Carbon stocks and sequestration rates of hardwood floodplain forests along the Middle Elbe River, Germany

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A hardwood floodplain forest dominated by *Quercus robur*

on the active floodplain of the Middle Elbe River.

Photo taken in 2019 by Heather A. Shupe.

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Abbreviations

ABI	aboveground biomass increment
ADF	acid detergent fiber
ADL	acid determined lignin
BAI	basal area increment
C	carbon
CO_2	carbon dioxide
CS	carbon stock
CSR	carbon sequestration rate
DBH	diameter at breast height
DWD	downed woody debris
HF	hardwood floodplain
N	nitrogen
NDF	neutral detergent fiber
SPEI	Standardized Precipitation Evaporation Index
TRW	tree ring width

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Chapter 1: General Introduction

1.1 Hardwood floodplain forests

Hardwood floodplain (HF) forests are highly productive yet endangered ecosystems dominated by hardwood tree species which are located on seasonally or irregularly flooded soils of floodplains. Globally, HF forests vary in terminology and characteristics such as species compositions. In literature, HF forests have also been referred to as mixed riparian floodplain and gallery woodlands (EUNIS 2012), alluvial hardwood forests (Schnitzler 1994, Bannister et al. 2015), *Querco-Ulmetum minoris* (Schnitzler 1994), *Alno-Ulmion* (Leuschner and Ellenberg 2017), *Ficario-Ulmetum* (Härdtle et al. 2020), riparian forests (Kozlowski 2002), and bottomland forests (Frye and Grosse 1992, Shoch et al. 2009, Ricker et al. 2016, King and Keim 2019). The HF forests referred to in this thesis are classified as EUNIS code T13: temperate hardwood riparian woodlands, and are currently listed as Endangered on the EU28+ Red List of Habitats (EEA 2022). This research focuses on northern European floodplains, and specifically on HF forests of the Middle Elbe River, Germany. The typical tree species iof T13 HF forests include *Quercus* spp., *Ulmus* spp., *Fraxinus* spp., and *Acer* spp. Pedunculate Oak (*Quercus robur*) is the dominant floodplain tree species in lowland northern Central Europe (Leuschner and Ellenberg 2017), which is also true for HF of the Middle Elbe River (Shupe et al. 2021).

1.2 Riverine floodplain dynamics and the effect on vegetation zonation and hardwood forests

Riverine floodplain dynamics create environmental gradients which affect vegetation zonation and the structure, species composition, and the function of HF forests. Because of a high level of spatial-temporal heterogeneity, riverine floodplains are among the most species-rich environments (Ward et al. 1999). The availability of oxygen, moisture, and nutrients in the soil as well as sediment sizes and other edaphic conditions determine which biota thrive in different areas of the floodplain, and these conditions are influenced by the hydrological regime and floodplain geomorphology (Junk et al. 1989, Hughes 1997, Gallardo 2003). Fluctuating periods of drought and flooding are common occurrences on the floodplain due to changes in water levels throughout the year, and the frequency, duration, and severity of these events varies over the years. Highly dynamic floodplains are subject to lateral overflow water, groundwater, upland sources, and precipitation (Tockner and Stanford 2002). Seasonal flooding in temperate areas is often associated with snowmelt in the spring. Heavy precipitation events can raise river water levels which can affect vegetation and sometimes be catastrophic for human settlements located near rivers, especially in degraded floodplains where floodwater retention areas have been reduced (Kiedrzyńska et al. 2014). Elevation on the floodplain is an indicator of flooding frequency, however, the complex geomorphology of floodplains and variability in environmental conditions also affects annual flooding duration. Drying and wetting cycles on floodplains affect decomposition processes and nutrient cycling which in turn affects vegetation communities (Junk et al. 1989, Robertson et al. 1999, Heffernan and Sponseller 2004). Perpendicular to rivers, there is generally an environmental gradient with many varying factors (e.g. edaphic characteristics, duration of flooding, and depth of the groundwater table) which shapes the zonation of riparian vegetation (Glenz et al. 2006). The frequency, duration, velocity, magnitude, and timing of flooding can all influence the community, vitality, and productivity of floodplain species (Blom 1999, Glaeser and Wulf 2009, Talbot et al. 2018). Tree species zonation and compositions of floodplains highly depends on hydrological conditions because flooding and drought tolerances vary by species (Frye and Grosse 1992). Species composition gradients strongly correlate with hydrology (Leyer 2004), with flooding and drought conditions selecting for the most well-adapted species. While softwood forests inhabit more frequently flooded areas, HF forests are located in relatively less frequently flooded areas (Siebel and Bouwma 1998, Blom 1999, Leuschner and Ellenberg 2017). Hardwood trees which thrive on floodplains can adapt to flooding and drought conditions, however, survival chances can vary by the amount of stress and tree age. While older HF trees can adapt to flooding and facilitate oxygen uptake during periods of inundation through the development of hypertrophied lenticels, aerenchyma tissues, and adventitious roots (Kozlowski 2002), saplings are more vulnerable to flooding (Blom 1999, Vreugdenhil et al. 2006). The chances of survival of hardwood seedlings decreases with increased flooding duration, depth, and frequency of flooding, but their survival capacity increases with age (Gill 1970, Blom 1999). Additionally, the timing of floods can impact the survival of HF tree species, with irregular high floods in late spring and summer decreasing the chance of seedling establishment (Siebel and Blom 1998). While too much water can have negative effects on the survival and growth of trees, too little water can also be detrimental. Drought can cause hydraulic failure and carbon starvation, both of which reduce tree productivity and eventually can result in tree mortality (Adams et al. 2017). Drought conditions on the floodplain can be overcome to a certain degree by HF tree species such as *Q. robur* through stomatal regulation and the development of long tap roots to access water (Thomsen et al. 2019). However, drought resilience is species-dependent and limited in younger trees which have shorter roots than mature trees (Leonova et al. 2022). While the highly dynamic nature of floodplain hydrology limits the areas suitable for HF forest establishment, flooding and drought stress can affect tree productivity, and it is with great interest that we determine the locations most suitable to maximize tree productivity and ecosystem services (see section 1.4) of HF forests.

