**Czech University of Life Sciences Prague**

**Faculty of Environmental Sciences**

**Department of Forest Ecology**

# Master's Thesis

## Tree growth and water deficit in a planted mixed forest in Germany

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# CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Environmental Sciences

# DIPLOMA THESIS ASSIGNMENT

Ing. Joana Camps Clot

Nature Conservation

Thesis title

**Tree growth and water deficit in a planted mixed forest in Germany**

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**Objectives of thesis**

Growing trees in species-rich, mixed forests instead of monocultures is considered as a key step for making planted forests more resilient and productive under climate change. However, there is still little empirical information on this issue from temperate forests of Central Europe. The thesis aims to study and compare tree growth and water deficit of trees in forest monocultures and species mixtures in a BIOTREE Kaltenborn experiment in Germany.

**Methodology**

Data for the thesis will be collected from automatic dendrometers, which were installed at a BIOTREE experiment near Kaltenborn (Germany) in March 2021 (before the growing season). In the experiment, four main species were planted in 2003: Picea abies, Pseudotsuga menziesii, Quercus robur, and Fagus sylvatica. These species were planted in monocultures and all possible species mixtures, with diversity levels ranging from 2 to 4 species. The automatic dendrometers are installed on 12 trees of each species in each species combination, on which they register stem diameter changes every 15 minutes. The data will be downloaded after the end of the growing season in 2021 and then will be processed and analyzed using R software. From the raw data, growth and water deficit will be derived for each tree at different temporal scales. For the statistical analyses, generalized additive models, as well as linear models, will be used.

**The proposed extent of the thesis**
30 pages

**Keywords**
tree diversity, planted forest, climate change, dendrometers.

**Recommended information sources**

Jucker, T., Bouriaud, O., Avacaritei, D., Coomes, D.A., 2014. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: Linking patterns and processes. Ecology Letters. 17, 1560–1569.

Jucker, T., Koricheva, J., Finér, L., Bouriaud, O., Iacopetti, G., Coomes, D.A., 2020. Good things take time—Diversity effects on tree growth shift from negative to positive during stand development in boreal forests. Journal of Ecology. 1365-2745.13464.

Paquette, A. a kol. 2018. A million and more trees for science. Nature Ecology and Evolution

Ratcliffe, S. a kol. 2017. Biodiversity and ecosystem functioning relations in European forests depend on environmental context. Ecology Letters. 20, 1414–1426.

Scherer-Lorenzen, M., Schulze, E.D., Don, A., Schumacher, J., Weller, E., 2007. Exploring the functional significance of forest diversity: A new long-term experiment with temperate tree species (BIOTREE). Perspect. Plant Ecol. Evol. Syst. 9, 53–70.

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# Tree growth and water deficit in a planted mixed forest in Germany

## Abstract

Droughts, wildfires or invasive insect outbreaks are some of the consequences of global warming, resulting in irreversible impacts on forest ecosystems. At tree species level, climate change effects remain largely unexplored. Mixed forests contribute to essential ecosystem services and provide more structural and species diversity than single-species forests. This study aims to evaluate the response of planted trees in the biodiversity experiment BIOTREE in Kaltenborn, Germany. I focus on four major central European tree species: European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*), common oak (*Quercus robur*), and Douglas fir (*Pseudotsuga menziesii*). Each species was examined in monoculture as well as two-, three- and four-species mixtures. Stem growth and tree water deficit were analysed and compared for each case (in forest monocultures and species mixtures). Data for the thesis was collected from dendrometers and processed using linear and generalized additive models. The study found that monocultures had the fastest growth but also were the most sensitive to tree water deficit. However, it was conducted in an exceptionally favorable growing season. Even though monocultures have shown higher radius growth, mixed-species forests could be essential to enhance productivity and ecosystem resilience under climate change.

# Růst stromu a nedostatek vody ve vysazeném smíšeném lese v Německu

**Abstrakt**

Sucha, požáry nebo masová reprodukce invazních druhů hmyzu jsou některými z důsledků globálního oteplování, které mají nezvratné dopady na lesní ekosystémy. Efekty klimatické změny na jednotlivé druhy stromů jsou z většiny neprozkoumané. Smíšené lesy se podílejí na základních ekosystémových službách a poskytují více strukturální a druhové diverzity než jednodruhové lesy. Tato práce se zaměřuje na zhodnocení účinku vysazených stromů v biodiverzitním experimentu BIOTREE v německém Kaltenbornu. Zaměřuji se na čtyři středoevropské druhy stromů: buk lesní (Fagus sylvatica), Smrk ztepilý (Picea abies), dub letní (Quercus robur) a douglasku tisolistou (Pseudotsuga menziesii). Každý z těchto druhů byl zkoumán v monokultuře, ale i ve smíšených lesích obsahujících dva, tři a čtyři druhy stromů. V monokultuře i v dříve uvedených smíšených lesích byl vždy analyzován a srovnán růst kmene a nedostatek vody. Data pro tuto diplomovou práci byla získána pomocí dendometrů a zpracována v R studiu, konkrétně byly využity "linear model" a "generalized additive model". Bylo zjištěno, že monokultury rychleji rostou, jsou ale také nejcitlivější k nedostatku vody. K tomuto závěru došlo ve vyjímečně příznivém růstovém období. Přestože monokultury prokázaly větší růst, smíšené lesy by mohly být zásadní ke zlepšení produktivity a ekosystémové odolnosti při klimatické změně.

**Klíčová slova:** diverzita stromů, vysázený les, klimatická změna, dendometry, nedostatek vody pro stromy, BIOTREE

# Table of content

# 1 Introduction

Forests are essential to humanity: they contribute to several crucial ecosystem services, provide us with a wealth of goods and services, support high levels of biodiversity, and presently encompass 30% of the planet's land surface (Gamfeld et al., 2013; Ratcliffe et al., 2017; Paquette et al., 2018). Susceptible to human population growth, nearly 30% of the Earth's forest area has been lost over the last 5.000 years, and it is steadily shrinking as a result of deforestation and agricultural conversion. (Paquette et al., 2018).

It is known that ecosystems, therefore forests, would ultimately lose most of their ability to function properly if biodiversity loss continues (Cardinale et al., 2012; Loreau & Hector, 2001). Simultaneously, the study that has been conducted over two decades about the relationship between variety and ecosystem functioning has shown that species loss frequently results in reductions in ecosystem functions (Hooper et al., 2012). As a result, diversity not only promotes but also stabilizes ecological functioning throughout time (Hautier et al., 2014).

Since the 90s, ecologists have been carefully seeking to understand how biodiversity loss may influence the functioning of ecosystems alarmed by the threat of a global biodiversity crisis (Scherer-Lorenzen et al., 2007).

Despite the overall favorable association between tree diversity and productivity, there is a degree of variation in how diversity influences tree growth (Jucker et al., 2014a). A large part of the variation is explained by differences in climate, soils, canopy structure and species composition, as recent research has demonstrated. (Ratcliffe et al., 2016; Baeten et al., 2019). However, little is understood about how and why the impacts of variety on tree growth alter over time as a stand develops (Taylor et al., 2020).

Reduced pest and disease burdens, trophic interactions, and greater nutrient and water- and efficiency below-ground have been proposed as mechanisms to explain the favorable impacts of diversity on tree growth in forests. (Sapijanskas et al., 2013; Ammer, 2019).

According to Jucker et al (2020), an important mechanism is the combination of species with different crown structures and the ability to tolerate shadow, which results in more efficient use of canopy space (Sapijanskas et al., 2014; Jucker et al., 2014a; Kunz et al., 2019). Crown complementarity effects can reduce light competition between trees, allowing them to develop faster in a mixed forest (Kunz et al., 2019; Searle & Chen, 2020). However, canopy filling is a slow process that occurs throughout several growing seasons when neighboring trees expand their crowns and compete for light. As a result, overyielding in which a combination of species outperforms a monoculture can take years to appear in regeneration stands (Jucker et al., 2020).

# 2   Objectives of the thesis

The thesis aims to study and compare tree growth and water deficit of four tree species planted in monocultures and species mixtures in Kaltenborn, a temperate forest in Germany as part of the BIOTREE net experiments.

This study focuses on the following topics:

- Tree growth response to different types of species mixtures and diversity.
- Tree water deficit (TWD) to different types of species mixtures and diversity.
- Relations of the previous factors with temperature.
- Implications of the findings for forest management in a context of climate change.

We expect that:

a) Drought will limit growth and increase TWD. Trees growing in a mixed-species plot will be less affected by TWD, and therefore will grow more than trees in a monoculture environment.
b) Mixed-species plots will have a stabilizing effect on trees. Growth rates in monocultures will be more affected by TWD as it will take more time to recover from drought.

# 3 Literature Review

## 3.1 Linking biodiversity and forest functioning

### 3.1.1 Forest loss and monocultures

Even though tree planting helps to restore forest cover and alleviates deforestation (Liu et al., 2018), almost all industrial plantations are single-species monocultures consisting primarily of fast-growing cultivars or hybrids: pine, eucalypt, acacia, spruce, poplar or larch (Carle & Holmgren, 2008) produced under a stable and predictable environment through intensive silviculture (Paquette et al., 2018).

Monocultures have long been the most common kind of plantation, and it is expected that by the middle of the century, they will provide more than half of all industrial timber (Carle & Holmgren, 2008). However, with a growing understanding of the environmental costs of high-input systems, a changing climate, an increase in exotic pests and diseases, and a greater emphasis on other ecosystem services provided by forests, the historical arguments in favor of monocultures are becoming less compelling (Bauhus et al., 2017). Thence, as climate change and resource scarcity worsen, mixed-species plantations are gaining popularity (Liu et al., 2018).

### 3.1.2 Mixed-species forests

Indeed, research over the last quarter-century has shown that higher diversity levels improve ecosystem functioning as well as ecosystem services provision, therefore tree species richness in production forests has positive correlations with multiple ecosystem services (Duffy et al., 2017). According to the study conducted by Gamfeldt et al. (2013), there is a favorable association between tree species richness and proxies for other biodiversity components. A mixed forest, defined by Bravo-Oviedo. et al (2014), is a forest unit where excluding linear formations, at least two tree species coexist at any developmental period, sharing common resources like light, water, and/or soil nutrients. Heinrich Cotta, who opposed monocultures as early as 1828, highlighted the benefits of mixed-species forests: "Since not all tree species utilize resources in the same manner, growth is more lively in mixed stands, and neither insects nor storms can do as much damage; also, a wider range of timber will be

available everywhere to satisfy different demands …" (translated in Scherer-Lorenzen et al., 2005).

Furthermore, mixed-species forests generally capture and store more carbon from the atmosphere than species-poor communities on an equal footing (Fichtner et al., 2018) while better coping with climate change-related stress and other biotic disturbances such as exotic pests (TreeDivNet, 2011a).

Forest diversity is therefore not just a conservation priority, but it also has crucial implications for forest management practices and climate change mitigation measures (Jucker et al., 2014b). To maintain the entire spectrum of services that forests provide to society, the management of production forests will benefit from considering diverse tree species, as no single tree species can promote all functions (Gamfeldt et al., 2013). Mixed-species plantations with up to four species can be more productive and have greater advantages in biodiversity, economy, and forest health than monocultures with proper planning and management (Liu et al., 2018).

