2018) ‘A spatio-temporal dataset of forest mensuration for the analysis of tree species structure and diversity in semi-natural mixed floodplain forests’, *Annals of Forest Science*, 75(1). Available at: https://doi.org/10.1007/s13595-018-0688-8.

Fartmann, T., Müller, C. and Poniatowski, D. (2013) ‘Effects of coppicing on butterfly communities of woodlands’, *Biological Conservation*, 159, pp. 396–404. Available at: https://doi.org/10.1016/j.biocon.2012.11.024.

Fisichelli, N.A., Frelich, L.E. and Reich, P.B. (2014) ‘Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures’, *Ecography*, 37(2), pp. 152–161. Available at: https://doi.org/10.1111/j.1600-0587.2013.00197.x.

Flexas, J. and Medrano, H. (2002) ‘Drought-inhibition of photosynthesis in C3 plants: Stomatal and non-stomatal limitations revisited’, *Annals of Botany*, 89(2), pp. 183–189. Available at: https://doi.org/10.1093/aob/mcf027.

Forrester, D.I. *et al.* (2017) ‘Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate’, *Forest Ecology and Management*, 396, pp. 160–175. Available at: https://doi.org/10.1016/J.FORECO.2017.04.011.

Franklin, J.F. (1989) ‘Importance of ecological diversity in maintaining long-term site productivity’, *Maintaining the long-term productivity of Pacific Northwest forest ecosystems*, pp. 82–97.

Franklin, J.F. *et al.* (2002) ‘Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example’, *Forest Ecology and Management*, 155(1–3), pp. 399–423. Available at: https://doi.org/10.1016/S0378-1127(01)00575-8.

Freese, A. *et al.* (2006) ‘Habitat use of the endangered butterfly Euphydryas maturna and forestry in Central Europe’, *Animal Conservation*, 9(4), pp. 388–397. Available at: https://doi.org/10.1111/j.1469-1795.2006.00045.x.

Frelich, L.E. (2002) *Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-Deciduous Forests. Cambridge University Press.*

De Frenne, P. *et al.* (2013) ‘Microclimate moderates plant responses to macroclimate warming.’, *Proceedings of the National Academy of Sciences of the United States of America*, 110(46), pp. 18561–5. Available at: https://doi.org/10.1073/pnas.1311190110.

De Frenne, P. *et al.* (2019) ‘Global buffering of temperatures under forest canopies’, *Nature Ecology & Evolution*, 3(5), pp. 744–749. Available at: https://doi.org/10.1038/s41559-019-0842-1.

Fujimori, T. (2001) *Ecological and silvicultural strategies for sustainable forest management*.

Gamfeldt, L. *et al.* (2013) ‘Higher levels of multiple ecosystem services are found in forests with more tree species’, *Nature Communications 2013 4:1*, 4(1), pp. 1–8. Available at: https://doi.org/10.1038/ncomms2328.

Gao, T. *et al.* (2014) ‘The role of forest stand structure as biodiversity indicator’, *Forest Ecology and Management*, 330, pp. 82–93. Available at: https://doi.org/10.1016/j.foreco.2014.07.007.

Gebeyehu, M.N. (2019) ‘Review on Effect of Climate Change on Forest Ecosystem’, *International Journal of Environmental Sciences & Natural Resources*, 17(4). Available at: https://doi.org/10.19080/ijesnr.2019.17.555968.

Gill, S.J., Biging, G.S. and Murphy, E.C. (2000) *Modeling conifer tree crown radius and estimating canopy cover*.

Glithero, N.J., Wilson, P. and Ramsden, S.J. (2013) ‘Prospects for arable farm uptake of Short Rotation Coppice willow and miscanthus in England’, *Applied Energy*, 107, pp. 209–218. Available at: https://doi.org/10.1016/j.apenergy.2013.02.032.

Götmark, F. (2013) ‘Habitat management alternatives for conservation forests in the temperate zone: Review, synthesis, and implications’, *Forest Ecology and Management*, 306, pp. 292–307. Available at: https://doi.org/10.1016/j.foreco.2013.06.014.

Granier, A. *et al.* (2007) ‘Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003’, *Agricultural and Forest Meteorology*, 143(1–2), pp. 123–145. Available at: https://doi.org/10.1016/j.agrformet.2006.12.004.

Gray, A.N., Spies, T.A. and Easter, M.J. (2002) ‘Microclimatic and soil moisture responses to gap formation in coastal Douglas-fir forests’, *Canadian Journal of Forest Research*, 32(2), pp. 332–343. Available at: https://doi.org/10.1139/x01-200.

Grimm, N.B. *et al.* (2013) ‘The impacts of climate change on ecosystem structure and function’, *Frontiers in Ecology and the Environment*, pp. 474–482. Available at: https://doi.org/10.1890/120282.

Grossiord, C. *et al.* (2017) ‘Tree water dynamics in a drying and warming world’, *Plant Cell and Environment*, 40(9), pp. 1861–1873. Available at: https://doi.org/10.1111/pce.12991.

Grossiord, C. *et al.* (2020) ‘Plant responses to rising vapor pressure deficit’, *New Phytologist*. Blackwell Publishing Ltd, pp. 1550–1566. Available at: https://doi.org/10.1111/nph.16485.

Guariguata, M.R. and A. Pinard, M. (1998) ‘Ecological knowledge of regeneration from seed in neotropical forest trees: Implications for natural forest management’, *Forest Ecology and Management*, 112(1–2), pp. 87–99. Available at: https://doi.org/10.1016/S0378-1127(98)00318-1.

Hartley, M.J. (2002) ‘Rationale and methods for conserving biodiversity in plantation forests’, *Forest Ecology and Management*, 155(1–3), pp. 81–95. Available at: https://doi.org/10.1016/S0378-1127(01)00549-7.

Harvey, B.J., Donato, D.C. and Turner, M.G. (2016) ‘High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches’, *Global Ecology and Biogeography*, 25(6), pp. 655–669. Available at: https://doi.org/10.1111/geb.12443.

Hédl, R., Kopecký, M. and Komárek, J. (2010) ‘Half a century of succession in a temperate oakwood: From species-rich community to mesic forest’, *Diversity and Distributions*, 16(2), pp. 267–276. Available at: https://doi.org/10.1111/j.1472-4642.2010.00637.x.

Van Der Heijden, M.G.A. and Horton, T.R. (2009) ‘Socialism in soil? the importance of mycorrhizal fungal networks for facilitation in natural ecosystems’, *Journal of Ecology*, 97(6), pp. 1139–1150. Available at: https://doi.org/10.1111/j.1365-2745.2009.01570.x.

Hérault, B. and Piponiot, C. (2018) ‘Key drivers of ecosystem recovery after disturbance in a neotropical forest: Long-term lessons from the Paracou experiment, French Guiana’, *Forest Ecosystems*, 5(1), pp. 1–15. Available at: https://doi.org/10.1186/s40663-017-0126-7.

Hobbie, S.E. and Stuart Chapin, F. (1998) ‘An experimental test of limits to tree establishment in Arctic tundra’, *Journal of Ecology*, 86(3), pp. 449–461. Available at: https://doi.org/10.1046/j.1365-2745.1998.00278.x.