Biodiversity in HF forests is typically higher than in upland forests because of the frequent disturbances and the complex geomorphology of floodplains that creates microsites for many species (Naiman et al. 1993, Postel and Carpenter 1997). The most species-rich communities on floodplains typically have intermediate levels of disturbance and intermediate flooding frequencies (Pollock et al. 1998) and ecosystem multifunctionality is highest at sites which are flooded regularly (Sendek 2021). Floodplain areas exposed to river flood pulses receive inputs of nutrients which are valuable for growth and are known to boost productivity of vegetation (Junk et al. 1989). Different floodplain compartments of major rivers (i.e. low sites on the active floodplain, high sites on the active floodplain, the seepage water zone behind dikes, or tributary floodplains) are exposed to different flooding dynamics, and the productivity of vegetation growing in these compartments may therefore be differently affected by the hydrological conditions.

1.3 Land use history of European floodplains and threats to hardwood floodplain forests

For centuries, human agricultural settlements have prospered from the highly fertile alluvial soils near large European rivers. Under natural conditions, the morphological floodplains would be inundated with river water on a recurring basis and nutrient-rich river pulses would continue to enhance the fertility of the soils (Junk et al. 1989). However, since the Middle Ages, river engineering in Europe has changed the flow of rivers to suit human needs. With the canalization, straightening and damming of the rivers, natural erosion and sedimentation processes now only occur in a few areas in Central Europe (Leuschner and Ellenberg 2017). The hydrological modifications split the floodplain into the active floodplain and the former floodplain. While nutrient-rich river pulses still inundate the active floodplain, the former floodplain areas behind the dikes are exposed to seepage water but disconnected from river pulses. As of 2021, only a third of the former floodplains in Germany can be flooded and a majority of the existing active floodplain is intensively used (BMU and BfN 2021). Across the entire Middle Elbe in Germany, the loss of flooded areas is between 50% and more than 90% (BMU and BfN 2021). While 43% of German floodplains is dominated by grassland, 16% is forested, and only a small fraction of the forested area is in a near-natural state and able to provide sufficient habitat to plants and animals typically thriving on the floodplain (BMU and BfN 2021). In Germany, natural HF forests have been reduced to less than 1% of the active floodplain area (BMU 2009, Brunotte et al.

2009, Scholz et al. 2012) and are threatened by dikes and river engineering, agricultural practices, forest fragmentation, disease, and climate change (King and Keim 2019).

Dike presence constrains the floodplain and prevents nutrient-rich flood pulses from reaching the forests located in the former floodplain's seepage water zone behind the dike (Figure 1.1). Dikes can affect the species compositions of forests on the seepage water zone by altering hydrological connectivity, sedimentation, and plant dispersal processes (Leyer 2004). Additionally, river straightening and the construction of dams, barrages, groynes, and bank reinforcements change the morphology of the floodplain and alter the natural disturbance regimes which maintain ecologically diverse floodplains (Naiman et al. 1993). Some species typically found in HF forests, such as *Ulmus* spp., are highly threatened by water regulation (Caudullo and de Rigo 2016).

Figure 1.1 Dike presence on the Middle Elbe floodplain constrains the floodplain and alters floodplain hydrology, with the active floodplain besides the river to the right of the dike and the seepage water zone in the former floodplain to the left. Photo taken near Wittenberge in 2018 by Heather A. Shupe.

Agricultural land dominates the floodplain and is managed to prevent natural succession. This form of land use management reduces the area available to HF forests and changes their connectivity and function. Many of today's remnants of HF forests are patchy and sparse, and dense HF forests with successful natural regeneration are rare (BMU and BfN 2021). Additionally, intensive understory grazing, harvesting of trees, and the use of heavy machinery changes the character and edaphic conditions of natural HF forests. Compaction of soil, crushing of understory vegetation, removal of deadwood, and increased edge effects can alter the understory species composition and change the character and habitat suitability for species typical for HF forests (Petrášová-Šibíková et al. 2017).

Along with human modifications to floodplains which reduces HF forest area, disease and insects also threatens remaining tree species typical for HF forests. Dutch elm disease caused by three different fungal pathogens in the genus *Ophiostoma* and transmitted by *Scolytus* beetles has devastated *Ulmus* spp. populations in Europe (Martín et al. 2018). Ash dieback caused by the fungal pathogen *Hymenoscyphus fraxineus* has decimated *Fraxinus excelsior* trees in HF forests and throughout Europe (Leuschner and Ellenberg 2017, Erfmeier et al. 2019). *Q. robur trees*, especially in monoculture plantations, can be susceptible to insect outbreaks. One notable caterpillar is the oak processionary moth (*Thaumetopoea processionea*). Not only are the toxic caterpillar hairs a public health hazard for humans, defoliation of the trees by caterpillars can reduce photosynthetic capacity and thus tree productivity while also weakening the trees, making them more vulnerable to other threats (e.g. drought conditions) (Groenen and Meurisse 2012, Tomlinson et al. 2015). Other threats to *Q. robur* include oak mildew (*Erysiphe alphitoides*), root pathogens, and the new and little understood syndrome Acute Oak Decline which may be associated with lowered groundwater tables and absence of flooding in combination with other factors such as climate change (Eaton et al. 2016).

Climate change driven by increasing concentrations of atmospheric gases such as carbon dioxide (CO_2) is a major threat to forests worldwide and has already resulted in mass tree mortalities due to rising temperatures and droughts, however, the severity of the threat at local scales is uncertain (Allen et al. 2010, Anderegg et al. 2012, IPCC 2021). The most severe regional climate-changeinduced issues in northern Germany include drought (particularly in the spring) and increased occurrences of extreme weather events such as torrential rains (Barkmann et al. 2017). Drought events have increased since the 1950s and higher temperatures and more frequent drought events are projected for Europe (IPCC 2021). Northern Hemisphere spring snow cover has decreased since 1950 (IPCC 2021), which can lower river water levels and worsen drought conditions if not offset by precipitation. It is projected that climate change will further alter the hydrological behavior of rivers and the hydrological conditions of floodplains (Pfeiffer and Ionita 2017), which will consequently affect floodplain biota. While forests can benefit from CO_2 fertilization and longer warmer growing seasons associated with climate change, drought events can reduce growth and increase stress and mortality of trees (Allen et al. 2010). It is not known how climate change may affect HF forests, but it is known that extreme drought events and changes to hydrological conditions negatively affect tree growth (Perkins et al. 2018). Irregular floodings and droughts are characteristic features on floodplains, and *Q. robur* can adapt to hydrological fluctuations, but the frequency and intensity of floods and droughts are expected to change in the future. Although *Q. robur* is to a certain degree resistant to drought, *Q. robur* trees are also at risk for hydraulic failure, xylem cavitation, and mortality under extreme or prolonged drought conditions (Urli et al. 2015). *Q. robur* are especially vulnerable to spring droughts (Bose et al. 2021). Decreases in water level as well as temperature increases can result in a decline of *Q. robur* growth on floodplains (Stojanović et al. 2015). However, higher temperatures in conjunction with high water availability could also increase tree productivity and carbon sequestration rates of forests (Seppälä 2009, Tatarinov and Cienciala 2009), and may be beneficial to the productivity of HF forests with ample water supply on the floodplain (Mikac et al. 2018). Because water availability on the floodplain is spatially and temporally variable, it is important to research the growth reactions of HF trees to drought and floods in different floodplain compartments to determine possible future outcomes and the effects on ecosystem services of HF forests in response to climate change.