## 3.2   Importance of woody species

Although biodiversity is thought to have a positive impact on a variety of services, research on natural systems at scales relevant to management is limited (Gamfeldt et al., 2013). For several reasons including the large size, slow growth, and long lifespans of trees, whether biodiversity is positively associated with ecosystem functioning has been a much-disputed topic and particularly challenging to study in arboreal systems (Paquette & Messier, 2011). Even though herbaceous plants are more convenient in experimental systems due to their fast-growing and small model systems, the shift towards the study of structurally more complex ecosystems such as woody species is one of the most recent developments in functional biodiversity research (Baeten et al., 2013; Paquette et al., 2018).

The capacity to focus on individuals rather than populations is a key advantage of employing trees rather than permanent grassland species, where individuals are frequently lost either to clonal growth or dense mingling of neighbors. Because of the emphasis on individuals, concerns about the role of biotic interactions and population dynamics as the basis of diversity-functioning relationships might now be assessed (Scherer-Lorenzen et al. 2007).

Since forestry is primarily interested in 1 or 2 species assemblages of commercially relevant species, existing mixture experiments in the context of forest management frequently lack intermediate and highly diversified treatments. Moreover, most forester-supported plantations are planted with varieties that have been genetically selected for high yield (Vilà et al., 2005; Scherer-Lorenzen et al., 2007).

## 3.3 Radial stem variations, swelling and shrinking, water potential

Although being a highly researched process, due to the multiple elements that influence tree growth, is still not clear the dependency of stem development on environmental circumstances, especially on short timescales (Chan et al., 2016). The environment has a direct impact on cambial processes such as cell division and expansion, but also on carbohydrate allocation, photosynthetic output and tree water relations (Hölttä et al., 2010).

Two processes produce variations in stem radius measured over living bark. On one hand, growth (GRO) is the irreversible cambial growth due to the buildup of new woody and bark tissue material, that causes the increase of the stem radius (SR hereafter). On the other hand, reversible tree water deficit-induced stem shrinkage and swelling (formerly known as TWD), provides knowledge on the relative water content of a plant concerning its hydration state (Zweifel et al., 2016). TWD is produced by imbalances between transpiration and root water intake (Zweifel et al., 2005), as well as processes that modify osmotic water potentials, such as sugar translocation in the phloem (Mencuccini et al., 2013; Chan et al., 2016).

Whereas GRO is a one-way process that always increases SR, the modulation of water potential is a bidirectional process that can lead to either an increase or decrease in SR (Chan et al., 2016). As a result, radial shortening of the stem is always attributed directly to lowering water potentials and hence rising TWD (assuming that the stem tissue structure is not structurally degraded). Radial growth, on the other hand, can be caused by either returning water and thus swelling tissues or by GRO (Drew & Downes, 2009; Chan et al., 2016).

To properly understand cambial growth and its interconnections with tree physiology and responses to environmental changes, short-term transpiration-driven variations in stem dimensions must be separated from longer-term variations (Chan et al., 2016).

While water-potential-driven fluctuations occur mainly during daylight, more progressive diameter changes occur when the osmotic concentration in the phloem fluctuates, which is triggered by changes in the soluble carbohydrate concentration (Sevanto et al. 2003). As a result, the osmotic concentration rises and water is drawn from the roots, increasing the stem diameter (Mencuccini et al., 2013). The diameter of the measured stem may progressively fluctuate due to changes in the humidity level of the bark (Gall et al., 2002).

## 3.4   Water restrictions

In a warming world, extreme climatic events are predicted to become more common (Rahmstorf & Coumou, 2011). Heatwave frequency and severity episodes have grown in recent decades and are expected to continue to rise throughout the twenty-first century (Barriopedro et al., 2011). Stomatal closure and the resulting inhibition of photosynthesis limit ecosystem carbon uptake when drought and heat stress are combined. Tree water reservoirs gradually deplete when soils dry up and canopy transpiration surpasses root water intake (Salomón et al., 2018). Forests' ability to sequester carbon in woody biomass is further hampered by poor stem water conditions, which limits growth (Steppe et al., 2015; Peters et al., 2021). Water released from internal stem reserves can temporarily buffer the harmful effects of drought on the vascular system integrity of trees in the short term (Meinzer et al., 2009).

Extended drought occurrences eventually produce hydraulic failure, along with tissue dehydration and damage, which could lead to drought-induced tree mortality (Martinez-Vilalta et al., 2019; Salomón et al., 2018).

## 3.5   Dendrometers

Dendrometers are measuring instruments used to determine the diameter of trees (Drew & Downes, 2009). Complex indicators integrating tree stem irreversible growth and reversible radial fluctuations due to stem water release and refill can be recorded using high-resolution dendrometers (Salomón et al., 2018). These fluctuations reflect bark tissue shrinking and swelling, which occurs on a sub-daily basis. As drought proceeds, this prolonged elastic reductions in stem diameter are commonly known as tree water deficit (Zweifel & Sterck, 2018). As a result, sub-daily dendrometer

observations of stem diameter variations might give useful in situ metrics on the long-term physiological response of trees to changing climate in terms of both growth and water status (Steppe et al., 2015; Zweifel et al., 2021). The findings emphasize dendrometer data's unique potential as an early warning system for detecting in situ responses as stress thresholds for tree vitality, growth and stem daily water stratus (Salomón et al., 2018), thereby identifying trees' response to changing environmental conditions or defining areas in danger of forest decline. Moreover, the thermocouple in the bottom section of the body allows the dendrometer to monitor the ambient temperature. Its rugged structure and high-capacity lithium battery make it resistant to a variety of harsh environments, allowing each autonomous device to measure and gather data for up to ten years without the need to replace the battery or delete outdated data.

## 3.6 The conceptual background: Experimental approaches to the study of forest biodiversity-ecosystem functioning relationships

Evaluating the functional relevance of biodiversity in complex ecosystems like forests will undoubtedly require a variety of complementary scientific approaches. In the case of 'observational studies', biodiversity and ecosystem processes are compared in existing forests of different tree diversity (Schulze et al., 1996; Caspersen & Pacala, 2001; Vilà et al., 2007), while statistically controlling for other productivity factors (Paquette & Messier, 2011). These experiments have reached some of the strongest evidence for the positive impact of forest diversity on productivity, as shown in recent studies that included data from all of the world's forest biomes (Liang et al., 2016). Although such studies have high relevance to real-world systems and are simple to conduct, they may be limited in their capacity to isolate the influence of tree diversity due to potential confounding (Paquette & Messier, 2011). 'Removal experiments', on the other hand, allow species removal from established communities while monitoring impacts on functioning (Diaz et al., 2003), but at the same time, the disturbance can confound the results. The third approach is to experimentally manipulate tree diversity and identity by planting trees in well-replicated designs (Verheyen et al., 2016). Plots with various levels of diversity are constructed in tree diversity experiments to monitor the impacts on ecosystem functioning and stability. Experiments offer the benefit of allowing researchers to better control confounding factors like species composition

and stem density, but they take time to construct, whereas evidence shows that diversification impacts grow over time (Meyer et al., 2016). Furthermore, many experiments manipulate not only tree species richness, but also other aspects of diversity such as species identity (plots with the same diversity level but different species combinations), intraspecific genetic diversity, functional or phylogenetic diversity, and evenness (Fichtner et al., 2017).

The studied case takes place within the framework of the Tree Diversity Network (TreeDivNet) experiments, which typically have long gradients and investigate not only the effect of mixture but the effects of tree diversity on multiple forest ecological functions (Paquette & Messier, 2011).

# 4 Methodology

## 4.1 Study area

The study is located near Kaltenborn (10° 13'E, 50° 47'N ) in the state of Thuringia, central Germany (Fig. 1), as part of the long-term research experiment BIOTREE. Influenced by the Rhön mountains and the neighboring Werra river valley, Kaltenborn has a sub-Atlantic climate. It has an elevation of 320-350 meters above sea level. In 2021 mean temperature recorded was 8.9°C, nevertheless, the mean temperature registered from 2011 to 2021 was 10°C, which means an increase over the past decade of 0.75 degrees, and an overall rise in recorded temperatures since 1979 of 2 degrees (data extracted from Meteoblue, 2022). It should be noted that the results of this thesis were obtained under exceptional rainfall conditions in the Kaltenborn study site since during 2021 mean precipitation values reached 1000.7 mm, being the rainiest year on record since 1981, which had mean precipitation of 1015.9 mm (Meteoblue, 2022). Even though, the annual precipitation trend in the study area has been generally stable since 1980, with an annual trend of around 775 mm. This is in line with the conclusions of IPCC regarding temperature global warming reports and heavy precipitation events (IPCC, 2021).
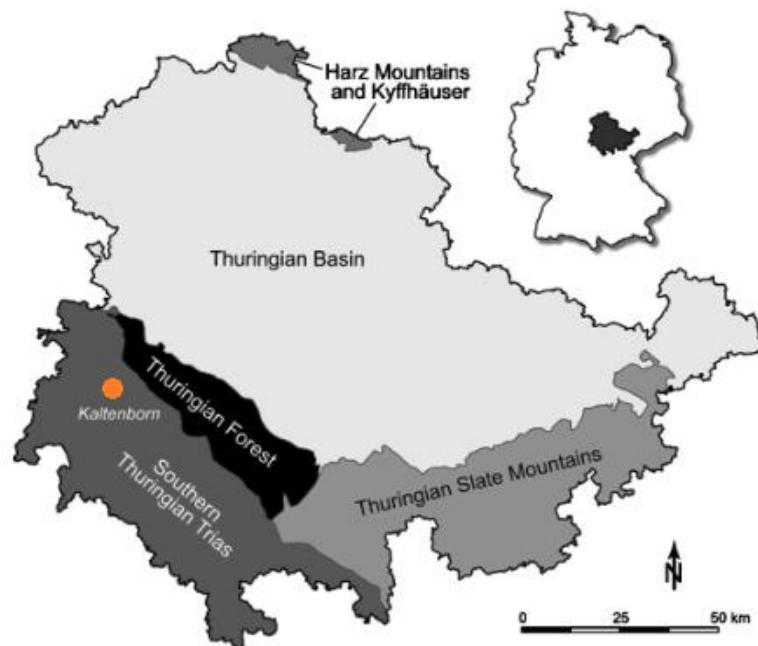


*Figure 1.  Main landscape units within Thuringia, Germany, and location of the BIOTREE experimental plantation Kaltenborn. Provided by: Scherer-Lorenzen et al. 2007, edited.*

This BIOTREE experimental afforestation site has an acidic bedrock: sandstone disrupted by some schist clay layers, along with natural vegetation of deciduous beech-dominated forests. Conifers would not grow naturally in the area, but have been introduced by forestry for more than 200 years and are an essential component of forest ecosystems nowadays. The plantation site is located neighboring a 20-hectare mixed pine–beech forest stand (Fig. 2). The land was utilized for agriculture until 1975 when it was turned into grassland managed by mowing once a year plus some cattle and sheep grazing (Scherer-Lorenzen et al., 2007).

## 4.2 Study design

### 4.2.1 Site preparation and planting: BIOTREE experiment

Using plants of regional provenances, rows of 30 cm width and 60 cm depth were planted at the Kaltenborn site during October/November 2003 and in March/April 2003 and 2004. Trees were between 3 and 4 years old when they were planted in the seedbed, and stood between 20 and 60 cm tall depending on the type. Because mortality had reached high levels as a result of the very dry and warm summer of 2003, replanting of species was carried out in November 2004 and March 2005 to assure an average establishment success of at least 85% in each plot (Scherer-Lorenzen et al., 2007).