Holl, K.D. (2017) ‘Research directions in tropical forest restoration’, *Annals of the Missouri Botanical Garden*, 102(2), pp. 237–250. Available at: https://doi.org/10.3417/2016036.

Holmgren, M., Scheffer, M. and Huston, M.A. (1997) ‘The interplay of facilitation and competition in plant communities’, *Ecology*, 78(7), pp. 1966–1975. Available at: https://doi.org/10.1890/0012-9658(1997)078[1966:TIOFAC]2.0.CO;2.

Hooper, D.U. and Vitousek, P.M. (1997) ‘The effects of plant composition and diversity on ecosystem processes’, *Science*, 277(5330), pp. 1302–1305. Available at: https://doi.org/10.1126/science.277.5330.1302.

Hopkins, W.G., Hiiner, N.P.A. and Wiley, W.J. (1995) *Introduction to Plant Physiology Fourth Edition*.

Howe, H.F. and Smallwood, J. (1982) ‘Ecology of Seed Dispersal’, *Source: Annual Review of Ecology and Systematics*, 13, pp. 201–228.

Hui, G. *et al.* (2019) ‘Methods of Forest Structure Research: a Review’, *Current Forestry Reports*, 5(3), pp. 142–154. Available at: https://doi.org/10.1007/s40725-019-00090-7.

Imai, N. *et al.* (2012) ‘Effects of selective logging on tree species diversity and composition of Bornean tropical rain forests at different spatial scales’, *Plant Ecology*, 213(9), pp. 1413–1424. Available at: https://doi.org/10.1007/s11258-012-0100-y.

Imamura, K., Saito, S. and Nakashizuka, T. (2017) ‘Abandoned forest ecosystem: Implications for Japan’s Oak Wilt disease’, *Journal of Forest Economics*, 29, pp. 56–61. Available at: https://doi.org/10.1016/J.JFE.2017.08.005.

IPCC 2007 - Climate Change (2007) ‘The Physical Science Basis: Working Group I Intergovernmental Panel on Climate Change.’ New York, Cambridge University Press: 104.

IPCC 2021 - Climate Change (2021) ‘The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change’ [Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., ... and Zhou, B. (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. doi:10.1017/9781009157896.

Ishii, H.T., Tanabe, S.I. and Hiura, T. (2004) ‘Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems’, *Forest Science*, 50(3), pp. 342–355. Available at: https://doi.org/10.1093/forestscience/50.3.342.

Itô, H., Hino, T. and Sakuma, D. (2012) ‘Species abundance in floor vegetation of managed coppice and abandoned forest’, *Forest Ecology and Management*, 269, pp. 99–105. Available at: https://doi.org/10.1016/j.foreco.2011.12.017.

De Jaegere, T., Hein, S. and Claessens, H. (2016) ‘A review of the characteristics of small-leaved lime (Tilia cordata Mill.) and their implications for silviculture in a changing clima’, *Forests*, 7(3), pp. 1–21. Available at: https://doi.org/10.3390/f7030056.

Jansen, P. and Kuiper, L. (2004) ‘Double green energy from traditional coppice stands in the Netherlands’, *Biomass and Bioenergy*, 26(4), pp. 401–402. Available at: https://doi.org/10.1016/J.BIOMBIOE.2003.08.004.

Janzen, D.H. (1970) ‘Herbivores and the Number of Tree Species in Tropical Forests’, *https://doi.org/10.1086/282687*, 104(940), pp. 501–528. Available at: https://doi.org/10.1086/282687.

Joys, A. C., Fuller, R.J. and Dolman, P.M. (2004) ‘Influences of deer browsing, coppice history, and standard trees on the growth and development of vegetation structure in coppiced woods in lowland England’, *Forest Ecology and Management*, 202(1–3), pp. 23–37. Available at: https://doi.org/10.1016/j.foreco.2004.06.035.

Jucker, T. *et al.* (2014) ‘Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes’, *Ecology Letters*, 17(12), pp. 1560–1569. Available at: https://doi.org/10.1111/ELE.12382.

Käber, Y. *et al.* (2021) 'Tree recruitment is determined by stand structure and shade tolerance with uncertain role of climate and water relations', *Ecology and Evolution,* 11(17), pp. 12182–12203. Available at: https://doi.org/10.1002/ece3.7984.

Kadavý, J., Kneifl, M. and Knott, R. (2011) 'Establishment and selected characteristics of the Hády coppice and coppice-with-standards research plot (TARMAG I) FRAMEADAPT-Frameworks and possibilities of forest adaptation measures and strategies connected with Climate change View project'. Available at: https://doi.org/10.17221/3233-JFS.

Kammesheidt, L. (1998) 'The role of tree sprouts in the restoration of stand structure and species diversity in tropical moist forest after slash-and-burn agriculture in Eastern Paraguay', *Plant Ecology*, 139, pp. 155–165. Available at: https://doi.org/10.1145/2820783.2820787.

Kattenberg, A., Giorgi, F., Grassl, H., Meehl, G.A., Mitchell, J.F.B., Stouffer, R.J., Tokioka, T., Weaver, A.J., Wigley, T.M.L., (1996) 'Climate models—projections of future climate'. In: Houghton, J.T., Meira Filho, L.G., Callander, B.A., Harris, N., Kattenberg, A., Maskell, K. (Eds.), Climate Change, 1995. The Science of Climate Change. Contribution of WG I to the 2nd Assessment Report of the IPCC. Cambridge University Press, Cambridge, pp. 285–357.

Kellomäki, S. and Kolström, M. (1993) 'Computations on the yield of timber by Scots pine when subjected to varying levels of thinning under a changing climate in southern Finland', *Forest Ecology and Management*, 59, pp. 237–255.

Kelty, M.J. (1992) 'Comparative productivity of monocultures and mixed-species stands', in, pp. 125–141. Available at: https://doi.org/10.1007/978-94-015-8052-6_8.

Kennard, D.K. *et al.* (2002) 'Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest', *Forest Ecology and Management*, 162(2–3), pp. 197–208. Available at: https://doi.org/10.1016/S0378-1127(01)00506-0.

Kerhoulas, L.P., Kolb, T.E. and Koch, G.W. (2017) 'The influence of monsoon climate on latewood growth of southwestern ponderosa pine', *Forests*, 8(5), p. 140. Available at: https://doi.org/10.3390/f8050140.

Kern, C.C. *et al.* (2013) 'Canopy gap size influences niche partitioning of the ground-layer plant community in a northern temperate forest', *Journal of Plant Ecology,* 6(1), pp. 101–112. Available at: https://doi.org/10.1093/jpe/rts016.

Kirby, K.J., Buckley, G.P. and Mills, J. (2017) ‘Biodiversity implications of coppice decline, transformations to high forest and coppice restoration in British woodland’, *Folia Geobotanica*, 52(1), pp. 5–13. Available at: https://doi.org/10.1007/s12224-016-9252-1.

Kirschbaum, M.U.F. (2000) ‘Forest growth and species distribution in a changing climate’, *Tree Physiology*, 20, pp. 309–322.