1.4 Ecosystem services of hardwood floodplain forests

Ecosystem services are the many benefits humans obtain from ecosystems and are categorized into four types: Provisioning, Regulating, Cultural, and Supporting services (Millenium Ecosystem Assessment 2005). Although there has been a rapid and extensive loss of ecosystems to meet the demand for food, water, timber, fiber, and fuel (Millenium Ecosystem Assessment 2005), measures to quantify and take action to maximize ecosystem services are also being made (Di Sacco et al. 2021). One measure to increase ecosystem services in some areas is reforestation of land that naturally would be forested if not for human intervention (Hornung et al. 2019), such as floodplains. Ecosystem services that are positively influenced by floodplain reforestation include carbon storage and sequestration, the retention of nutrients, flood risk and mass flow/ sediment regulation, soil formation, local temperature regulation/ cooling, the provision of wild animals and fish, the provision of surface- and ground-water for drinking, and the maintenance of habitats (Hornung et al. 2019). Floodplain reforestation can also have a positive influence on cultural services such as landscape aesthetics, natural and cultural heritage, and water-related activities (Hornung et al. 2019). Potentially negative trade-offs of floodplain reforestation may be the reduction of cultivated crops and plant resources for agricultural use (Hornung et al. 2019). The quantification and weighing of the positive and negative outcomes of floodplain management measures is important to provide science-based advice on how to maximize ecosystem services. Although it is important to be aware of all ecosystem services and trade-offs when determining suitable floodplain management measures, in this body of research, we focus mainly on carbon storage and sequestration of HF forests.

Management measures such as reforestation of HF forests may increase carbon stocks (as storage) and carbon flows (as sequestration) of the floodplain and contribute to the ecosystem service of global climate regulation (Keith et al. 2021), however, it is important to accurately quantify these services and keep the potential contribution of reforestation in perspective with the global carbon cycle.

The carbon cycle is important to understand and correctly quantify because it is directly tied to one of the most pressing challenges of our time: climate change. There is no scientific doubt that the increase of CO_2 in the atmosphere since the Industrial Revolution is directly linked to climate change (IPCC 2021). Global atmospheric CO_2 levels have increased due to high rates of anthropogenic combustion of organic carbon as well as the destruction of natural carbon sinks such as forests (Bakwin et al. 1998, Pan et al. 2011). Globally, it is estimated that terrestrial vegetation stores 450 Gigatonnes (Gt) of carbon and there is a CO_2 sink of 3.1 ± 0.6 Gt of carbon per year by the land (Figure 1.2) (Canadell et al. 2022, Friedlingstein et al. 2022). The amount of carbon stored in forests (live and dead vegetation and soil) is about 862 Gt, and the total forest carbon sink is 2.4 ± 0.4 Gt of carbon per year (Pan et al. 2011). The latest decadal average (2011–2020) annual flux of CO_2 into the atmosphere from fossil fuels is 9.5 ± 0.5 Gt of carbon, which is more than three times greater than the global vegetation sink (Canadell et al. 2022, Friedlingstein et al. 2022). To meet the goals of the Paris Agreement's legally binding international treaty on climate change (UN 2015a), the increase of carbon sinks (along with great reductions of fossil fuel emissions) is imperative. Although the global carbon cycle has been estimated through models, there is still considerable uncertainty and spatial and temporal variability associated with the terrestrial carbon sink (Poulter et al. 2011).

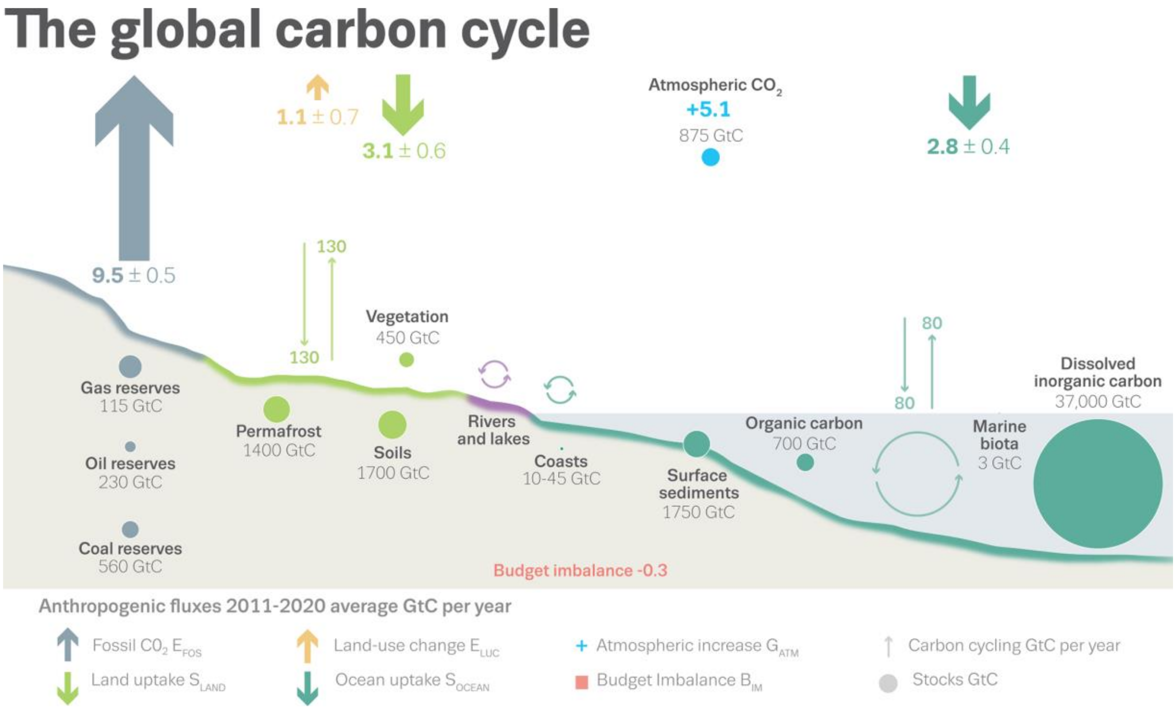


Figure 1.2 Schematic representation of the global carbon cycle and anthropogenic fluxes, averaged for the decade 2011–2020. The anthropogenic perturbation is shown with arrows on top of stocks and fluxes of the active carbon cycle shown with circles (Canadell et al. 2022, Price and Warren 2022). Figure from Friedlingstein et. al., 2022.