### 4.2.2 Experimental layout

To achieve the greatest diversity, four main species were planted in 2003: Norway spruce *(Picea abies),* Douglas fir *(Pseudotsuga menziesii),* common oak *(Quercus robur)* and European beech *(Fagus sylvatica).* From monocultures to all possible species mixtures, a gradient in tree species richness was established at the site, therefore diversity levels were ranging from 1 to 4 species (Fig. 2).
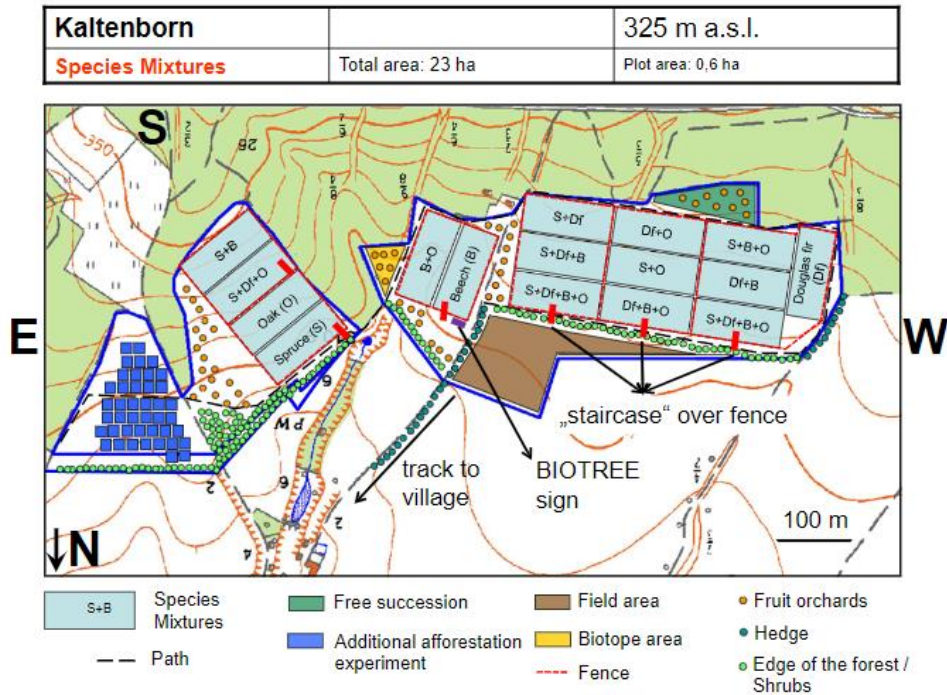
*Figure 2. Species mixtures in Kaltenborn experiment. Provided by: M. Scherer-Lorenzen [unpublished]*

Within the locations, a total of 16 plots of 16x16 m size with different levels of variety were assigned at random (Table 1). Scherer-Lorenzen et al., (2007) used various combinations to duplicate each species-diversity level, preventing any misunderstanding between species identification and the impact of species number (Schmid et al., 2002b). There were no duplicates of specific mixes. As a result, while the major characteristic of interest – species richness – is satisfactorily duplicated, this design does not allow for a statistical evaluation of composition effects (Scherer-Lorenzen et al., 2007) (Fig. 3).

*Table 1. The number of mixtures at each diversity level.*

| Kaltenborn site | | | | | Number of plots |
| --- | --- | --- | --- | --- | --- |
| Species number | 1 | 2 | 3 | 4 | |
| Replicates | 4 | 6 | 4 | 4 | 16 |

| Kaltenborn | | 325 m a.s.l. |
|---|---|---|
| Species Number | Total area: 23 ha | Plot area: 0,6 ha |
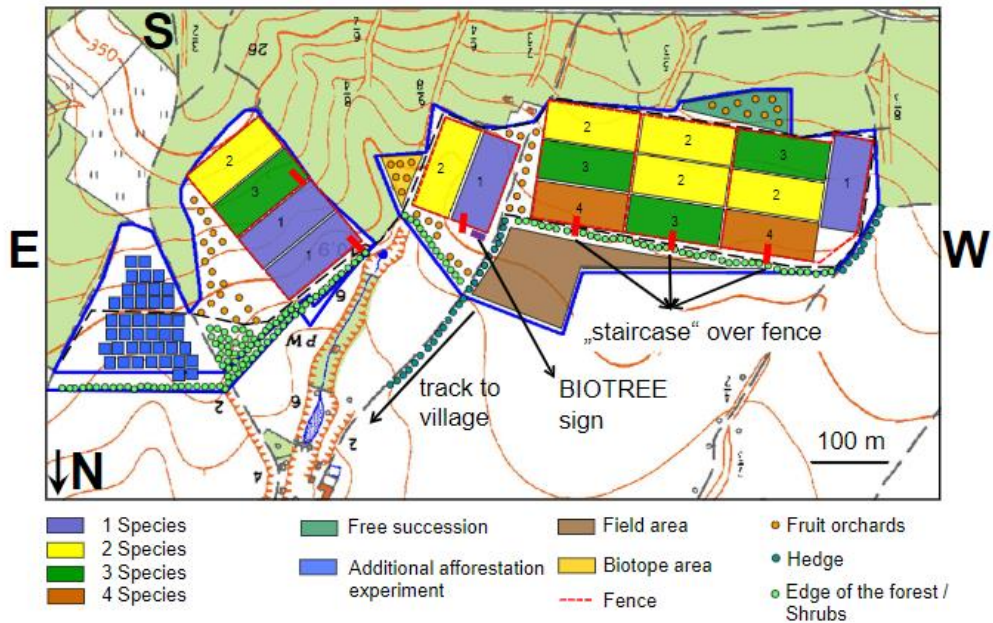
*Figure 3. Species number in Kaltenborn experiment. Provided by: M. Scherer-Lorenzen [unpublished]*

## 4.3 Data collection

Data for the thesis was collected from point dendrometers installed at the BIOTREE experiment in Kaltenborn in March 2021 before the growing season (Fig. 4).

*Figure 4. Tomst dendrometers installed in Kaltenborn study site. From: Radim Matula*

Dendrometers were installed in the following manner: on each plot, 12 trees of each species were selected randomly, and a dendrometer was installed in every one of them. For instance, if the plot was monocultural, 12 dendrometers were installed, while if the plot had a combination of four species, 48 dendrometers were placed. The selection of trees was random, even so, it was necessary to find groups of trees of different species that were growing side by side (Fig. 5).
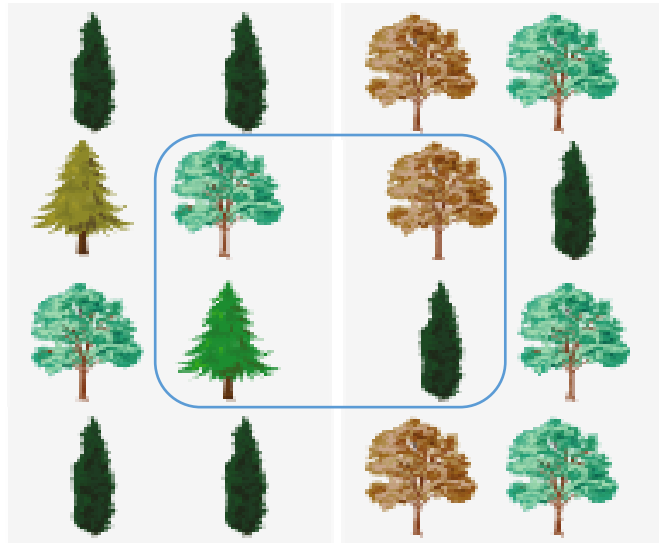
*Figure 5. Trees within the quadrant were the ones possibly selected due to their coexistence with other species. Adjusted from: Paquette et al., 2018, edited.*

The dendrometers placed on the trees register stem diameter changes every 15 minutes. However, for purely practical reasons, the study has been performed taking into account just one measurement every hour, being the average of the four hourly data recorded.

Measurements were collected from 372 trees at Kaltenborn site. For each monitored tree, information on the (i) species, (ii) plot composition, (iii) species richness, (iv) forest type, (v) radius growth, (vi) tree water deficit (TWD) and (vii) temperature was collected. Collected data encompass the period between May to October 2021.

Data collection was carried out over three days, from 17th to 19th November 2021, after the end of the growing season 2021. Data is easily downloaded using an adapter, which is connected to the PC via a USB cable. Lolly is the software that allows Tomst dendrometers to collect and analyze data (Fig. 6).
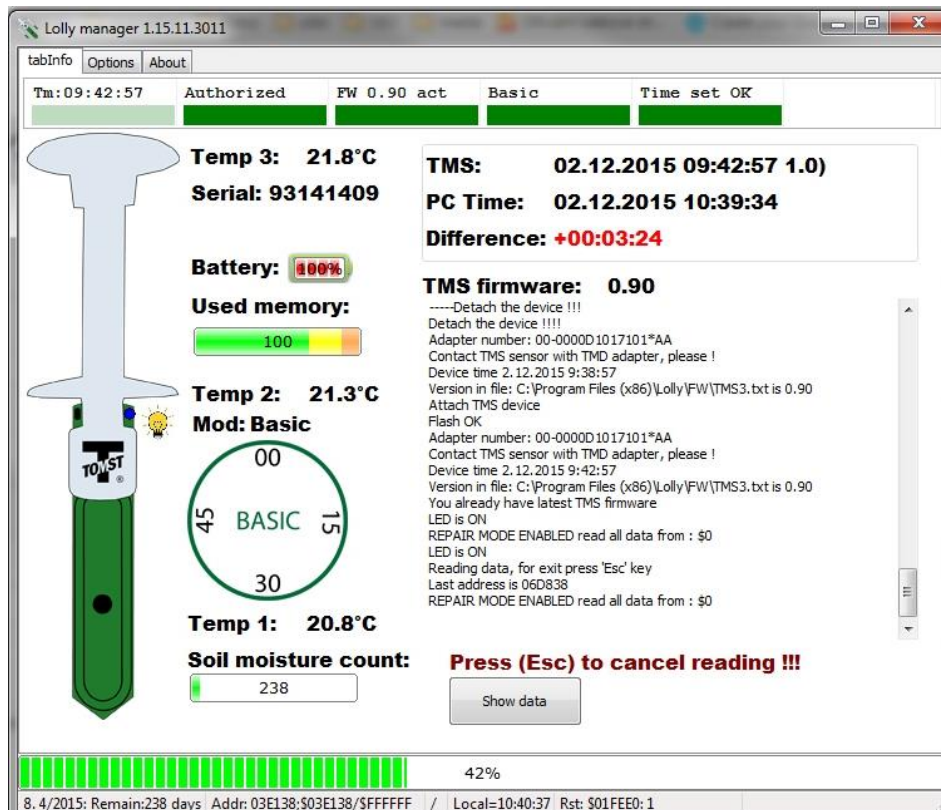
*Figure 6. Screenshot of Lolly software in use. From: Tomst.com*

## 4.4 Statistical methods

After downloading, data extracted from the dendrometers were processed and analyzed using 'PLOTeR', a special R package. Raw data were treated and homogenised to correct some technical anomalies (Fig. 7). Following this, all data were merged excluding information not needed for the study, such as some offset and unknown loggers.
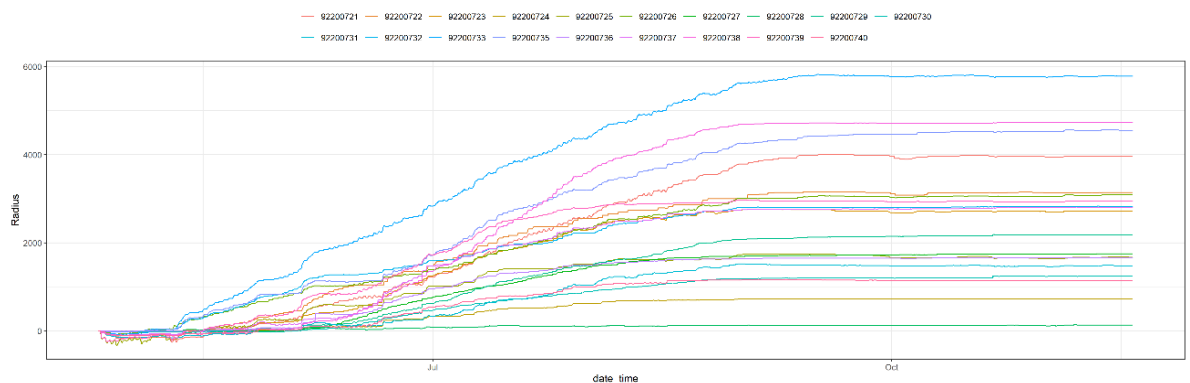


*Figure 7. Data of 20 dendrometers while being processed using the R package 'PLOTeR'.*

Using the cleaned dendrometer data set, water-related and growth-related components of stem radius variation were calculated according to the zero-growth concept (Zweifel et al., 2016). The followed approach presumes that growth begins when the previous maximum stem diameter is exceeded and concludes when the stem begins to shrink. A period of tree water deficit is defined as diameter variations below the previous maximum stem diameter (Dietrich et al., 2018; Salomón et al., 2022).