Kitajima, K. and Fenner, M. (2009) ‘Ecology of seedling regeneration.’, *Seeds: the ecology of regeneration in plant communities*, pp. 331–359. Available at: https://doi.org/10.1079/9780851994321.0331.

Klopcic, M., Poljanec, A. and Boncina, A. (2012) ‘Modelling natural recruitment of European beech (Fagus sylvatica L.)’, *Forest Ecology and Management*, 284, pp. 142–151. Available at: https://doi.org/10.1016/j.foreco.2012.07.049.

Knapp, B.O., Olson, M.G. and Dey, D.C. (2017) ‘Early Stump Sprout Development after Two Levels of Harvest in a Midwestern Bottomland Hardwood Forest’, *Forest Science*, 63(4), pp. 377–387. Available at: https://doi.org/10.5849/fs-2016-029r2.

Kopecký, M., Hédl, R. and Szabó, P. (2013) ‘Non-random extinctions dominate plant community changes in abandoned coppices’, *Journal of Applied Ecology*, 50(1), pp. 79–87. Available at: https://doi.org/10.1111/1365-2664.12010.

Kroschel, W.A., King, S.L. and Keim, R.F. (2016) ‘Tree Regeneration by Seed in Bottomland Hardwood Forests: A Review’, *https://doi.org/10.1656/058.015.sp907*, 15(sp9), pp. 42–60. Available at: https://doi.org/10.1656/058.015.SP907.

Krstić, M.R., Kanjevac, B.R. and Babić, V.P. (2018) ‘Effects of extremely high temperatures on some growth parameters of sessile oak (Quercus petraea/Matt./Liebl.) seedlings in northeastern Serbia’, *Archives of Biological Sciences*, 70(3), pp. 521–529. Available at: https://doi.org/10.2298/ABS171215013K.

Kuehne, C. *et al.* (2020) ‘Seedling development and regeneration success after 10 years following group selection harvesting in a sessile oak (Quercus petraea [Mattuschka] Liebl.) stand’, *Annals of Forest Science*, 77(3). Available at: https://doi.org/10.1007/s13595-020-00972-y.

Kuznetsova, A., Brockhoff, P.B. and Christensen, R.H.B. (2017) ‘lmerTest Package: Tests in Linear Mixed Effects Models ’, *Journal of Statistical Software*, 82(13). Available at: https://doi.org/10.18637/jss.v082.i13.

Kvasnica, J. *et al.* (2023) ‘Forest Ecology and Management Multi-stemming enhances tree survival and growth in Borneo ’ s logged forests’, 544(April). Available at: https://doi.org/10.1016/j.foreco.2023.121140.

Langley, J.A., Drake, B.G. and Hungate, B.A. (2002) ‘Extensive belowground carbon storage supports roots and mycorrhizae in regenerating scrub oaks’, *Oecologia 2002 131:4*, 131(4), pp. 542–548. Available at: https://doi.org/10.1007/S00442-002-0932-6.

Langvall, O. and Nilsson, U. (2001) ‘Frost damage to planted Norway spruce seedlings Ð in¯uence of site preparation and seedling type’, *Forest Ecology and Management*, 141, pp. 223–235.

Larsson, L.A., (2003) ‘CDendro: Cybis Dendro dating program’, Cybis Elektronik & Data AB, Saltsjobaden, Sweden.

Lasch, P. *et al.* (2002) ‘Regional impact assessment on forest structure and functions under climate change—the Brandenburg case study’, *Forest Ecology and Management*, 162(1), pp. 73–86. Available at: https://doi.org/10.1016/S0378-1127(02)00051-8.

Lendzion, J. and Leuschner, C. (2008) ‘Growth of European beech (Fagus sylvatica L.) saplings is limited by elevated atmospheric vapour pressure deficits’, *Forest Ecology and Management*, 256(4), pp. 648–655. Available at: https://doi.org/10.1016/j.foreco.2008.05.008.

Lenth, R. V, Bolker, B., Buerkner, P., Vázquez, I.G., Herve, M., Jung, M., Love, J., Miguez, F., Piaskowski, J., Riebl, H., Singmann, H., (2024) ‘emmeans: Estimated Marginal Means, aka Least-Squares Means’, (https://cran.r-project.org/web/packages/emmeans/index.html)

Leonardsson, J. and Götmark, F. (2015) ‘Differential survival and growth of stumps in 14 woody species after conservation thinning in mixed oak-rich temperate forests’, *European Journal of Forest Research*, 134(1), pp. 199–209. Available at: https://doi.org/10.1007/s10342-014-0843-1.

Lett, S. and Dorrepaal, E. (2018) ‘Global drivers of tree seedling establishment at alpine treelines in a changing climate’, *Functional Ecology*, 32(7), pp. 1666–1680. Available at: https://doi.org/10.1111/1365-2435.13137.

Leuschner, C. *et al.* (2024) ‘A multi-criteria drought resistance assessment of temperate Acer, Carpinus, Fraxinus, Quercus, and Tilia species’, *Perspectives in Plant Ecology, Evolution and Systematics*, 62(November 2023), p. 125777. Available at: https://doi.org/10.1016/j.ppees.2023.125777.

Leuschner, C. and Meier, I.C. (2018) ‘The ecology of Central European tree species: Trait spectra, functional trade-offs, and ecological classification of adult trees’, *Perspectives in Plant Ecology, Evolution and Systematics*, 33(April), pp. 89–103. Available at: https://doi.org/10.1016/j.ppees.2018.05.003.

Lévesque, M., Walthert, L. and Weber, P. (2016) ‘Soil nutrients influence growth response of temperate tree species to drought’, *Journal of Ecology*, 104(2), pp. 377–387. Available at: https://doi.org/10.1111/1365-2745.12519.

Li, R. *et al.* (2022) ‘Effects of logging on the trade-off between seed and sprout regeneration of dominant woody species in secondary forests of the Natural Forest Protection Project of China’, *Ecological Processes*, 11(1). Available at: https://doi.org/10.1186/S13717-022-00363-3.

Linares, J.C. *et al.* (2009) ‘Competition and drought limit the response of water-use efficiency to rising atmospheric carbon dioxide in the Mediterranean fir Abies pinsapo’, *Oecologia*, 161(3), pp. 611–624. Available at: https://doi.org/10.1007/s00442-009-1409-7.

Lindenmayer, D.B. and Franklin, J.F. (2013) *Conserving forest biodiversity: a comprehensive multiscaled approach*. Island press.

Lindenmayer, D.B. and Laurance, W.F. (2012) ‘A history of hubris - Cautionary lessons in ecologically sustainable forest management’, *Biological Conservation*, pp. 11–16. Available at: https://doi.org/10.1016/j.biocon.2011.10.032.

Linder, M. (2000) ‘Developing adaptive forest management strategies to cope with climate change.’, *Tree physiology*, 20(5_6), pp. 299–307. Available at: https://doi.org/10.1093/treephys/20.5-6.299.

Lindner, M. *et al.* (1997) ‘Regional impacts of climatic change on forests in the state of Brandenburg, Germany’, *Agricultural and Forest Meteorology*, 84, pp. 123–135.