To reduce uncertainty in carbon cycle modelling, knowledge about parameters such as carbon stocks, sequestration rates, and carbon cycling in highly variable ecosystems such as HF forests is required (Larocque et al. 2008). The nature-based solution of reforestation is considered a strategy which can contribute to the reduction of atmospheric CO_2 (Griscom et al. 2017), but not all trees and not all locations for reforestation may provide the same carbon sink benefit. Forests can both store carbon (carbon stocks) and sequester carbon from the atmosphere (carbon sequestration). The ecosystem service of carbon storage can be estimated by taking an inventory of the carbon stocks of different carbon pools in an ecosystem at one point in time, while carbon sequestration can be estimated by calculating the change in the carbon stocks over time (usually the change over a year, which can be averaged over several years). During a forest inventory, different organic carbon pools such as above- and below-ground biomass in living trees, shrubs, and standing dead wood, downed woody debris, leaf litter, and soil are measured (UNFCCC 2015b). A second inventory can be taken years after the first inventory to determine the change in the carbon stock, and thus the carbon sequestration rate (CSR). Some of the many factors which may influence the CSR of HF forests include the hydrological situation, climate, forest stand structure, decomposer communities, and vegetative species composition (Giese et al. 2000, Battin et al. 2009, Freschet et al. 2012). Also, different structures of organic carbon can influence carbon cycling pathways and decomposition rates, which in turn can affect the CSR. Carbon is the universal building block of life and is able to form a great variety of complex yet stable molecules with itself and other elements (Schulze-Makuch and Irwin 2004). Through the process of photosynthesis, trees use the sun's energy to convert atmospheric CO_2 into complex biological structures such as cellulose, hemicellulose, and lignin. Different carbon pools have highly variable turnover and residence times in specific carbon pools depending on the biochemical characteristics, surrounding conditions, and annual environmental changes (Sierra et al. 2017). Once converted into biomass, there are many pathways the organic carbon can take. It can be stored for long periods of time as the structure of living trees, eaten by animals or decomposers and partially respired back into the atmosphere and partially converted into other forms of biomass, or combusted and released back into the atmosphere. While deadwood can take centuries to decompose and the carbon thus remains stored in the deadwood carbon pool until then, leaf litter can be decomposed in less than a year (Kurz et al. 2009), potentially reducing the annual CSR of the leaf litter pool. The decomposition rate of different organic carbon pools is therefore an important part of carbon accounting in an ecosystem, and is required for carbon budget modelling (i.e. in the Carbon Budget Model of the Canadian Forest Sector CBM-CFS3) (Kurz et al. 2009). Because local conditions can highly influence decomposition rates, investigations into how these conditions may influence decomposition are necessary. The quantification of carbon stocks, CSRs, and decomposition rates of different carbon pools within highly variable HF forests can improve the scientific understanding of the impact that management measures such as floodplain reforestation can make on the carbon cycle, and can be valuable for improving climate change projections.

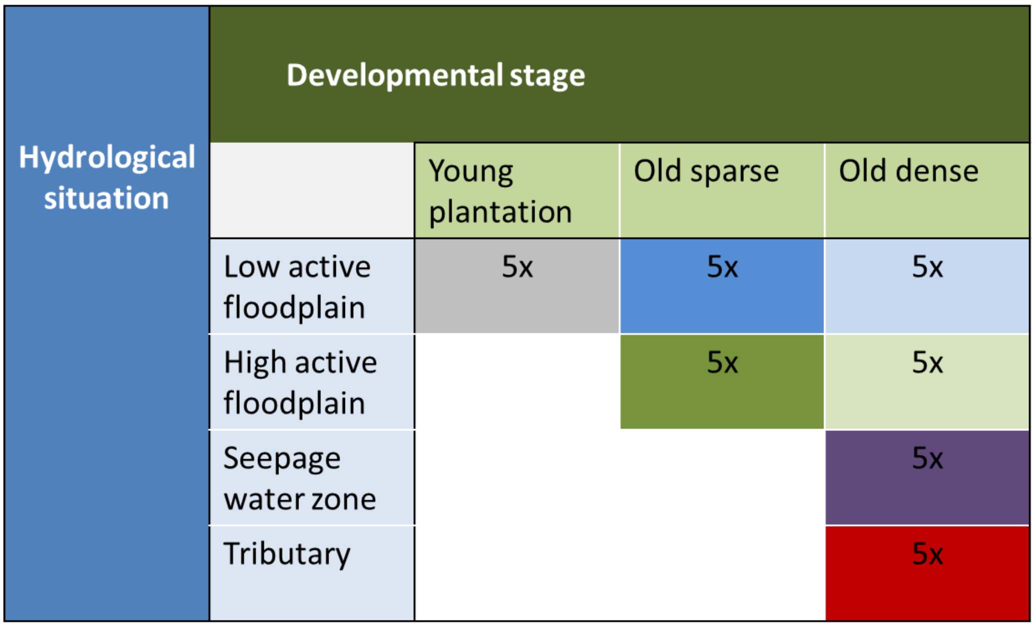
1.5 Restoration of hardwood floodplain forests

Efforts to relocate dikes and enlarge active floodplain areas have been made in Central Europe to both minimize the destruction of floods and to restore the biodiversity of species typical for floodplains (Schwartz et al. 2003, Damm 2013, BMU and BfN 2021). The three dike relocation projects Lödderitzer Forst (600 hectares), Lenzen (420 hectares) and Hohe Garbe (420 hectares) conducted along the Middle Elbe are among the largest dike relocation projects in Germany (BMU and BfN 2021). Through dike relocations in Germany, 7,100 hectares of active floodplain have been reclaimed between 1983 and 2020, which is a 1.5% increase in active floodplain area. However, this is small in comparison to the potential to restore tens of thousands of hectares of active floodplain areas in Germany (BMU and BfN 2021). The goal of Germany's National Strategy on Biological Diversity (Nationalen Strategie zur Biologischen Vielfalt) to increase the natural floodplains on rivers by 10% has still not been met, and thus calls for the continued restoration and reforestation of floodplains. Along with flood risk reduction and meeting national as well as global biodiversity goals (UN 2015b), reforestation of the floodplain with HF forests can also increase other ecosystem services such as the carbon storage and sequestration of floodplain ecosystems (Hornung et al. 2019). The understanding and quantification of these services is therefore required.