We have related the tree responses to the explanatory variables using linear models as well as generalized additive model (GAM). This model has been used to interpret data in other research with comparable vegetation response analyses, which supports the decision to utilize this type of statistical analysis (Bio et al., 1998).

The analysis has been divided into 4 models: (i) radius responses to tree mixtures over time, comparing the different tree mixtures for each tree species; (ii) radius responses to specific species combinations over time for each tree species; (iii) tree water deficit response over time, comparing the different tree mixtures for each tree species; (iv) radius responses to temperature over time, comparing the different tree mixtures for each tree species.

# 5 Results

## 5.1 General overview

In Figure 8, findings are grouped by species richness. Thus, species studied in this experiment have not been clustered, instead, the graph displays the average radius growth collected grouped regarding species richness.

At first appearance, the results (Fig. 8) exhibit the most significant growth in the plots under monoculture. In this case, where species richness equals 1, radius shows a mean growth above 3500 mm. These results are outperforming the other types of plantations, which show a minor growth rate. Three mixed-species plantation exhibits an average radius growth of 3000 mm at the end of the growing season, while the mean growth of 4- and 2-mixed species crops was around 2750 mm. In general terms, remarkable growth is observed from mid-May to the beginning of September, stabilizing from autumn onwards.

*Figure 8. The graphic shows results from GAM analysis representing average species richness (sr) in the study plots without species differentiation. Forest mixtures are: monoculture (1), mix of two species (2), mix of three species (3), and mix of four species (4). Lines display mean radius growth (mm) over the growing season (May – October), with confidence intervals shadowed in gray.*

In the case of TWD, the graph shown below (Fig. 9) indicates a fairly similar response for all different types of plantations. From a general perspective, a remarkable deficit is observed at the beginning of the growing season, when data collection began, although it is reduced to almost 0 within a month. In mid-June, a slight decrease is perceived to recover hydration again in July, where it gently falls again and does not recover its complete hydration until the end of summer. From mid-September onwards, a large decline is noticed, affecting particularly 4-mixed species plantations. It is worth highlighting that, although all plantations have fluctuations, the plantation that shows the most TWD peaks is the one consisting of the average monoculture plots, whereas the most stable plantation appears to be the 3-species mixture.
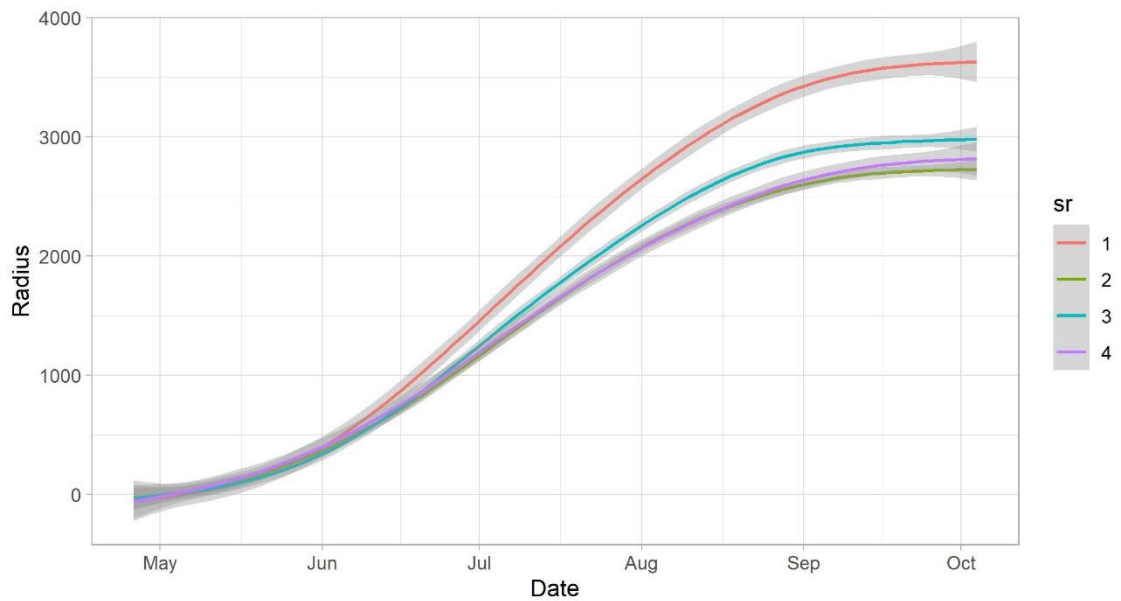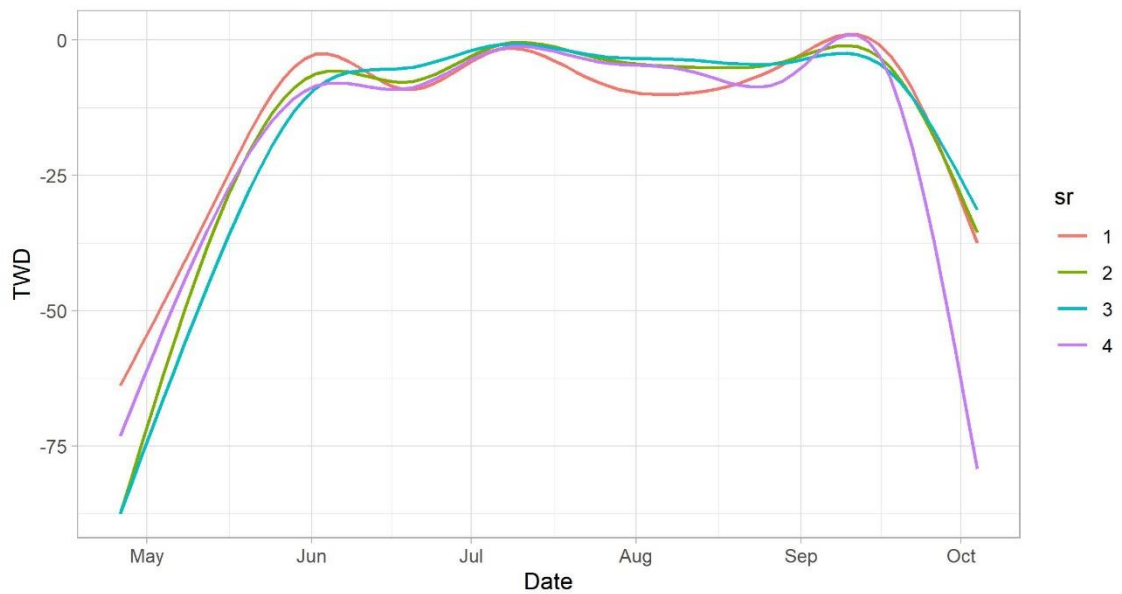
*Figure 9. The graphic shows results from GAM analysis representing average tree water deficit (TWD) in the study plots without species differentiation. Forest mixtures are: monoculture (1), mix of two species (2), mix of three species (3), and mix of four species (4). Lines display tree water deficit (TWD), in (μm), of each species over the growing season (May – October).*

## 5.2 Radius responses to tree-mixtures

Results show that in the case of beech (Fig. 10), the radius of trees displays a strong growth between June and September, stabilizing completely at the beginning of autumn. The maximum growth of the radius of this species occurs when the tree grew in monoculture, reaching almost 5000 mm. This growth doubles the radius recorded when the species is found in mixed plantations of 2 and 3 species (2500 mm), where also the while the lowest growth occurs in plots with all 4 species (1500 mm).

It is observed that Douglas fir (Fig. 10) performs a linear growth from May until September. Any major variations are hardly seen in the different species compositions and species richness levels, in all cases the radius average is between 3000 mm - 35000 mm.

Results for oak (Fig. 10) also show a significant growth throughout the summer. In monoculture plots it shows a much greater growth, reaching a radius of 3500 mm, similarly to the case of beech. On the other hand, the three types of mixed plantations have the same growth curve, and the average radius in this species composition oscillates around 2000 mm.

Starting in early May, the four Norway spruce (Fig. 10) plantations grew at about the same time until mid-summer. At this point, the fastest growth is recorded for trees planted in plots of 3 different species, reaching a radius of 4500 mm. They are then followed by plantations of 2 and 4 species, both with a radius close to 4000. Finally, Norway spruce growing in monocultures show a radius of around 2550 mm.
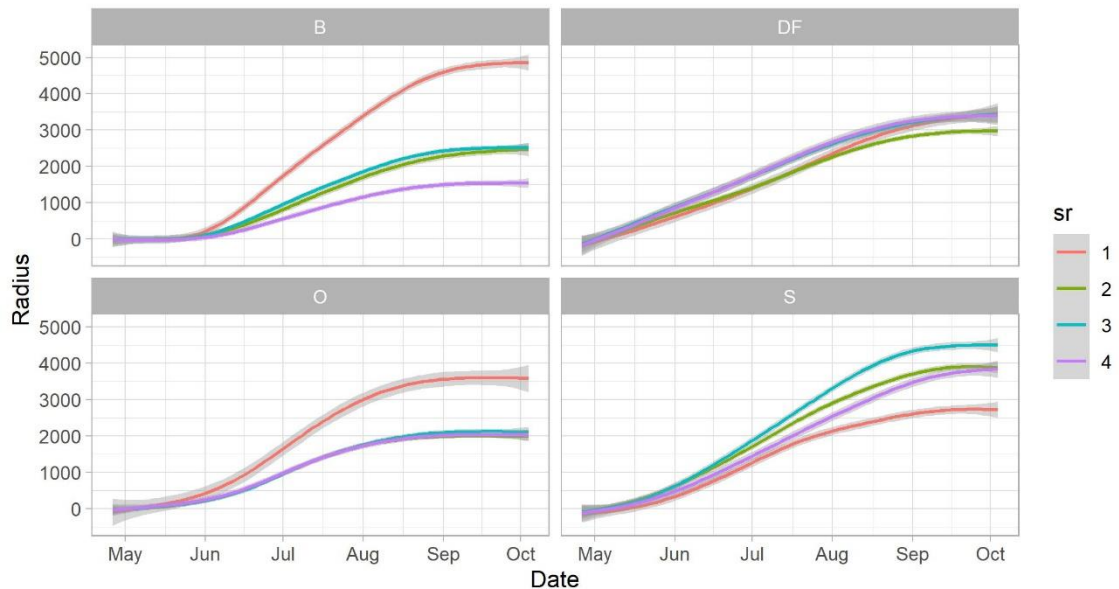


*Figure 10. Each graphic represents results from GAM analysis for each tree species: beech (B), Douglas fir (DF), oak (O), and Norway spruce (S). Lines display radius growth (mm) of each species over the growing season (May – October), with confidence intervals shadowed in gray. Different colors of the lines represent species richness (sr) in the study plots, the different forest mixtures are: monoculture of each respective species (1), mix of two species (2), mix of three species (3), and mix of four species (4).*

## 5.3   Radius responses to inter-specific interaction

This set of graphs (Fig. 11) exhibits that in the case of beech, the highest growth occurs when it is single-crop, i.e. in plots cultivated only with beech, growing up to 5000 mm during the whole season. On the other hand, when beech is combined with one or two other species, it is observed that it grows between 2500-3000mm, except in the case of beech-oak, which, being the plot with the lowest growth, only reaches 1000 mm. Lastly, the combination of the four species does not give a good yield for beech either, since the growth that has been recorded only amounts to 1500 mm.