Lindner, M. *et al.* (2010) ‘Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems’, *Forest Ecology and Management*, 259(4), pp. 698–709. Available at: https://doi.org/10.1016/j.foreco.2009.09.023.

Loik, M.E. *et al.* (2004) ‘A multi-scale perspective of water pulses in dryland ecosystems: Climatology and ecohydrology of the western USA’, *Oecologia*, pp. 269–281. Available at: https://doi.org/10.1007/s00442-004-1570-y.

Longa, G. Della *et al.* (2020) ‘Coppicing and plant diversity in a lowland wood remnant in North–East Italy’, *Plant Biosystems*, 154(2), pp. 173–180. Available at: https://doi.org/10.1080/11263504.2019.1578276.

Loranger, H., Zotz, G. and Bader, M.Y. (2016) ‘Early establishment of trees at the alpine treeline: Idiosyncratic species responses to temperature-moisture interactions’, *AoB PLANTS*, 8. Available at: https://doi.org/10.1093/aobpla/plw053.

Lüdecke, D., Bartel, A., Schwemmer, C., Powell, Ch. Djalovski, A., Titz, J., (2024) ‘sjPlot: Data Visualization for Statistics in Social Science’, (https://cran.r-project.org/package=sjPlot)

Marchi, A. and Paletto, A. (2010) *Relationship between forest canopy and natural regeneration in the subalpine spruce-larch forest (north-east Italy).*

Mårell, A. *et al.* (2018) ‘The effect of deer browsing and understory light availability on stump mortality and sprout growth capacity in sessile oak’, *Forest Ecology and Management*, 430, pp. 134–142. Available at: https://doi.org/10.1016/J.FORECO.2018.08.015.

Martín-Benito, D. *et al.* (2008) ‘Growth response to climate and drought in Pinus nigra Arn. trees of different crown classes’, *Trees - Structure and Function*, 22(3), pp. 363–373. Available at: https://doi.org/10.1007/s00468-007-0191-6.

Mason, C.F. and Macdonald, S.M. (2002) ‘Responses of ground flora to coppice management in an English woodland - A study using permanent quadrats’, *Biodiversity and Conservation*, 11(10), pp. 1773–1789. Available at: https://doi.org/10.1023/A:1020395014155.

Matías, L., Zamora, R. and Castro, J. (2012) ‘Sporadic rainy events are more critical than increasing of drought intensity for woody species recruitment in a Mediterranean community’, *Oecologia*, 169(3), pp. 833–844. Available at: https://doi.org/10.1007/s00442-011-2234-3.

Matoušková, M. *et al.* (2022) ‘Coppicing modulates physiological responses of sessile oak (Quercus petraea Matt. Lieb.) to drought’, *Forest Ecology and Management*, 517, p. 120253. Available at: https://doi.org/10.1016/J.FORECO.2022.120253.

Matthews, J. (1989) *Silvicultural systems*.

Matula, R. *et al.* (2012) ‘The sprouting ability of the main tree species in Central European coppices: Implications for coppice restoration’, *European Journal of Forest Research*, 131(5), pp. 1501–1511. Available at: https://doi.org/10.1007/s10342-012-0618-5.

Matula, R. *et al.* (2015) ‘Measuring biomass and carbon stock in resprouting woody plants’, *PLoS ONE*, 10(2), pp. 12–15. Available at: https://doi.org/10.1371/journal.pone.0118388.

Matula, R. *et al.* (2019) ‘Pre-disturbance tree size, sprouting vigour and competition drive the survival and growth of resprouting trees’, *Forest Ecology and Management*, 446, pp. 71–79. Available at: https://doi.org/10.1016/j.foreco.2019.05.012.

Matula, R. *et al.* (2020) ‘Resprouting trees drive understory vegetation dynamics following logging in a temperate forest’, *Scientific Reports*, 10(1), pp. 1–10. Available at: https://doi.org/10.1038/s41598-020-65367-5.

Maurent, E. *et al.* (2023) ‘A common framework to model recovery in disturbed tropical forests: Common model for disturbed forest recovery’, *Ecological Modelling*, 483(June). Available at: https://doi.org/10.1016/j.ecolmodel.2023.110418.

McElhinny, C., Gibbons, P. and Brack, C. (2006) ‘An objective and quantitative methodology for constructing an index of stand structural complexity’, *Forest Ecology and Management*, 235(1–3), pp. 54–71. Available at: https://doi.org/10.1016/j.foreco.2006.07.024.

McEuen, A.B. and Curran, L.M. (2004) ‘Seed dispersal and recruitment limitation across spatial scales in temperate forest fragments’, *Ecology*, 85(2), pp. 507–518. Available at: https://doi.org/10.1890/03-4006.

McEvoy, T.J. (1995) ‘Introduction to forest ecology and silviculture’, *BR (USA)* [Preprint].

Mcgrath, M.J. *et al.* (2015) ‘Reconstructing European forest management from 1600 to 2010’, *Biogeosciences*, 12, pp. 4291–4316. Available at: https://doi.org/10.5194/bg-12-4291-2015.

Mejstřík, M. *et al.* (2024) ‘Differential roles of seed and sprout regeneration in forest diversity and productivity after disturbance’, *Forest Ecosystems*, 11(October 2023). Available at: https://doi.org/10.1016/j.fecs.2024.100198.

Mejstřík, M., Šrámek, M. and Matula, R. (2022) ‘The effects of stand density, standards and species composition on biomass production in traditional coppices’, *Forest Ecology and Management*, 504(September 2021). Available at: https://doi.org/10.1016/j.foreco.2021.119860.

Mészáros, I. *et al.* (2022) ‘Long-term radial growth and climate-growth relationships of Quercus petraea (Matt.) Liebl. and Quercus cerris L. in a xeric low elevation site from Hungary’, *Dendrochronologia*, 76(October). Available at: https://doi.org/10.1016/j.dendro.2022.126014.

Michelot, A. *et al.* (2012) ‘Differing growth responses to climatic variations and soil water deficits of Fagus sylvatica, Quercus petraea and Pinus sylvestris in a temperate forest’, *Forest Ecology and Management*, 265, pp. 161–171. Available at: https://doi.org/10.1016/j.foreco.2011.10.024.

Midgley, J.J. (1996) ‘Why the World’s Vegetation Is Not Totally Dominated by Resprouting Plants; Because Resprouters Are Shorter than Reseeders’, 19(1), pp. 92–95.

Miklín, J. and Čížek, L. (2014) ‘Erasing a European biodiversity hot-spot: Open woodlands, veteran trees and mature forests succumb to forestry intensification, succession, and logging in a UNESCO Biosphere Reserve’, *Journal for Nature Conservation*, 22(1), pp. 35–41. Available at: https://doi.org/10.1016/j.jnc.2013.08.002.

Millar, C.I., Stephenson, N.L. and Stephens, S.L. (2007) ‘Climate change and forests of the future: Managing in the face of uncertainty’, *Ecological Applications*, 17(8), pp. 2145–2151. Available at: https://doi.org/10.1890/06-1715.1.

Miller, A. *et al.* (2012) ‘Interactions between frequency and size of disturbance affect competitive outcomes’, *Ecological Research*, 27(4), pp. 783–791. Available at: https://doi.org/10.1007/S11284-012-0954-4.