1.6 MediAN project

The main goal of the MediAN (Mechanisms of ecosystem services in hardwood floodplain forests: Scientific analysis and optimization of conservation management) project is to better understand the mechanisms underlying the ecosystem services of HF forests and to quantify the spatial and temporal variability of the services. It is a joint effort by scientists from the fields of plant ecology (University of Hamburg), soil science (University of Hamburg), soil zoology (Senckenberg Gesellschaft Görlitz), nature conservation research (Helmholtz Center for Environmental Research Leipzig) and landscape economics (TU Berlin). As a part of the MediAN project, the research complied in this dissertation investigates the carbon stocks of trees, shrubs, deadwood, and leaf litter, as well as the carbon sequestration of HF forests along the Middle Elbe.

The original study design of the MediAN project included the investigation of seven different HF forest strata classes differing in hydrological situations and forest developmental stages: (1) old dense forests on the low active floodplain, (2) old sparse forests on the low active floodplain, (3) young plantations on the low active floodplain, (4) old dense forests on the high active floodplain, (5) old sparse forests on the high active floodplain, (6) old forests in the former floodplain and seepage water zone behind the dike, and (7) old forests on tributaries (Figure 1.3). Although the original goal was to study seven replicate plots per strata class, not enough suitable replicates were identified, and this thesis thus includes five replicate plots per strata class. The plots are interspersed along approximately 100 km of the Middle Elbe River (Figure 1.4). Forests on the active floodplain were selected based on an estimated 25-year (1990-2016) mean annual flooding duration. Both elevation and floodplain morphology were considered in the model to determine flooding duration (Weber in prep). An example of a map used for site selection is shown in Figure 1.5.



Hydrological situation	Developmental stage			
		Young plantation	Old sparse	Old dense
	Low active floodplain	5x	5x	5x
	High active floodplain		5x	5x
	Seepage water zone			5x
	Tributary			5x

Figure 1.3 Seven strata classes of the MediAN project. Five replicate plots per strata class were identified and studied for the purpose of this thesis.

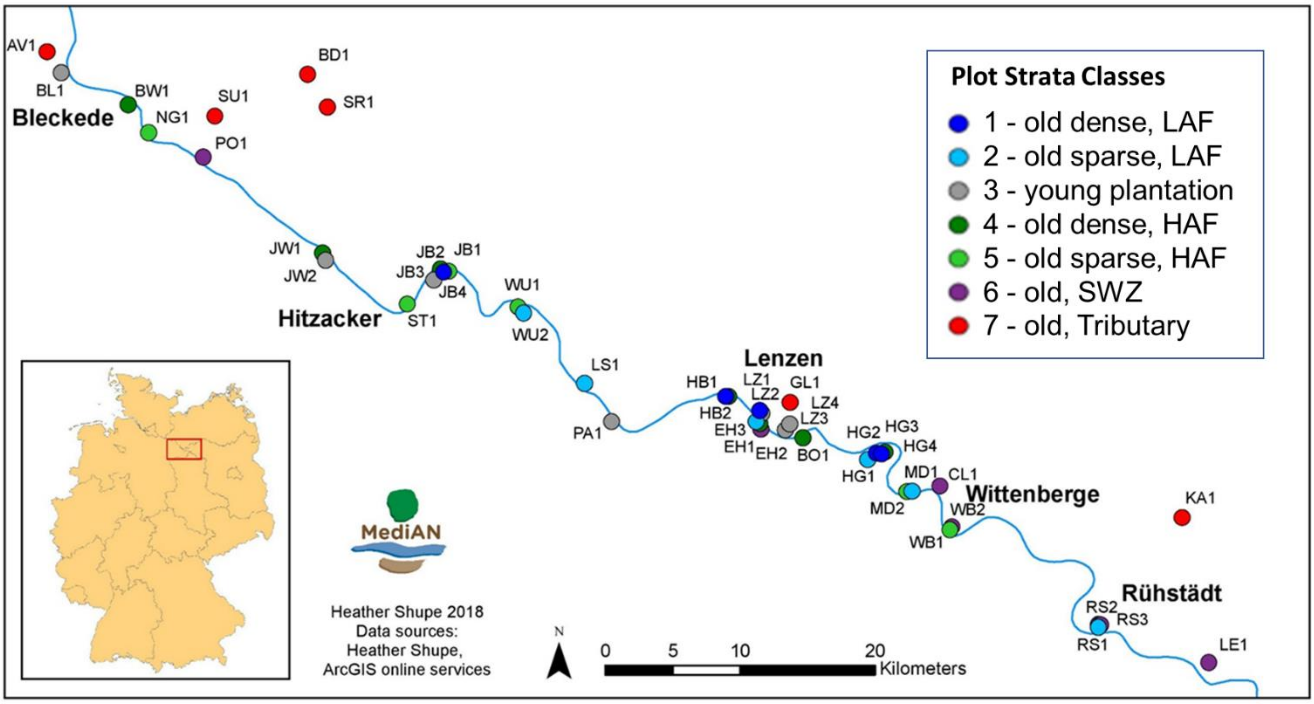
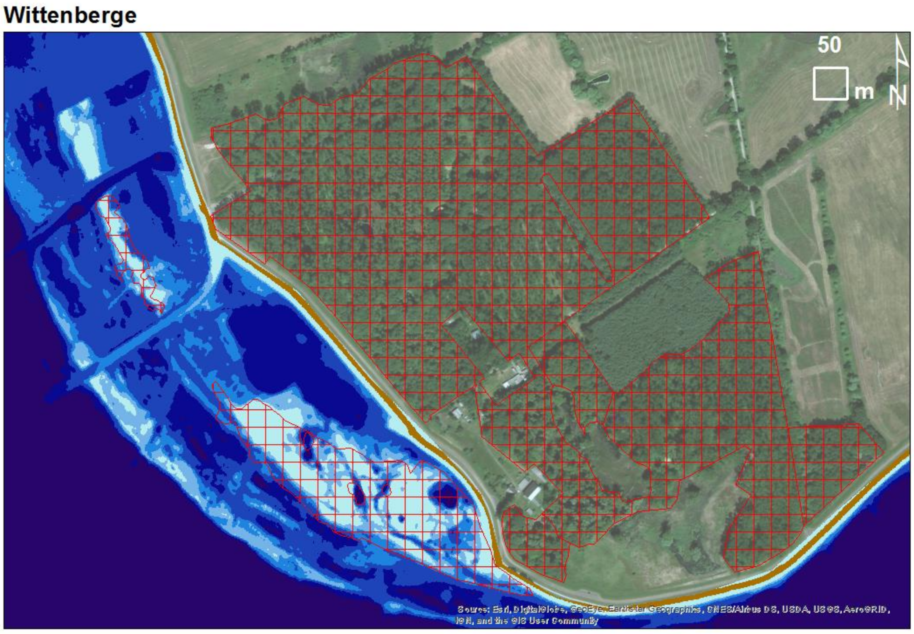