*Figure 11. Each graphic represents results from GAM analysis for a different combination of species in the study plots, focused on beech (b). Lines display stem diameter growth (mm) over the growing season (May – October). Different colors of the lines represent species richness (sr) in the study plots, the different forest mixtures are: monoculture of each respective species (1), mix of two species (2), mix of three species (3), and mix of four species (4).*

Results for Douglas fir (Fig. 12), it is observed that there is almost no variation in the different species mixtures. Except for the combinations with Norway spruce and Douglas fir (separately), both showing a growth of 2500 mm, all other combinations including the monoculture, grew by 3500 mm.



*Figure 12. Each graphic represents results from GAM analysis for a different combination of species in the study plots, focused on Douglas fir (df). Lines display stem diameter growth (mm) over the growing season (May – October). Different colors of the lines represent species richness (sr) in the study plots, the different forest mixtures being: monoculture of each respective species (1), mix of two species (2), mix of three species (3), and mix of four species (4).*

Results from oak combination (Fig. 13) display a great radius growth for this specie in monoculture plots, exceeding 3500 mm. It can be noticed that when there is a species richness of 2 or 4 species, the growth does not vary, it is found in all cases at 2000 mm. On the other hand, in the 3 species mixture samples, the growth varies from 1500 mm to almost 3000 mm.
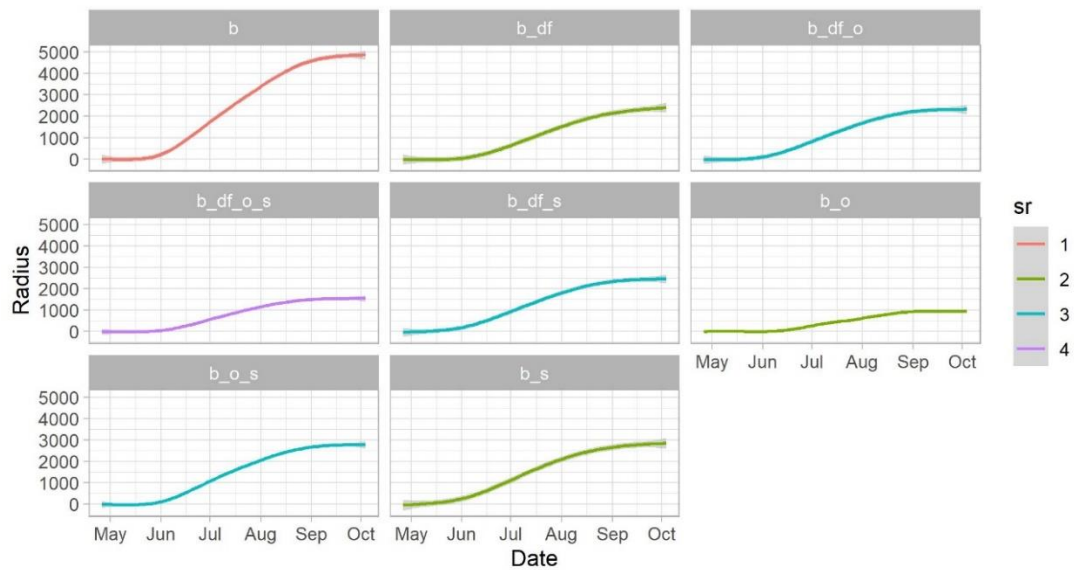


*Figure 13. Each graphic represents results from GAM analysis for a different combination of species in the study plots, focused on oak (o). Lines display stem diameter growth (mm) over the growing season (May – October). Different colors of the lines represent species richness (sr) in the study plots, the different forest mixtures being: monoculture of each respective species (1), mix of two species (2), mix of three species (3), and mix of four species (4).*

The Norway spruce set of graphs (Fig. 14) presents the monoculture as the plantation that has grown the least, not reaching 3000 mm, followed by the combination of Norway spruce and beech. it is observed that most other crops have grown around 4000 mm, except for the Douglas fir-beech-Norway spruce combination, where growth of almost 6000 mm is measured.
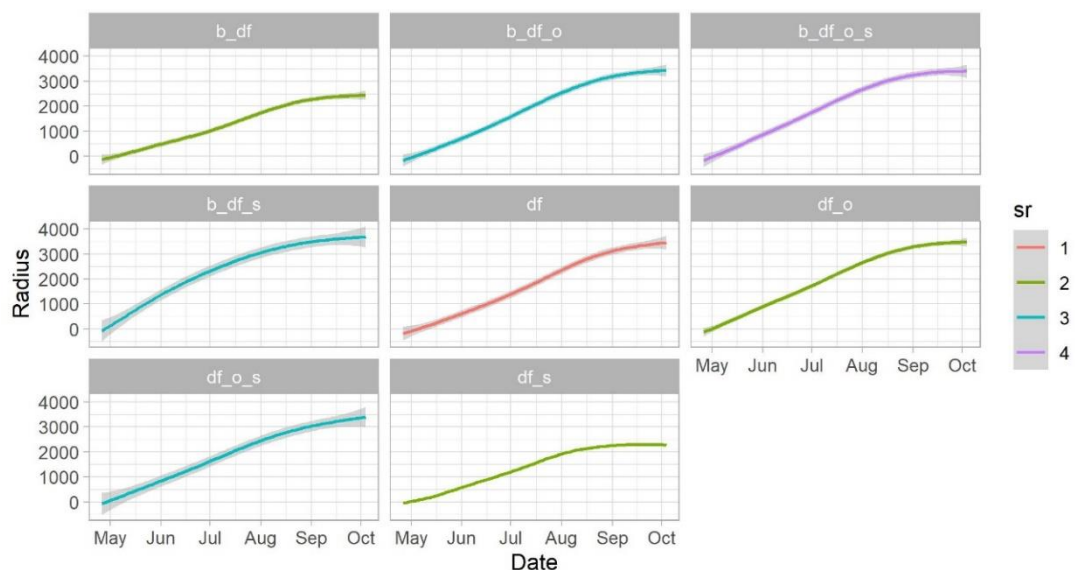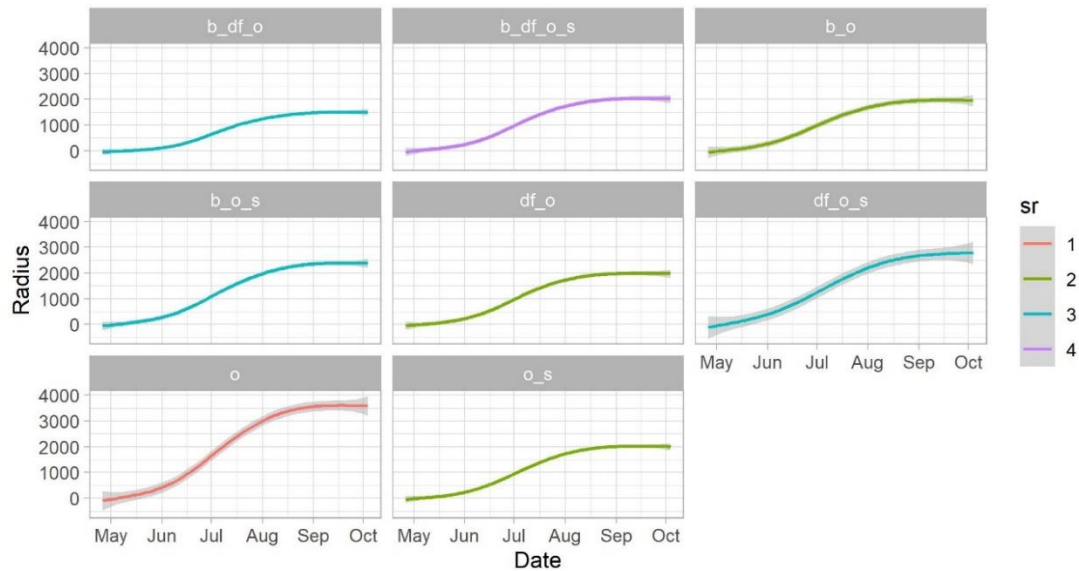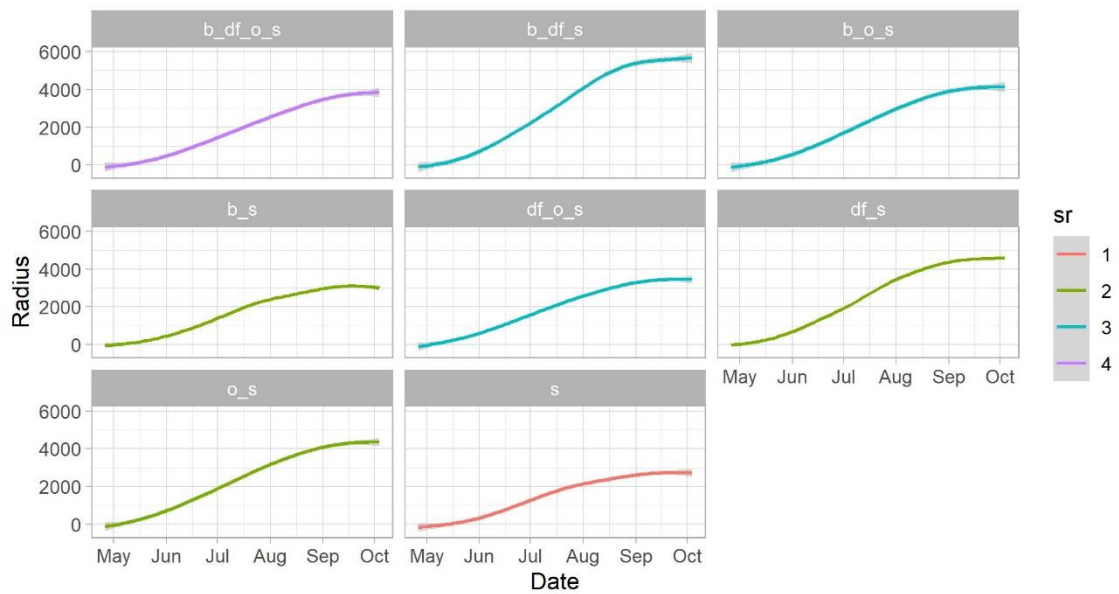
*Figure 14. Each graphic represents results from GAM analysis for a different combination of species in the study plots, focused on Norway spruce (s). Lines display stem diameter growth (mm) over the growing season (May – October). Different colors of the lines represent species richness (sr) in the study plots, the different forest mixtures are: monoculture of each respective species (1), mix of two species (2), mix of three species (3), and mix of four species (4).*

## 5.4   Tree water deficit response

In the case of beech (Fig. 15), the lowest TWD values are reached during the first month of the growing season (May to June). The results exhibit a more prolonged deficit for those plots in 4-species mixed forests. Following, 2- and 3- mixed-species plots have also low values, while faster recovery. On the other hand, it is remarkable how little deficit monoculture plantations suffer, as well as their fast recovery rate. By mid-June, no matter in which plot was it located, the trees returned to a fully hydrated state. TWD consistently remained around zero during the whole summer, however, in early September it is disturbed by a minimal irregular drop in the plots consisting of 2 species-mixture.