Millet, J., Bouchard, A. and Édelin, C. (1998) ‘Plant Succession and Tree Architecture: An Attempt at Reconciling Two Scales of Analysis of Vegetation Dynamics’, *Acta Biotheoretica* , 46, pp. 1–22.

Mina, M. *et al.* (2018) ‘The symmetry of competitive interactions in mixed Norway spruce, silver fir and European beech forests’, *Journal of Vegetation Science*, 29(4), pp. 775–787. Available at: https://doi.org/10.1111/jvs.12664.

Mirabel, A. *et al.* (2023) ‘Increasing atmospheric dryness reduces boreal forest tree growth’, *Nature Communications*, 14(1). Available at: https://doi.org/10.1038/s41467-023-42466-1.

Modrý, M., Hubený, D. and Rejšek, K. (2004) ‘Differential response of naturally regenerated European shade tolerant tree species to soil type and light availability’, *Forest Ecology and Management*, 188(1–3), pp. 185–195. Available at: https://doi.org/10.1016/j.foreco.2003.07.029.

Mohr, H. and Schopfer, P. (2012) *Plant physiology*. Springer Science & Business Media.

Monteith, J. and Unsworth, M. (2013) Principles of environmental physics: plants, animals, and the atmosphere. Academic press.

Montgomery, R.A. and Chazdon, R.L. (2001) ‘Forest structure, canopy architecture, and light transmittance in tropical wet forests’, *Ecology*, 82(10), pp. 2707–2718. Available at: https://doi.org/10.1890/0012-9658(2001)082[2707:FSCAAL]2.0.CO;2.

Moreno-Fernández, D. *et al.* (2018) ‘Regeneration dynamics of mixed stands of Pinus pinaster Ait. and Pinus pinea L. in Central Spain’, *European Journal of Forest Research*, 137(1), pp. 17–27. Available at: https://doi.org/10.1007/s10342-017-1086-8.

Morin, X. *et al.* (2011) ‘Tree species richness promotes productivity in temperate forests through strong complementarity between species’, *Ecology Letters*, 14(12), pp. 1211–1219. Available at: https://doi.org/10.1111/J.1461-0248.2011.01691.X.

Mostacedo, B. *et al.* (2009) ‘Contributions of root and stump sprouts to natural regeneration of a logged tropical dry forest in Bolivia’, *Forest Ecology and Management*, 258(6), pp. 978–985. Available at: https://doi.org/10.1016/j.foreco.2008.09.059.

Müllerová, J. *et al.* (2016) ‘Detecting Coppice Legacies from Tree Growth’. Available at: https://doi.org/10.1371/journal.pone.0147205.

Müllerová, J., Hédl, R. and Szabó, P. (2015) ‘Coppice abandonment and its implications for species diversity in forest vegetation’, *Forest Ecology and Management*, 343, pp. 88–100. Available at: https://doi.org/10.1016/J.FORECO.2015.02.003.

Müllerová, J., Szabó, P. and Hédl, R. (2014) ‘The rise and fall of traditional forest management in southern Moravia: A history of the past 700 years’, *Forest Ecology and Management*, 331, pp. 104–115. Available at: https://doi.org/10.1016/j.foreco.2014.07.032.

Munier, A. *et al.* (2010) ‘The interacting effects of temperature, ground disturbance, and herbivory on seedling establishment: Implications for treeline advance with climate warming’, *Plant Ecology*, 210(1), pp. 19–30. Available at: https://doi.org/10.1007/s11258-010-9724-y.

Myers, J.A. and Harms, K.E. (2009) ‘Seed arrival, ecological filters, and plant species richness: A meta-analysis’, *Ecology Letters*, 12(11), pp. 1250–1260. Available at: https://doi.org/10.1111/j.1461-0248.2009.01373.x.

Naeem, S. *et al.* (1994) ‘Declining biodiversity can alter the performance of ecosystems’, *Nature*, 368(6473), pp. 734–737. Available at: https://doi.org/10.1038/368734a0.

Nakagawa, S., Johnson, P.C.D. and Schielzeth, H. (2017) ‘The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded’, *Journal of the Royal Society Interface*, 14(134). Available at: https://doi.org/10.1098/rsif.2017.0213.

Nestorovski, L. *et al.* (2009) ‘Contribution towards energetic potential and possibilities for forestry biomass energy utilization from coppice forests in some countries of South-Eastern Europe’, *Silva Balcanica*, (10), pp. 63–67.

N’Guessan, A.E. *et al.* (2019) ‘Drivers of biomass recovery in a secondary forested landscape of West Africa’, *Forest Ecology and Management*, 433(November 2018), pp. 325–331. Available at: https://doi.org/10.1016/j.foreco.2018.11.021.

Norby, R.J. *et al.* (2005) *Forest response to elevated CO 2 is conserved across a broad range of productivity*. Available at: www.pnas.orgcgidoi10.1073pnas.0509478102.

Norden, N. *et al.* (2009) ‘Resilience of tropical rain forests: Tree community reassembly in secondary forests’, *Ecology Letters*, 12(5), pp. 385–394. Available at: https://doi.org/10.1111/j.1461-0248.2009.01292.x.

Novick, K.A. *et al.* (2016) ‘The increasing importance of atmospheric demand for ecosystem water and carbon fluxes’, *Nature Climate Change*, 6(11), pp. 1023–1027. Available at: https://doi.org/10.1038/nclimate3114.

Ojeda', F. (1998) 'Biogeography of seeder and resprouter Erica species in the Cape Floristic Region—Where are the resprouters?', *Biological Journal of the Linnean Society*, 63(3), pp. 331–347. Available at: https://doi.org/10.1111/J.1095-8312.1998.TB01521.X.

Ollikainen, M. (2014) 'Forestry in bioeconomy – smart green growth for the humankind', *Scandinavian Journal of Forest Research*, 29(4), pp. 360–366. Available at: https://doi.org/10.1080/02827581.2014.926392.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., (2016) 'Vegan: Community Ecology Package', R Package Version 2.3-5.

Pan, Y. *et al.* (2011) 'A Large and Persistent Carbon Sink in the World's Forests', *Science*, 333(6045), pp. 988–993. Available at: https://doi.org/10.1126/science.1201609.

Pan, Y. *et al.* (2013) 'The Structure, Distribution, and Biomass of the World's Forests', *Annual Review of Ecology, Evolution, and Systematics*, 44(1), pp. 593–622. Available at: https://doi.org/10.1146/annurev-ecolsys-110512-135914.

Paquette, A. *et al.* (2018) 'Climate Change Could Negate Positive Tree Diversity Effects on Forest Productivity: A Study Across Five Climate Types in Spain and Canada', *Ecosystems*, 21(5), pp. 960–970. Available at: https://doi.org/10.1007/s10021-017-0196-y.

Paquette, A. and Messier, C. (2011) 'The effect of biodiversity on tree productivity: From temperate to boreal forests', *Global Ecology and Biogeography*, 20(1), pp. 170–180. Available at: https://doi.org/10.1111/j.1466-8238.2010.00592.x.