Figure 1.4 MediAN study plots along approximately 100 km of the Middle Elbe River, Germany. Seven strata classes were identified: (1) old dense forests on the low active floodplain (LAF), (2) old sparse forests on the LAF, (3) young plantations on the LAF, (4) old dense forests on the high active floodplain (HAF), (5) old sparse forests on the HAF, (6) old forests in the former floodplain behind the dike in the seepage water zone (SWZ), and (7) old forests on tributaries. Acronyms are included for each plot.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 1.5 An example site selection map of the area by Wittenberge, Germany. Red checkered squares indicate potential hardwood forest. The orange line outlines the dike which divides the active floodplain from the seepage water zone. The blue to white color gradient indicates estimated flooding duration, with the darker blue indicating greater annual flooding duration (typically lower elevation) and white indicating less annual flooding duration (typically higher elevation). Map produced by Timo Hartmann using GIS Software Version: Esri 1999 – 2018, ArcGIS Desktop 10.7.0 10450 and 25-year (1990-2016) mean flooding duration estimates from the hyd1D model (Weber in prep).

1.7 Aim and Structure of Thesis

A review of endangered HF forests and how they are affected by floodplain hydrology, land use history and other threats, as well as a review of their ecosystem services and recent restoration of HF forests shows that there is even more potential to increase the presence of HF forests and by doing so increase ecosystem services of floodplains. In order to understand the importance and impact of HF restoration, ecosystem services must be quantified. Therefore, the aim of this thesis is to quantify specifically the ecosystem services of carbon storage and sequestration rates of HF forests and determine the spatial and temporal variation of these services. With the knowledge gained through this research, science-based landscape management advice for the Middle Elbe floodplain as well as suggestions for future research is provided.

Chapter 2 explores carbon stocks of trees, deadwood, and leaf litter in HF forests differing in developmental stages and hydrological conditions. It also provides a logarithmic relationship between forest age and carbon stock and estimates the carbon stock of different tree species in different hydrological conditions.

Chapter 3 provides a method on how to calculate annual CSRs of *Q. robur* using diameter at breast height and tree ring width measurements from tree cores.

Chapter 4 uses the equation in Chapter 3 to estimate CSRs of dominant *Quercus robur* trees in (a) different forest developmental stages, (b) different hydrological conditions, and (c) different hydrological conditions during flood and drought years.

Chapter 5 explores leaf litter decomposition of the two main tree species (*Q. robur* and *Ulmus laevis*) on the active floodplain and provides decomposition rates that may be useful for carbon cycle modelling.

Chapter 6 synthesizes the key findings of each chapter, offers upscaled estimates of the CSRs of different HF forest types while also discussing the inherent challenges and limitations as well as future research recommendations to improve these estimates, discusses carbon budget models, mentions other challenges, offers recommendations for floodplain reforestations, and provides conclusions and outlook for other future research.

2

Chapter 2: Carbon stocks of hardwood floodplain forests along the Middle Elbe: the influence of forest age, structure, species, and hydrological conditions

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2.1 Abstract

Hardwood floodplain (HF) forests can store a considerable amount of carbon (C), and floodplains may be good candidates for reforestation to provide natural C sinks. In this study, we use nondestructive inventory methods to estimate the C stocks of different tree species and C pools within HF forests of varying age and structure and located at sites differing in hydrological conditions (low and high active floodplain, seepage water zone, tributaries). The study was carried out along the Elbe River (Germany). Average C stocks for young plantations in the active floodplain were significantly lower (50.2 ±10.8 SE Mg ha^{-1}) than those of old dense (140.6 ± 11.6 SE Mg ha^{-1}) and old sparse forests (180.4 ± 26.6 SE Mg ha^{-1}) with comparable hydrological conditions. C stocks of old dense forests did not significantly vary from old sparse forests. Additionally, C stocks of old forests did not significantly vary according to hydrological conditions. The highest amount of C was stored in *Quercus robur* for all hydrological conditions. *Ulmus laevis* stored the second-highest amount of C on the active floodplain. We conclude that sparse and dense forests as well as forests under different hydrological conditions provide the same C storage function.

2.2 Introduction

Hardwood floodplain (HF) forests can store a considerable amount of carbon (C) in woody biomass and provide many ecological services such as climate regulation through long-term C storage (Brown et al. 1997, Sutfin et al. 2016, Dybala et al. 2019). Globally, HF forests have declined substantially during the last centuries, and in Germany, natural HF forests have been reduced to less than 1% of the active floodplain area (BMU 2009, Brunotte et al. 2009, Scholz et al. 2012). The destruction of European HF forests began in the Middle Ages and continued with the expansion of agricultural land and the construction of dikes (Naiman et al. 2005). Only 10–20% of the former floodplains of the major river catchments in Germany are left, and these active floodplain areas are dominated by managed grasslands (Brunotte et al. 2009, Scholz et al. 2012). HF forests also grow on the seepage water zone behind the dike and on tributary floodplains, but they have different hydrological site conditions which may influence their function. Many of today’s remnants of HF forests are patchy and sparse, and dense HF forests with successful natural regeneration are rare.