Regarding Douglas fir analyses, TWD fluctuations are very noticeable (Fig. 15). Results exhibit low values during the early weeks of the research, reaching -65 µm on average. The tendency to suffer TWD decreased from mid-May onwards, although a milder deficit peak is observed at the beginning of summer. July is the month when Douglas fir seems to be more hydrated and stable. Yet, again it shows TWD increase

peaks along August. From mid-September onwards, it gradually declines again, most remarkably in 4-mixed species plots, which reach -125 µm.

Our results for oak display a rather low TWD at the beginning of the experiment (Fig. 15). In May, the largest deficit is seen in 3-mixed species plots (-130 µm), whereas monocultures are the least affected. Nevertheless, water deficit is gradually getting closer to 0 by the end of June. It remains relatively stable during summer with a few peaks in August, then begins to smoothly decline again in autumn.

Lastly, Norway spruce shows uneven results (Fig. 15). Although a huge generalized TWD is observed in May, the deficit decreases during June and July, presenting some peaks although with certain stability near 0. In August there are strong spikes in all plot combinations, although they are most prominent in 1-species plots. After a short stabilization through September, a sudden drop begins, reaching the lowest values recorded (-170 µm).



Figure 15. Each graphic represents results from GAM analysis for each tree species: beech (B), Douglas fir (DF), oak (O), and Norway spruce (S). Lines display tree water deficit (TWD), in (µm), of each species over the growing season (May – October). Different colors of the lines represent species richness (sr) in the study plots, the different forest mixtures being: monoculture of each respective species (1), mix of two species (2), mix of three species (3), and mix of four species (4).

## 5.5  Radius responses to temperature

The following set of graphs (Fig. 16) illustrates a general trend: for all species and plantations, there is a sharp growth peak around 13-14 °C and a smaller one that occurs near 4-8 °C.

Beech results exhibit the highest growth in monoculture plots, reaching almost 4000 mm. The 2- and 3-species crops approach 2000 mm of growth also at 13 °C, while the crop least affected by temperature is the 4-species mix.

Concerning the findings obtained for Douglas fir, a similar trend is observed. There is a small peak at around 7 °C and a larger one at 14 °C. Even so, the differences between plantations are very minimal.

In the case of oak, while all species mixtures have a similar response, the monoculture crop grows noticeably at the peak of 14 °C, reaching nearly 3000 mm.

Ultimately, the results for Norway spruce show a fairly similar trend between mixtures. However, the largest peak is dominated by the planting of 3 species reaching almost 3500 mm, while the monoculture is the one that grows the least at 13-14 °C.
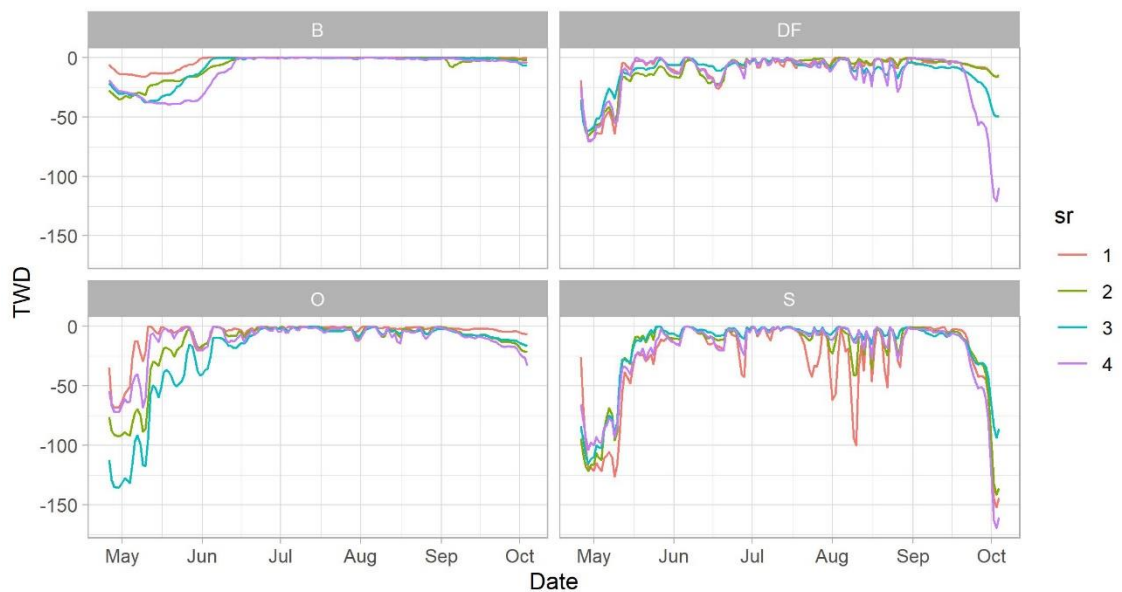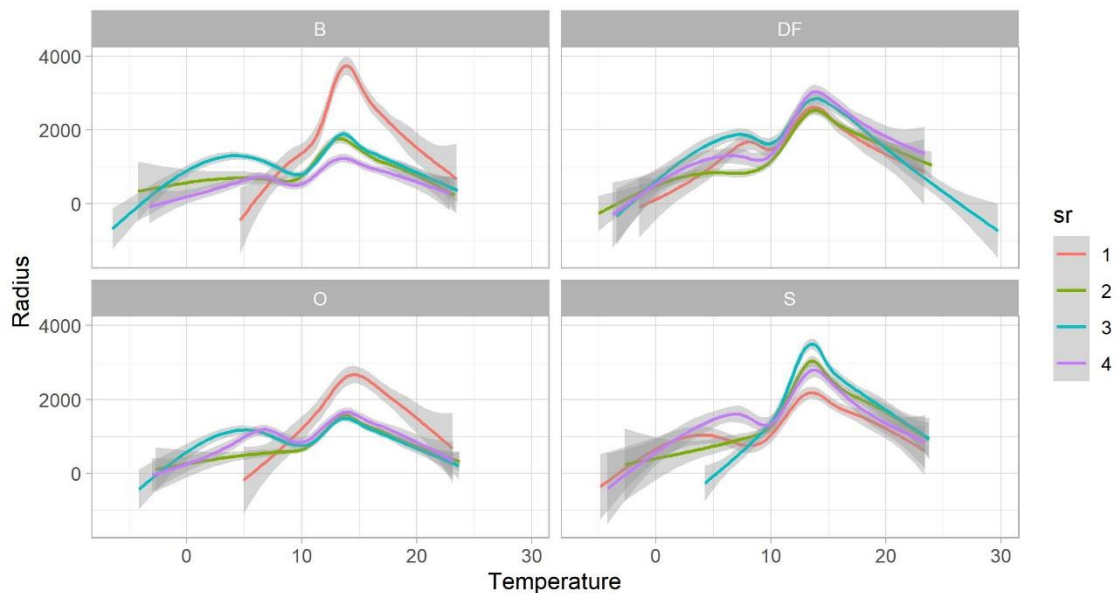


*Figure 16. Each graphic represents results from GAM analysis for each tree species: beech (B), Douglas fir (DF), oak (O), and Norway spruce (S). Lines display radius growth (mm) of each species according to temperature (°C), with confidence intervals shadowed in grey. Different colors of the lines represent species richness (sr) in the study plots, the different forest mixtures are: monoculture of each respective species (1), mix of two species (2), mix of three species (3), and mix of four species (4).*

# 6 Discussion

## 6.1 Monocultural performance

The results do not agree with the hypotheses that trees growing in a mixed-species plot will be less affected by TWD. The performed analysis demonstrates that beech has a higher growth rate when planted in monoculture. This fact may be explained by different factors. Firstly, it is observed that in the case of beech the greatest tree growth occurs between June to August (both included). According to the data recorded in Kaltenborn during this period in 2021, the average temperature of these three months was 14,1°C (Table 2). The results are consistent since the peak of beech growth is observed when the environmental temperature is found in the range of 13-14 degrees, as shown in the previous results. Beech is, at the same time, the tree in the study that suffers the least from TWD, which undoubtedly helps to propel its growth during the summer period.

Table 2. Monthly mean and standard deviation of the recorded temperatures (°C) in Kaltenborn from April to October 2021.

| Month | April | May | June | July | August | September | October |
|-------|-------|------|------|------|--------|-----------|---------|
| Mean  | 8,6   | 13,9 | 14,3 | 10,1 | 14,1   | 22,5      | 21,5    |
| SD    | 2,6   | 3,6  | 3,6  | 5,4  | 3,6    | 5,4       | 0,2     |

This result ties well with the conclusion reached by Rukh et al. (2020), who reported that beech trees were shown to be more resistant and resilient at individual tree level in monocultural stands.

Findings on Douglas fir interactions do not show a wide variation among the different mixtures. All plots have a remarkably homogeneous growth, as well as a very similar reaction to temperature changes. This suggests that, in a year of abundant precipitations and suitable temperatures as is the case, this species can perform a successful growth on any plantation. Douglas fir's capacity to adapt and mitigate climate change is known (Spiecker et al., 2019).

The outcomes regarding oak plantations suggest that similar assumptions to those adopted concerning beech, the other deciduous tree in the study, can be made. With a very similar reaction pattern in both temperature and drought conditions, it can therefore be assumed that oak grows well in monoculture when given the ideal climatic circumstances during the growing season. Moreover, access to deep soil water by roots might be a key component in species-specific responses to water scarcity (Brinkmann et al., 2019). As a deep-rooted plant, oak may be less affected by water deficit (Salomón et al., 2022), as this study results are previously shown. Findings on Norway spruce at least hint that of all the studied trees is the one most affected by TWD. Contrary to the studied deciduous species, it does not perform very well in monocultures, instead, it grows best in a mixed forest. It has been demonstrated that mixture seems to enhance the water supply of Norway spruce trees, which should increase the stability of this species in a time of climatic warming (Schäfer et al., 2019; Rukh et al., 2020). Moreover, as a shallow-rooted species, spruce is not able to access deep groundwater, therefore is hindered in disadvantaged water conditions (Salomón et al., 2022).

## 6.2 Species mixtures performance

As suggested by the number of studies recently carried out, there is a growing interest in beech and spruce mixed plantations in Central Europe (Pretzsch et al., 2018; Schäfer et al., 2019; Hilmers et al., 2019). The study conducted by Gayler et al. (2006) states that higher morphological plasticity of beech relative to Norway spruce is the main mechanism for competitiveness when both species have comparable heights at the time of canopy closure. Thus, greater flexibility would be a disadvantage for beech, causing it to be outcompeted by the more robust Norway spruce. Contrary to their findings, in my experiment, it is observed that beech and spruce mixed plantations grow well together since both species reached a growth of 3000 mm when studied in the mixture.

Superior results are seen for the combination of beech, Norway spruce and Douglas fir. Results confirm that this species-mixture plot performs very well in propitius growing seasons. In this 3-mixed plot, beech records a radius growth of 2500 mm, Douglas Fir exceeds 3500 mm, and spruce also increases its radius by 6000 mm.