Pardos, M. *et al.* (2021) 'The greater resilience of mixed forests to drought mainly depends on their composition: Analysis along a climate gradient across Europe', *Forest Ecology and Management*, 481(September 2020), p. 118687. Available at: https://doi.org/10.1016/j.foreco.2020.118687.

Park, J. *et al.* (2019) 'The influence of tree structural and species diversity on temperate forest productivity and stability in Korea', *Forests*, 10(12). Available at: https://doi.org/10.3390/f10121113.

Parker, G.G. (1995) 'Structure and microclimate of forest canopies', *Forest Canopy* [Preprint].

Pau, M. *et al.* (2022) ‘Site index as a predictor of the effect of climate warming on boreal tree growth’, *Global Change Biology*, 28(5), pp. 1903–1918. Available at: https://doi.org/10.1111/gcb.16030.

Peng, C. *et al.* (2011) ‘A drought-induced pervasive increase in tree mortality across Canada’s boreal forests’, *Nature Climate Change*, 1(9), pp. 467–471. Available at: https://doi.org/10.1038/nclimate1293.

Penuelas, J. and Filella, I. (2003) ‘Deuterium labelling of roots provides evidence of deep water access and hydraulic lift by Pinus nigra in a Mediterranean forest of NE Spain’, *Environmental and Experimental Botany*, 49(5), p. 201?/ 208. Available at: https://doi.org/10.1139/y75-101.

Peterken GF (1996) ‘Natural woodland’. Cambridge University Press, Cambridge

Pietras, J. *et al.* (2016) ‘Oak sprouts grow better than seedlings under drought stress’, *http://iforest.sisef.org/*, 9(4), p. 529. Available at: https://doi.org/10.3832/IFOR1823-009.

Pigott, C.D. and Pigott, S. (1993) ‘Water as a Determinant of the Distribution of Trees at the Boundary of the Mediterranean Zone’, *Journal of Ecology*, 81(3), pp. 557–566. Available at: https://doi.org/10.2307/2261534.

Piotto, D. (2008) ‘A meta-analysis comparing tree growth in monocultures and mixed plantations’, *Forest Ecology and Management*, 255(3–4), pp. 781–786. Available at: https://doi.org/10.1016/j.foreco.2007.09.065.

Poorter, L. and Markesteijn, L. (2008) ‘Seedling traits determine drought tolerance of tropical tree species’, *Biotropica*, 40(3), pp. 321–331. Available at: https://doi.org/10.1111/j.1744-7429.2007.00380.x.

Premoli, A.C. and Steinke, L. (2008) ‘Genetics of sprouting: Effects of long-term persistence in fire-prone ecosystems’, *Molecular Ecology*, 17(17), pp. 3827–3835. Available at: https://doi.org/10.1111/j.1365-294X.2008.03889.x.

Pretzsch, H. (2009) ‘Forest Dynamics, Growth, and Yield’, in H. Pretzsch (ed.) *Forest Dynamics, Growth and Yield: From Measurement to Model*. Berlin, Heidelberg: Springer Berlin Heidelberg, pp. 1–39. Available at: https://doi.org/10.1007/978-3-540-88307-4_1.

Pretzsch, H. *et al.* (2013) ‘Productivity of mixed versus pure stands of oak (Quercus petraea (Matt.) Liebl. and Quercus robur L.) and European beech (Fagus sylvatica L.) along an ecological gradient', *European Journal of Forest Research*, 132(2), pp. 263–280. Available at: https://doi.org/10.1007/s10342-012-0673-y.

Pretzsch, H. *et al.* (2020) 'Stand growth and structure of mixed-species and monospecific stands of Scots pine (Pinus sylvestris L.) and oak (Q. robur L., Quercus petraea (Matt.) Liebl.) analysed along a productivity gradient through Europe', *European Journal of Forest Research*, 139(3), pp. 349–367. Available at: https://doi.org/10.1007/s10342-019-01233-y.

Pretzsch, H. and Zenner, E.K. (2017) 'Toward managing mixed-species stands: from parametrization to prescription', *Forest Ecosystems*, 4(1). Available at: https://doi.org/10.1186/s40663-017-0105-z.

Pyttel, P.L. *et al.* (2013) 'The effect of harvesting on stump mortality and re-sprouting in aged oak coppice forests', *Forest Ecology and Management*, 289, pp. 18–27. Available at: https://doi.org/10.1016/J.FORECO.2012.09.046.

R Core Team, (2022) 'A language and environment for statistical computing'. R Foundation for Statistical Computing (4.2.0), R Foundation for Statistical Computing. https://www.r-project.org/

Rackham, O. (2003) 'Ancient woodland: its history, vegetation and uses in England (revised edition) ', Castlepoint Press, Dalbeattie, Scotland

Rackham, O., (2006) 'Woodlands', vol. 284. Collins, London.

Rackham, O., (2008) 'Ancient woodlands: modern threats', New Phytologist 180, 571– 586.

Radoglou, K. *et al.* (2009) 'A review on the ecology and silviculture of limes: (Tilia cordata Mill., Tilia platyphyllos Scop, and Tilia tomentosa Moench.) in Europe', *Bodenkultur*, 60(3), pp. 9–19.

Radtke, A. *et al.* (2013) 'Traditional coppice forest management drives the invasion of Ailanthus altissima and Robinia pseudoacacia into deciduous forests', *Forest Ecology and Management*, 291, pp. 308–317. Available at: https://doi.org/10.1016/j.foreco.2012.11.022.

Reich, P.B. *et al.* (1998) 'Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light', *Functional Ecology*, 12(3), pp. 327–338. Available at: https://doi.org/10.1046/j.1365-2435.1998.00208.x.

Reyer, C. *et al.* (2014) ‘Projections of regional changes in forest net primary productivity for different tree species in Europe driven by climate change and carbon dioxide’, *Annals of Forest Science*, 71(2), pp. 211–225. Available at: https://doi.org/10.1007/s13595-013-0306-8.

Reyer, C.P.O. *et al.* (2013) ‘A plant’s perspective of extremes: Terrestrial plant responses to changing climatic variability’, *Global Change Biology*, pp. 75–89. Available at: https://doi.org/10.1111/gcb.12023.

del Río, M. *et al.* (2022) ‘Emerging stability of forest productivity by mixing two species buffers temperature destabilizing effect’, *Journal of Applied Ecology*, 59(11), pp. 2730–2741. Available at: https://doi.org/10.1111/1365-2664.14267.

Rossi, S., Anfodillo, T. and Menardi, R. (2006) ‘Trephor: A New Tool for Sampling Microcores from tree stems’, *IAWA Journal*, 27(1), pp. 89–97. Available at: https://doi.org/10.1163/22941932-90000139.

Salamanca, Á.E. (2022) ‘Effects of Climate Change on Forest Regeneration in Central Spain’, *Atmosphere*, 13(7). Available at: https://doi.org/10.3390/atmos13071143.

Scheller, R.M. and Mladenoff, D.J. (2004) ‘A forest growth and biomass module for a landscape simulation model, LANDIS: Design, validation, and application’, *Ecological Modelling*, 180(1), pp. 211–229. Available at: https://doi.org/10.1016/j.ecolmodel.2004.01.022.