Land management which increases the C storage of ecosystems is known as a natural climate solution, and reforestation has garnered global attention as a climate change mitigation measure (Griscom et al. 2017). Initiatives such as the Bonn Challenge and ECCA30 have set targets to restore millions of hectares of degraded and deforested lands by 2030 (Dave et al. 2019). To meet these targets, suitable locations for reforestation must be identified. Highly productive floodplains are good candidates for reforestation (Dybala et al. 2019), where other ecosystem services such as habitat provisioning to increase biodiversity and flood risk reduction of agricultural lands could also be maximized by reforestation (Hornung et al. 2019). Many studies have identified positive effects of floodplain vegetation on flood risk reduction, concluding that floodplain vegetation reduces flood risks by increasing hydraulic resistance, reducing flow velocity, and reducing peak magnitude at the catchment outflow (Thomas and Nisbet 2007, Leyer et al. 2012, Dixon et al. 2016). However, vegetation with high roughness can also potentially increase flood risks in upstream areas, and to what degree the roughness of vegetation affects flooding in different locations is still under debate (Leyer et al. 2012). Flow resistance may be influenced by forest age and density (Mckenney et al. 1995, Antonarakis and Milan 2020), and the ecosystem services and functions (i.e. C storage) of different forest ages and structures must therefore be quantified and assessed in parallel with other ecosystem services such as flood risk reduction to determine suitable floodplain management advice (Bennett et al. 2009). Reforestation of HF forests is also possible on the seepage water zone behind dikes and on the tributary floodplains, but it is not well known whether the C storage function of these forests with different hydrological conditions is equal to the active floodplain of the main river channel.

The few available studies on C stocks in HF forests report a wide range of C stocks of the standing biomass (7.5-281 Mg ha^{-1}) (Sutfin et al. 2016). On the Danube floodplain in Austria, C stock in aboveground biomass of HF forests is highest (281 ± 59 Mg ha^{-1}) compared to softwood (163 ± 26 Mg ha^{-1}), cottonwood (199 ± 29 Mg ha^{-1}), and reforestations (35 ± 17 Mg ha^{-1}) (Cierjacks et al. 2010). Interestingly, in another study for the same area of the Danube floodplain, much lower aboveground C stocks (123 ± 26 Mg ha^{-1}) were reported for mixed hardwood and softwood riparian forests (Rieger et al. 2013). While differences between inventory methods may have contributed to the wide range of C stock estimates, other site-specific conditions such as forest age and structure as well as hydrological and other abiotic conditions and species composition could also play a role here.

Stand structure and forest age affects the growth and yield of trees (Pretzsch 2009) and the C storage function of forests (Thom and Keeton 2019). Management of forest stands, i.e. timber extraction, understory livestock grazing, and the clearance of deadwood and thinning of trees to enhance the growth and dimensions of a few harvestable trees, is a long-standing practice in Europe (Assman 1970, Bergmeier and Roellig 2014, Schulze E.D et al. 2019). In Germany, timber extraction occurs in a majority of floodplain forests, and only a few near-natural stands remain (Schindler et al. 2016). The few remaining patches of dense forests which are multilayered and exhibit a well-developed shrub layer and overstory are contrasted with sparse forests which lack a well-developed shrub layer. Sparse and dense forests most likely represent differences in former and current management. Both sparse and dense forest are present on the active floodplain, but it is not known how C stocks differ according to these forest structures.

Trees in HF forests must withstand large hydrological fluctuations resulting in hypoxic or anoxic soils during flooding events and drought in dry periods. Annual flooding duration of HF forests on the active floodplain is related to elevation, with relatively low-lying HF forests subject to longer periods of hypoxia and those at higher elevations more prone to drought. Soil texture affects the water holding capacity and plant available water of the soil, with loamy soil able to hold more water than sandy soil during dry periods (Reichardt and Timm 2020). In lowland floodplains, soils are commonly loamy in low-elevated and sandy in high-elevated sites (Schwartz et al. 2003), where plant available water may therefore be additionally reduced during dry periods. HF forests are typically dominated by *Fraxinus*, *Ulmus*, and *Quercus* taxa (European Commission 2013). *Quercus robur* and *Ulmus laevis* are two characteristic tree species for European HF forests which are adapted to cope with flooding and reduced soil oxygen availability through the development of adventitious roots and hypertrophied lenticels (Parelle et al. 2006, Li et al. 2015). Additionally, the capacity to regulate stomatal conductance and long tap roots allow *Q. robur* to survive moderate drought stress. However, *Q. robur* is also prone to hydraulic failure due to vessel cavitation resulting in increased mortality under prolonged drought conditions (Urli et al. 2015). *U. laevis* thrives in damp soils and is highly vulnerable to vessel cavitation and mortality as a result of drought stress (Venturas et al. 2013, Urli et al. 2015). It is not well known how much these adaptations affect the growth of trees in different hydrological conditions, and how this in turn influences C stocks of HF forests on the active floodplain, the seepage water zone and tributaries.

In this study, we aim to answer (a) how C storage of HF forests develops with age, (b) whether sparse forests fulfill the same C storage function as dense forests, (c) how C storage of HF forests differs between typical hydrological conditions and (d) how C storage differs by taxon under different hydrological conditions.

2.3 Materials and Methods

2.3.1 Study area and forest types

The study area is a part of the UNESCO-biosphere reserve Flusslandschaft Elbe and spans approximately 100 km along the lower Middle Elbe River within the German states Saxony-Anhalt, Brandenburg, and Lower Saxony (Figure 2.1). The study area is located within the central European temperate climate region. The Lenzen weather station (53.08°N 11.48°E) records a mean annual precipitation of 615 mm and a mean annual temperature of 9.3°C for 1981-2010 (DWD 2022). Characteristic soils of the Elbe floodplain include Gleysols, Fluvisols, and Cambisols (Schwartz et al. 2003).

The biosphere reserve Flusslandschaft Elbe is used as a model system for anthropogenically altered European floodplains. With a history of diking, deforestation and agriculture on the active floodplain, todays' HF forests represent only small remnants of the former contiguous ecosystem type. On the active floodplain confined by dikes, HF forests are more frequently flooded on the lower sites and less frequently flooded on the higher sites. Flooding events mainly occur on the active floodplain (Leyer 2004) after snow melt during winter and spring and after intense rain events during summer. The duration of flooding is related to elevation on the active floodplain.

Typical species in HF forests, also referred to as mixed riparian forests (NATURA 2000 Code 91F0), include pedunculate oak (Quercus robur), European white, field, and wych elm (Ulmus laevis, Ulmus minor, and Ulmus glabra), European hornbeam (Carpinus betulus), and European ash (Fraxinus excelsior). Typical understory vegetation includes Crataegus monogyna, Sambucus nigra, and Cornus sanguinea.

2.3.2 Study sites and sampling

This study investigates six different forest types (n=5 per type). In total, 30 plots (2,500 m^2 each) were studied. A sketch of the study design is shown in Figure 2.2 and site characteristics for each forest type are presented in Table 2.1.