Douglas fir and beech are presumably more drought-tolerant than Norway spruce. Nevertheless, recent studies have shown that Douglas fir was more drought-stressed in the mixture (Vitali et al., 2018), while, as mentioned above, the mixture seems to enhance the water supply of Norway spruce trees (Schäfer et al., 2019; Rukh et al., 2020).

It was observed that beech was suppressed by Douglas fir in mixed stands. As a reaction to the strong above-ground domination of Douglas fir, beech develops a rooting strategy that ensures the possibility of above-ground expansion when the growth of Douglas fir declines (Hendriks & Bianchi, 1995).

## 6.3   Tree water deficit on broadleaves and coniferous

TWD was recorded at night since this is usually the minimum TWD daily since it is buffered against diurnal oscillation due to day-time transpirational water loss and so reflects periodic drought stress, which is mostly regulated by soil moisture availability (Salomón et al., 2018).

As recently studied by Salomón et al., (2018), heavy drought periods (i.e. 2018 European heatwave), caused dehydration in trees, however regular growth decreases were not recorded. Moreover, no differences between broadleaf and conifer species were noticed.

It is important to highlight the differences in TWD depending on the groups of the species studied. This experiment shows less water deficit in broadleaf species (beech and oak) than coniferous species (Douglas fir and spruce). These findings are in accordance with the conclusions reported by Salomón et al., (2018). They pointed out that under similar hydrometeorological circumstances, conifers species showed larger stem dehydration than broadleaves. Overall, during the growing season broadleaves stems returned more easily than coniferous species to a fully hydrated state, which could be classified as no deficit period (Nehemy et al., 2021).

## 6.4  Implications for forest management

Considering all of the mentioned during the present study, it is reasonable that the beech monoculture has had great growth during the growing season in which the study was conducted. However, it has already been pointed out that the study was conducted in a year of extreme precipitation. In the context of climate change as is expected in the coming years, planting monocultures would not necessarily be the most resilient option (Felton et al., 2010; Coll et al., 2018).

On the other hand, the results suggest that a more sustainable option would be the promotion of mixed forests involving the Douglas fir, beech and spruce triad. Although beech productivity drops in this type of plantation, the growth of Douglas fir and especially spruce increases significantly. During years with a less favorable environment over the growing season, the production of these species is likely to be higher in mixed-species than in monoculture plantations. However, according to the results from Paquette & Messier (2011), in temperate forests that grow in a more stable and productive environment, complementarity may be less relevant, while beneficial interactions between species become more important in stressful environments.

European forests are intended to ensure biodiversity, supply renewable resources and offer other ecosystem services while also assisting us in mitigating and adapting to climate change. For that reason, forest management should take into account all the scientific work that is being carried out. Understanding biodiversity-ecosystem functions and how forest management may impact or assure both economic and ecological sustainability is essential. Thus, this study strongly encourages taking species diversity into account when managing forests. Even mixed forests may take years to outperform forests planted in monoculture (Kambach et al., 2019). But long-term studies prove that mixed-species stands over-yielding monocultures are higher on poor soils and in low-grow years (Pretzsch, 2014). For this reason, it is fundamental to further study and create awareness about the importance of forest management.

Ecosystem benefits provided by mixed forests are important. According to the "insurance hypothesis", their response to disturbance will be less severe and their recovery will be faster than monocultures (Bravo-Oviedo et al., 2014). A similar conclusion was reached by Rukh et al., (2020), who stated that despite the lack of a

clear benefit of tree diversity on drought resistance, pursuing species-rich forests allows for risk-sharing among multiple species and enhanced provision of a variety of ecosystem services.

In central Europe, global warming might have important consequences for forests, as harsher droughts and precipitation could negatively affect tree growth. Under more severe conditions (i.e. the recent 2018 heatwave episode), the results of this study would probably be substantially different due to the scarcity of water or extreme climate conditions. According to Scherer-Lorenzen et al., (2007), large species effects are already being observed in extreme climate events. Thus, in more extreme conditions, the results displayed from Kalternborn plots would be completely different. At the same time, it must be considered that this ecosystem, both in terms of species composition and ecological processes, will experience long-term changes (Scherer-Lorenzen et al., 2007). Therefore, even if the external conditions are the same as in the present study, the species reaction to the environment will vary over the years.

It is well understood that if biodiversity loss continues, ecosystems, and hence forests, will lose the majority of their capacity to operate effectively. (Cardinale et al., 2012). In terms of yield and resilience to windthrows and bark beetle attacks, mixed stands have consistently outperformed monospecific stands (Rukh et al., 2020), and previous studies claim that forest biodiversity is thought to help regulate disease impacts (Liu et al., 2020). In my research, although some monocultures perform great radius growth, other studies provide evidence that single-species forests that monocultures do not provide the resilience required to cope with the effects of climate change.

It should be reminded that the results were obtained during a very favorable growing season for the studied trees, with optimum rainfall and temperature for their development. Taking into consideration the exceptionality of the year in which the field data were collected, the responses given by the studied trees may be slightly biased. Therefore, as the measurement used is the most precise possible, it is suggested further replication of the experiment using the same methodology. This will allow the analysis of the response of the targeted species under the environmental and climatic circumstances to which they might be exposed.

Because of the lack of data, I decided to not investigate how trees reacted to different kinds of management options, thus it would be interesting to consider it in forthcoming research. Mixed forest success may be influenced by below-ground interactions as well as canopy cover. Therefore, root and crown architecture studies could be fundamental to better comprehend the interaction between individual trees. In addition, further research is needed about species interaction and its dependence on environmental conditions. Long-term observations will be required to assess how the studied forest will react to the threatening climate changes.

# 7 Conclusions

The present study compares tree growth and water deficit in forest monocultures and different species mixtures in a BIOTREE experiment located in Kaltenborn, Germany. Radius responses to different tree mixtures, specific species combinations, temperature, and tree water deficit responses were studied during the growing season using dendrometers. Results demonstrated the fastest growth of beech and oak in monocultural plots. The coniferous species Norway spruce had a better stem growth in mixed-forest plantations, while tree mixture did not affect significantly Douglas fir stem growth. Regarding TWD, oak and beech showed a very mild water deficit, while Norway spruce and Douglas fir fluctuations were very noticeable. All species mixtures were affected by temperature, having a growing peak of around 14 °C. Note that environmental conditions throughout the recorded months were exceptionally favorable for the tree. The findings of this work suggest that beech monoculture is the most productive plantation in optimal environmental situations. These results may not be reliable in a scenario of climate change, where conditions will become harsher. However, beech combined with Norway spruce and Douglas fir also presents a fast growth, besides being a more resilient plantation.

Therefore, it is recommended to further study the responses of species in different tree mixtures in less favorable growing seasons. Thus, it is highly needed to evaluate the impacts that these different forestry mixtures may have on forest biodiversity and climate change mitigation.

# 8 Bibliography

Ammer, C. (2019). Diversity and forest productivity in a changing climate. *New Phytologist*, *221*(1), 50-66.

Baeten, L., Bruelheide, H., van der Plas, F., Kambach, S., Ratcliffe, S., Jucker, T., ... & Scherer-Lorenzen, M. (2019). Identifying the tree species compositions that maximize ecosystem functioning in European forests. *Journal of Applied Ecology*, *56*(3), 733-744.

Baeten, L., Verheyen, K., Wirth, C., Bruelheide, H., Bussotti, F., Finér, L., ... & Scherer-Lorenzen, M. (2013). A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. *Perspectives in Plant Ecology, Evolution and Systematics*, *15*(5), 281-291.

Barriopedro, D., Fischer, E. M., Luterbacher, J., Trigo, R. M., & García-Herrera, R. (2011). The hot summer of 2010: redrawing the temperature record map of Europe. *Science*, *332*(6026), 220-224.

Bauhus, J., Forrester, D. I., & Pretzsch, H. (2017). From observations to evidence about effects of mixed-species stands. In *Mixed-Species Forests* (pp. 27-71). Springer, Berlin, Heidelberg.

Bio, A. M. F., Alkemade, R., & Barendregt, A. (1998). Determining alternative models for vegetation response analysis: a non-parametric approach. *Journal of Vegetation Science*, *9*(1), 5-16.

Brinkmann, N., Eugster, W., Buchmann, N., & Kahmen, A. (2019). Species-specific differences in water uptake depth of mature temperate trees vary with water availability in the soil. *Plant Biology*, *21*(1), 71-81.

Bravo-Oviedo, A., Pretzsch, H., Ammer, C., Andenmatten, E., Barbati, A., Barreiro, S., ... & Zlatanov, T. (2014). European mixed forests: definition and research perspectives.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., ... & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*(7401), 59-67.

Carle, J., & Holmgren, P. (2008). Wood from planted forests. *Forest Products Journal*, *58*(12), 6.

Caspersen, J. P., & Pacala, S. W. (2001). Successional diversity and forest ecosystem function. *Ecological Research*, *16*(5), 895-903.

Chan, T., Hölttä, T., Berninger, F., Mäkinen, H., Nöjd, P., Mencuccini, M., & Nikinmaa, E. (2016). Separating water-potential induced swelling and shrinking from measured radial stem variations reveals a cambial growth and osmotic concentration signal. *Plant, Cell & Environment*, *39*(2), 233-244.

*Climate Change Kaltenborn*. (n.d.). Meteoblue. Retrieved March 20, 2022, from https://www.meteoblue.com/en/climate-change/kaltenborn_germany_2893620

Coll, L., Ameztegui, A., Collet, C., Löf, M., Mason, B., Pach, M., ... & Ponette, Q. (2018). Knowledge gaps about mixed forests: what do European forest managers want to know and what answers can science provide?. *Forest Ecology and Management*, *407*, 106-115.

Dıaz, S., Symstad, A. J., Chapin III, F. S., Wardle, D. A., & Huenneke, L. F. (2003). Functional diversity revealed by removal experiments. *Trends in Ecology & Evolution*, *18*(3), 140-146.

Dietrich, L., Zweifel, R., & Kahmen, A. (2018). Daily stem diameter variations can predict the canopy water status of mature temperate trees. *Tree Physiology*, *38*(7), 941-952.

Drew, D. M., & Downes, G. M. (2009). The use of precision dendrometers in research on daily stem size and wood property variation: a review. *Dendrochronologia*, *27*(2), 159-172.

Duffy, J. E., Godwin, C. M., & Cardinale, B. J. (2017). Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature*, *549*(7671), 261-264.

Felton, A., Lindbladh, M., Brunet, J., & Fritz, Ö. (2010). Replacing coniferous monocultures with mixed-species production stands: an assessment of the potential benefits for forest biodiversity in northern Europe. *Forest ecology and management*, *260*(6), 939-947.

Fichtner, A., Härdtle, W., Li, Y., Bruelheide, H., Kunz, M., & von Oheimb, G. (2017). From competition to facilitation: how tree species respond to neighbourhood diversity. *Ecology Letters*, *20*(7), 892-900.

Fichtner, A., Härdtle, W., Bruelheide, H., Kunz, M., Li, Y., & Von Oheimb, G. (2018). Neighbourhood interactions drive overyielding in mixed-species tree communities. *Nature communications*, *9*(1), 1-8.

Gall, R., Landolt, W., Schleppi, P., Michellod, V., & Bucher, J. B. (2002). Water content and bark thickness of Norway spruce (Picea abies) stems: phloem water capacitance and xylem sap flow. *Tree Physiology*, *22*(9), 613-623.

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., ... & Bengtsson, J. (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature communications*, *4*(1), 1-8.