Schulze, E.-D., Beck, E. and Müller-Hohenstein, K. (2005) *Plant ecology*. Springer Science & Business Media.

Seidl, R. *et al.* (2017) ‘Forest disturbances under climate change’, *Nature Climate Change*, 7(6), pp. 395–402. Available at: https://doi.org/10.1038/nclimate3303.

Senf, C. and Seidl, R. (2022) ‘Post-disturbance canopy recovery and the resilience of Europe’s forests’, *Global Ecology and Biogeography*, 31(1), pp. 25–36. Available at: https://doi.org/10.1111/geb.13406.

Shiferaw, W., Demissew, S. and Bekele, T. (2018) ‘Ecology of soil seed banks: Implications for conservation and restoration of natural vegetation: A review’, *International Journal of*

Biodiversity and Conservation, 10(10), pp. 380–393. Available at: https://doi.org/10.5897/ijbc2018.1226.

Silva Pedro, M., Rammer, W. and Seidl, R. (2016) ‘A disturbance-induced increase in tree species diversity facilitates forest productivity’, *Landscape Ecology*, 31(5), pp. 989–1004. Available at: https://doi.org/10.1007/s10980-015-0317-y.

Sjölund, M.J. and Jump, A.S. (2013) ‘The benefits and hazards of exploiting vegetative regeneration for forest conservation management in a warming world’, *Forestry*, 86(5), pp. 503–513. Available at: https://doi.org/10.1093/forestry/cpt030.

Smith, F.W. and Long, J.N. (1989) ‘The Influence of Canopy Architecture on Stemwood Production and Growth Efficiency of Pinus contorta Var. latifolia’, *The Journal of Applied Ecology*, 26(2), p. 681. Available at: https://doi.org/10.2307/2404092.

Song, X. *et al.* (2020) ‘When do Janzen – Connell effects matter? A phylogenetic meta-analysis of conspecific negative distance and density dependence experiments’, *Ecology Letters*, 24(3), pp. 608–620. Available at: https://doi.org/10.1111/ele.13665.

Spies, T.A. (1998) ‘Forest Structure: A Key to the Ecosystem’, *Northwest Scientific Association*, 72(2), pp. 34–39.

Spinelli, R., Ebone, A. and Gianella, M. (2014) ‘Biomass production from traditional coppice management in northern Italy’, *Biomass and Bioenergy*, 62, pp. 68–73. Available at: https://doi.org/10.1016/j.biombioe.2014.01.014.

Spitzer, L. *et al.* (2008) ‘Does closure of traditionally managed open woodlands threaten epigeic invertebrates? Effects of coppicing and high deer densities’, *Biological Conservation*, 141(3), pp. 827–837. Available at: https://doi.org/10.1016/j.biocon.2008.01.005.

Šplíchalová, M. *et al.* (2012) ‘Probability model of sessile oak (Quercus petraea (Matt.) Liebl.) stump sprouting in the Czech Republic’, *European Journal of Forest Research*, 131(5), pp. 1611–1618. Available at: https://doi.org/10.1007/s10342-012-0628-3.

Šrámek, M. *et al.* (2020) ‘Effective determination of biomass in oak coppices’, *Trees - Structure and Function* [Preprint], (0123456789). Available at: https://doi.org/10.1007/s00468-020-01987-8.

Šrámek, M. *et al.* (2023) ‘Effective woody biomass estimation in poplar short-rotation coppices – Populus nigra × P. maximowiczii’, *iForest - Biogeosciences and Forestry*, 16(4), pp. 202–209. Available at: https://doi.org/10.3832/ifor4200-016.

Steckel, M. *et al.* (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(February), p. 117908. Available at: https://doi.org/10.1016/j.foreco.2020.117908.

Stevens-Rumann, C.S. *et al.* (2018) ‘Evidence for declining forest resilience to wildfires under climate change’, *Ecology Letters*. Blackwell Publishing Ltd, pp. 243–252. Available at: https://doi.org/10.1111/ele.12889.

Stojanović, M., Sánchez-Salguero, R., *et al.* (2017) ‘Forecasting tree growth in coppiced and high forests in the Czech Republic. The legacy of management drives the coming Quercus petraea climate responses’, *Forest Ecology and Management*, 405, pp. 56–68. Available at: https://doi.org/10.1016/J.FORECO.2017.09.021.

Stojanović, M., Szatniewska, J., *et al.* (2017) ‘Transpiration and water potential of young Quercus petraea (M.) Liebl. coppice sprouts and seedlings during favourable and drought conditions’, *Journal of Forest Science*, 63(7), pp. 313–323. Available at: https://doi.org/10.17221/36/2017-JFS.

Stojanović, Marko *et al.* (2016) ‘Responses in young Quercus petraea: coppices and standards under favourable and drought conditions’, 76, pp. 127–136. Available at: https://doi.org/10.12657/denbio.076.012.

Strubelt, I. *et al.* (2019) ‘Inter-annual variation in species composition and richness after coppicing in a restored coppice-with-standards forest’, *Forest Ecology and Management*, 432, pp. 132–139. Available at: https://doi.org/10.1016/j.foreco.2018.09.014.

Svátek, M. and Matula, R. (2015) ‘Fine-scale spatial patterns in oak sprouting and mortality in a newly restored coppice’, *Forest Ecology and Management*, 348, pp. 117–123. Available at: https://doi.org/10.1016/j.foreco.2015.03.048.

Swanson, M.E. *et al.* (2011) ‘The forgotten stage of forest succession: Early-successional ecosystems on forest sites’, *Frontiers in Ecology and the Environment*, 9(2), pp. 117–125. Available at: https://doi.org/10.1890/090157.

Szabó, P. (2010) ‘Driving forces of stability and change in woodland structure: A case-study from the Czech lowlands’, *Forest Ecology and Management*, 259(3), pp. 650–656. Available at: https://doi.org/10.1016/j.foreco.2009.11.026.

Szabó, P. and Hédl, R. (2013) ‘Socio-Economic Demands, Ecological Conditions and the Power of Tradition: Past Woodland Management Decisions in a Central European Landscape’, *Landscape Research*, 38(2), pp. 243–261. Available at: https://doi.org/10.1080/01426397.2012.677022.

Thom, D. and Seidl, R. (2016) ‘Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests’, *Biological reviews of the Cambridge Philosophical Society*, 91(3), pp. 760–781. Available at: https://doi.org/10.1111/brv.12193.

Thompson, Ian. *et al.* (2009) *Forest resilience, biodiversity, and climate change : a synthesis of the biodiversity, resilience, stabiblity relationship in forest ecosystems*. Secretariat of the convention on the biological diversity.

Tiebel, K., Huth, F. and Wagner, S. (2018) ‘Soil seed banks of pioneer tree species in european temperate forests: A review’, *IForest*, 11(1), pp. 48–57. Available at: https://doi.org/10.3832/ifor2400-011.

Toïgo, M. *et al.* (2020) ‘Temporal trends in tree defoliation and response to multiple biotic and abiotic stresses’, *Forest Ecology and Management*, 477(February), p. 118476. Available at: https://doi.org/10.1016/j.foreco.2020.118476.

Török, P. *et al.* (2018) ‘Beyond the species pool: modification of species dispersal, establishment, and assembly by habitat restoration’, *Restoration Ecology*, 26(June), pp. S65–S72. Available at: https://doi.org/10.1111/rec.12825.

Travis Swaim, J. *et al.* (2016) ‘Predicting the height growth of oak species (Quercus) reproduction over a 23-year period following clearcutting’, *Forest Ecology and Management*, 364, pp. 101–112. Available at: https://doi.org/10.1016/J.FORECO.2016.01.005.

Del Tredici, P. (2001) ‘Sprouting in temperate trees: A morphological and ecological review’, *Botanical Review*. New York Botanical Garden Press, pp. 121–140. Available at: https://doi.org/10.1007/BF02858075.

Trouvé, R. *et al.* (2014) ‘Growth partitioning in forest stands is affected by stand density and summer drought in sessile oak and Douglas-fir’, *Forest Ecology and Management*, 334, pp. 358–368. Available at: https://doi.org/10.1016/j.foreco.2014.09.020.

Unrau A, Becker G, Spinelli R, Lazdina D, Magagnotti N, Nicolescu VN, Buckley P, Bartlett D, Kofman PD. editors. (2018) ‘Coppice forests in Europe’. Freiburg i. Br. Germany: Albert Ludwig University.

Valbuena, R. *et al.* (2012) ‘Diversity and equitability ordering profiles applied to study forest structure’, *Forest Ecology and Management*, 276, pp. 185–195. Available at: https://doi.org/10.1016/j.foreco.2012.03.036.

Valiente-Banuet, A. and Verdú, M. (2008) ‘Temporal shifts from facilitation to competition occur between closely related taxa’, *Journal of Ecology*, 96(3), pp. 489–494. Available at: https://doi.org/10.1111/j.1365-2745.2008.01357.x.

Valladares, F. and Niinemets, Ü. (2008) ‘Shade tolerance, a key plant feature of complex nature and consequences’, *Annual Review of Ecology, Evolution, and Systematics*, 39, pp. 237–257. Available at: https://doi.org/10.1146/annurev.ecolsys.39.110707.173506.

Vanhellemont, M. *et al.* (2019) ‘Distinct growth responses to drought for oak and beech in temperate mixed forests’, *Science of the Total Environment*, 650, pp. 3017–3026. Available at: https://doi.org/10.1016/j.scitotenv.2018.10.054.

Vayreda, J. *et al.* (2012) ‘Recent climate changes interact with stand structure and management to determine changes in tree carbon stocks in Spanish forests’, *Global Change Biology*, 18(3), pp. 1028–1041. Available at: https://doi.org/10.1111/j.1365-2486.2011.02606.x.

Vilà, M. *et al.* (2007) ‘Species richness and wood production: A positive association in Mediterranean forests’, *Ecology Letters*, 10(3), pp. 241–250. Available at: https://doi.org/10.1111/j.1461-0248.2007.01016.x.

Vilà, M. *et al.* (2013) ‘Disentangling Biodiversity and Climatic Determinants of Wood Production’, *PLoS ONE*, 8(2). Available at: https://doi.org/10.1371/journal.pone.0053530.

Vild, O. *et al.* (2013) ‘Experimental restoration of coppice-with-standards: Response of understorey vegetation from the conservation perspective’, *Forest Ecology and Management*, 310, pp. 234–241. Available at: https://doi.org/10.1016/J.FORECO.2013.07.056.

Vodka, Š. and Cizek, L. (2013) ‘The effects of edge-interior and understorey-canopy gradients on the distribution of saproxylic beetles in a temperate lowland forest’, *Forest Ecology and Management*, 304, pp. 33–41. Available at: https://doi.org/10.1016/j.foreco.2013.04.007.

Weigel, D.R. and Joanne Peng, C.Y. (2002) ‘Predicting stump sprouting and competitive success of five oak species in southern Indiana’, *Canadian Journal of Forest Research*, 32(4), pp. 703–712. Available at: https://doi.org/10.1139/x02-042.

Weil, R. and Brady, N. (2017) *The Nature and Properties of Soils. 15th edition*.

Whitehead, D. (2011) ‘Forests as carbon sinks - Benefits and consequences’, *Tree Physiology*, 31(9), pp. 893–902. Available at: https://doi.org/10.1093/treephys/tpr063.

Wickham H (2009) ‘ggplot2: elegant graphics for data analysis’. Springer, New York

Wyckoff, P.H. and Clark, J.S. (2005) ‘Tree growth prediction using size and exposed crown area’, *Canadian Journal of Forest Research*, 35(1), pp. 13–20. Available at: https://doi.org/10.1139/x04-142.

Xue, Y. *et al.* (2014) ‘Relative importance of various regeneration recruits in different recovery stages of Quercus variabilis forest after selective logging’, *Forest Systems*, 23(2), pp. 199–208. Available at: https://doi.org/10.5424/fs/2014232-03263.

Yamamoto, S.-I. (2000) *Invited Review Forest Gap Dynamics and Tree Regeneration*, *J. For. Res*.

Yan, Q.L., Zhu, J.J. and Yu, L.Z. (2012) ‘Seed Regeneration Potential of Canopy Gaps at Early Formation Stage in Temperate Secondary Forests, Northeast China’, *PLOS ONE*, 7(6), p. e39502. Available at: https://doi.org/10.1371/JOURNAL.PONE.0039502.

Zapater, M. *et al.* (2011) ‘Evidence of hydraulic lift in a young beech and oak mixed forest using 18O soil water labelling’, *Trees - Structure and Function*, 25(5), pp. 885–894. Available at: https://doi.org/10.1007/s00468-011-0563-9.

Zell, J. *et al.* (2019) ‘Modeling ingrowth for empirical forest prediction systems’, *Forest Ecology and Management*, 433, pp. 771–779. Available at: https://doi.org/10.1016/j.foreco.2018.11.052.

Zellweger, F. *et al.* (2020) ‘Forest microclimate dynamics drive plant responses to warming’, *Science*, 368, pp. 772–775. Available at: https://www.

Zhang, T. *et al.* (2018) ‘Restoring temperate secondary forests by promoting sprout regeneration: Effects of gap size and within-gap position on the photosynthesis and growth of stump sprouts with contrasting shade tolerance’, *Forest Ecology and Management*, 429(March), pp. 267–277. Available at: https://doi.org/10.1016/j.foreco.2018.07.025.

Zhang, Y., Chen, H.Y.H. and Reich, P.B. (2012) ‘Forest productivity increases with evenness, species richness and trait variation: A global meta-analysis’, *Journal of Ecology*, 100(3), pp. 742–749. Available at: https://doi.org/10.1111/j.1365-2745.2011.01944.x.

Zurbriggen, N. *et al.* (2013) ‘Performance of germinating tree seedlings below and above treeline in the Swiss Alps’, *Plant Ecology*, 214(3), pp. 385–396. Available at: https://doi.org/10.1007/s11258-013-0176-z.

Zweifel, R. *et al.* (2021) ‘Why trees grow at night’, *New Phytologist*, 231(6), pp. 2174–2185. Available at: https://doi.org/10.1111/nph.17552.