Gayler, S., Grams, T. E. E., Kozovits, A. R., Winkler, J. B., Luedemann, G., & Priesack, E. (2006). Analysis of competition effects in mono-and mixed cultures of juvenile beech and spruce by means of the plant growth simulation model PLATHO. *Plant Biology*, *8*(04), 503-514.

Hautier, Y., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., Hillebrand, H., ... & Hector, A. (2014). Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature*, *508*(7497), 521-525.

Hendriks, C. M. A., & Bianchi, F. J. J. A. (1995). Root density and root biomass in pure and mixed forest stands of Douglas-fir and beech. *Netherlands Journal of Agricultural Science*, *43*(3), 321-331.

Hilmers, T., Avdagić, A., Bartkowicz, L., Bielak, K., Binder, F., Bončina, A., ... & Pretzsch, H. (2019). The productivity of mixed mountain forests comprised of Fagus sylvatica, Picea abies, and Abies alba across Europe. *Forestry: An International Journal of Forest Research*, *92*(5), 512-522.

Hölttä, T., Mäkinen, H., Nöjd, P., Mäkelä, A., & Nikinmaa, E. (2010). A physiological model of softwood cambial growth. *Tree Physiology*, *30*(10), 1235-1252.

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E., Hungate, B. A., Matulich, K. L., ... & O'Connor, M. I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, *486*(7401), 105-108.

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., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. Cambridge University Press. In Press.

Jucker, T., Bouriaud, O., Avacaritei, D., & Coomes, D. A. (2014a). Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. *Ecology Letters*, *17*(12), 1560-1569.

Jucker, T., Bouriaud, O., Avacaritei, D., Dănilă, I., Duduman, G., Valladares, F., & Coomes, D. A. (2014b). Competition for light and water play contrasting roles in driving diversity–productivity relationships in Iberian forests. *Journal of Ecology*, *102*(5), 1202-1213.

Jucker, T., Koricheva, J., Finér, L., Bouriaud, O., Iacopetti, G., & Coomes, D. A. (2020). Good things take time—Diversity effects on tree growth shift from negative to positive during stand development in boreal forests. *Journal of Ecology*, *108*(6), 2198-2211.

Kambach, S., Allan, E., Bilodeau-Gauthier, S., Coomes, D. A., Haase, J., Jucker, T., ... & Bruelheide, H. (2019). How do trees respond to species mixing in experimental compared to observational studies?. Ecology and evolution, 9(19), 11254-11265.

Kunz, M., Fichtner, A., Härdtle, W., Raumonen, P., Bruelheide, H., & von Oheimb, G. (2019). Neighbour species richness and local structural variability modulate aboveground allocation patterns and crown morphology of individual trees. Ecology Letters, 22(12), 2130-2140.

Liang, J., Crowther, T. W., Picard, N., Wiser, S., Zhou, M., Alberti, G., ... & Reich, P. B. (2016). Positive biodiversity-productivity relationship predominant in global forests. *Science*, *354*(6309), aaf8957.

Liu, C. L. C., Kuchma, O., & Krutovsky, K. V. (2018). Mixed-species versus monocultures in plantation forestry: Development, benefits, ecosystem services and perspectives for the future. *Global Ecology and Conservation*, *15*, e00419.

Loreau, M., & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, *412*(6842), 72-76.

Martinez-Vilalta, J., Anderegg, W. R., Sapes, G., & Sala, A. (2019). Greater focus on water pools may improve our ability to understand and anticipate drought-induced mortality in plants. *New Phytologist*, *223*(1), 22-32.

Meinzer, F. C., Johnson, D. M., Lachenbruch, B., McCulloh, K. A., & Woodruff, D. R. (2009). Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology*, *23*(5), 922-930.

Mencuccini, M., Hölttä, T., Sevanto, S., & Nikinmaa, E. (2013). Concurrent measurements of change in the bark and xylem diameters of trees reveal a phloem-generated turgor signal. New phytologist, 198(4), 1143-1154.

Meyer, S. T., Ebeling, A., Eisenhauer, N., Hertzog, L., Hillebrand, H., Milcu, A., ... & Weisser, W. W. (2016). Effects of biodiversity strengthen over time as ecosystem functioning declines at low and increases at high biodiversity. *Ecosphere*, *7*(12), e01619.

Nehemy, M. F., Benettin, P., Asadollahi, M., Pratt, D., Rinaldo, A., & McDonnell, J. J. (2021). Tree water deficit and dynamic source water partitioning. *Hydrological Processes*, *35*(1), e14004.

Paquette, A., & Messier, C. (2011). The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography*, *20*(1), 170-180.

Paquette, A., Hector, A., Castagneyrol, B., Vanhellemont, M., Koricheva, J., Scherer-Lorenzen, M., & Verheyen, K. (2018). A million and more trees for science. *Nature ecology & evolution*, *2*(5), 763-766.

Peters, R. L., Steppe, K., Cuny, H. E., De Pauw, D. J., Frank, D. C., Schaub, M., ... & Fonti, P. (2021). Turgor–a limiting factor for radial growth in mature conifers along an elevational gradient. *New Phytologist*, *229*(1), 213-229.

Pretzsch, H. (2014). Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *Forest Ecology and Management*, *327*, 251-264.

Pretzsch, H., Schütze, G., & Biber, P. (2018). Drought can favour the growth of small in relation to tall trees in mature stands of Norway spruce and European beech. *Forest Ecosystems*, *5*(1), 1-19.

Rahmstorf, S., & Coumou, D. (2011). Increase of extreme events in a warming world. *Proceedings of the National Academy of Sciences*, *108*(44), 17905-17909.

Ratcliffe, S., Liebergesell, M., Ruiz-Benito, P., Madrigal González, J., Muñoz Castañeda, J. M., Kändler, G., ... & Wirth, C. (2016). Modes of functional biodiversity control on tree productivity across the European continent. *Global ecology and biogeography*, *25*(3), 251-262.

Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., ... & Baeten, L. (2017). Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecology letters*, *20*(11), 1414-1426.

Rukh, S., Poschenrieder, W., Heym, M., & Pretzsch, H. (2020). Drought Resistance of Norway Spruce (Picea abies [L.] Karst) and European Beech (Fagus sylvatica [L.]) in Mixed vs.

Monospecific Stands and on Dry vs. Wet Sites. From Evidence at the Tree Level to Relevance at the Stand Level. *Forests*, *11*(6), 639.

Salomón, R. L., Peters, R. L., Zweifel, R., Sass-Klaassen, U. G., Stegehuis, A. I., Smiljanic, M., ... & Steppe, K. (2022). The 2018 European heatwave led to stem dehydration but not to consistent growth reductions in forests. *Nature communications*, *13*(1), 1-11.

Salomón, R. L., De Schepper, V., Valbuena-Carabaña, M., Gil, L., & Steppe, K. (2018). Daytime depression in temperature-normalised stem $CO_2$ efflux in young poplar trees is dominated by low turgor pressure rather than by internal transport of respired $CO_2$. New Phytologist, 217(2), 586-598.

Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N., & Loreau, M. (2014). Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. *Ecology*, *95*(9), 2479-2492.

Sapijanskas, J., Potvin, C., & Loreau, M. (2013). Beyond shading: litter production by neighbors contributes to overyielding in tropical trees. *Ecology*, *94*(4), 941-952.

Schäfer, C., Rötzer, T., Thurm, E. A., Biber, P., Kallenbach, C., & Pretzsch, H. (2019). Growth and tree water deficit of mixed Norway spruce and European beech at different heights in a tree and under heavy drought. *Forests*, *10*(7), 577.

Scherer-Lorenzen, M., Potvin, C., Koricheva, J., Schmid, B., Hector, A., Bornik, Z., ... & Schulze, E. D. (2005). The design of experimental tree plantations for functional biodiversity research. In *Forest diversity and function* (pp. 347-376). Springer, Berlin, Heidelberg.

Scherer-Lorenzen, M., Schulze, E. D., Don, A., Schumacher, J., & Weller, E. (2007). Exploring the functional significance of forest diversity: A new long-term experiment with temperate tree species (BIOTREE). *Perspectives in Plant Ecology, Evolution and Systematics*, *9*(2), 53-70.

Schulze, E. D., Bazzaz, F. A., Nadelhoffer, K., Koike, T., & Takatsuki, S. (1996). Biodiversity and ecosystem function of temperate deciduous broad-leaved forests. In *Functional roles of biodiversity: a global perspective* (pp. 71-98). John Wiley.

Searle, E. B., & Chen, H. Y. (2020). Complementarity effects are strengthened by competition intensity and global environmental change in the central boreal forests of Canada. Ecology Letters, 23(1), 79-87.

Sevanto, S., Vesala, T., Perämäki, M., & Nikinmaa, E. (2003). Sugar transport together with environmental conditions controls time lags between xylem and stem diameter changes. *Plant, Cell & Environment*, *26*(8), 1257-1265.

Spiecker, H., Lindner, M., & Schuler, J. (2019). Douglas-fir-What Science Can Tell Us–an option for Europe.

Steppe, K., Sterck, F., & Deslauriers, A. (2015). Diel growth dynamics in tree stems: linking anatomy and ecophysiology. *Trends in plant science*, *20*(6), 335-343.

Taylor, A. R., Gao, B., & Chen, H. Y. (2020). The effect of species diversity on tree growth varies during forest succession in the boreal forest of central Canada. *Forest Ecology and Management*, *455*, 117641.

*TreeDivNet*. (2011a). TreeDivNet. Retrieved February 11, 2022, from https://treedivnet.ugent.be/ProjectMixForChange.html

*TreeDivNet*. (2011b). TreeDivNet. Retrieved February 18, 2022, from https://treedivnet.ugent.be/ProjectMixForChange.html

Verheyen, K., Vanhellemont, M., Auge, H., Baeten, L., Baraloto, C., Barsoum, N., ... & Scherer-Lorenzen, M. (2016). Contributions of a global network of tree diversity experiments to sustainable forest plantations. *Ambio*, *45*(1), 29-41.

Vilà, M., Inchausti, P., Vayreda, J., Barrantes, O., Gracia, C., Ibáñez, J. J., & Mata, T. (2005). Confounding factors in the observational productivity-diversity relationship in forests. In *Forest diversity and function* (pp. 65-86). Springer, Berlin, Heidelberg.

Vilà, M., Vayreda, J., Comas, L., Ibáñez, J. J., Mata, T., & Obón, B. (2007). Species richness and wood production: a positive association in Mediterranean forests. *Ecology letters*, *10*(3), 241-250.

Vitali, V., Forrester, D. I., & Bauhus, J. (2018). Know your neighbours: drought response of Norway spruce, silver fir and Douglas fir in mixed forests depends on species identity and diversity of tree neighbourhoods. *Ecosystems*, *21*(6), 1215-1229.

Zweifel, R., Haeni, M., Buchmann, N., & Eugster, W. (2016). Are trees able to grow in periods of stem shrinkage?. *New Phytologist*, *211*(3), 839-849.

Zweifel, R., & Sterck, F. (2018). A conceptual tree model explaining legacy effects on stem growth. Frontiers in Forests and Global Change, 1, 9.

Zweifel, R., Sterck, F., Braun, S., Buchmann, N., Eugster, W., Gessler, A., ... & Etzold, S. (2021). Why trees grow at night. *New Phytologist*, *231*(6), 2174-2185.

Zweifel, R., Zimmermann, L., & Newbery, D. M. (2005). Modeling tree water deficit from microclimate: an approach to quantifying drought stress. Tree physiology, 25(2), 147-156.