The effect of forest age and structure on the C storage of HF forests was studied for 15 plots located on the low active floodplain only. Here, five replicate plots of young plantations, old sparse, and old dense HF forests were sampled. The five young plantations are composed of woody species (mainly *Q. robur* and *U. laevis*) which were actively planted on a mix of former grasslands and forests. Dense forests are characterized as multilayered forests with a well-developed overstory and shrub layer, while sparse forests lack the well-developed shrub layer. The age of the young plantations ranged from 18-27 years while the old forests ranged from 80-200 years.

HF forests are found behind the dikes in the seepage water zone of the fossil floodplain and at floodplains of the tributaries. In this study, the possible effects of hydrological conditions on C storage of old dense HF forests were analyzed by sampling five replicate plots of these four forest types (low active floodplain, high active floodplain, seepage water zone, tributary; Figure 2). Hydrological conditions for high and low plots on the active floodplain were selected based on the average number of days the sites were flooded per year: a categorical mean of 0-5 days of flooding for high plots and greater than five days of flooding for the low plots. Flooding duration was estimated using a 35 year mean from 1990-2016 with a 1-dimensional model that integrates data from various databases (Weber in prep).

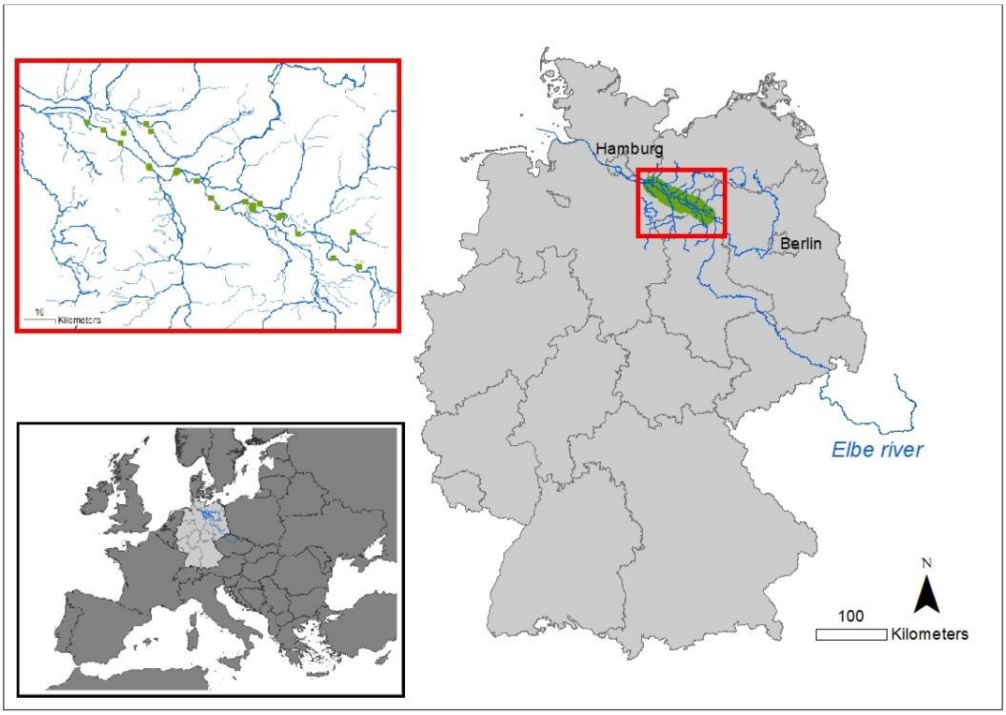

Figure 2.1 Map of the study area along the Middle Elbe River, Germany. The red box outlines the area which spans approximately 100 km along the Elbe River and the green dots represent the locations of each 2500 km^2 plot in the different studied forest types.

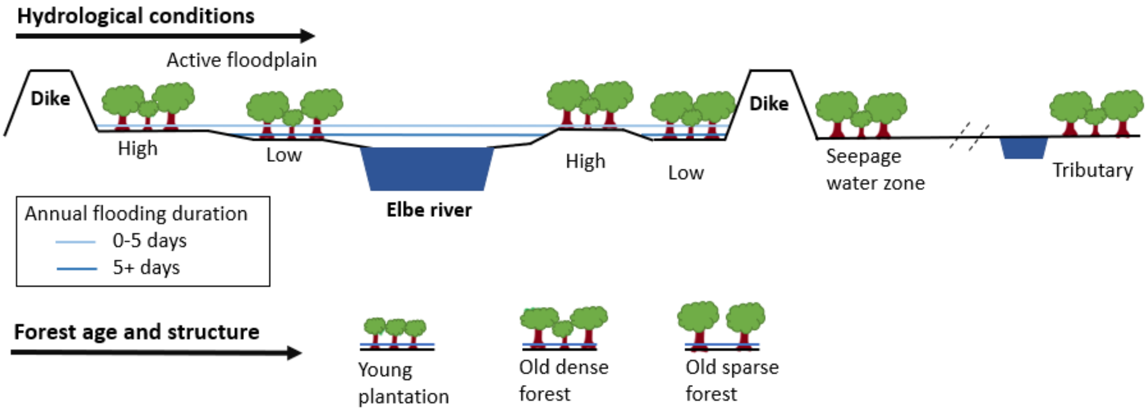

Figure 2.2 Study design showing old dense HF forests with different hydrological conditions (high active floodplain, low active floodplain, seepage water zone, and tributary) and HF forests with different ages and structure (young plantation, old sparse, and old dense) on the low active floodplain. Softwood floodplain forests and other land cover and ecosystem types are not represented in this sketch.

Table 2.3 Characteristics of each studied forest type showing minimum (min), maximum (max), and mean values with standard deviation (SD). Each forest type has a sample size of five replicate plots. DBH= diameter at breast height. x indicates a lack of data related to the spatial limitations of the flooding duration model.

	Low active floodplain, young		**Low active floodplain, old dense**		**Low active floodplain, old sparse**		**High active floodplain**		**Seepage water zone**		**Tributary**	
	Min Max	**Mean ±SD**	**Min Max**	**Mean ±SD**	**Min Max**	**Mean ±SD**	**Min Max**	**Mean ±SD**	**Min Max**	**Mean ±SD**	**Min Max**	**Mean ±SD**
Forest age (years)	18 27	23 ±4	104 200	141 ±36	129 167	144 ±14	108 186	134 ±33	81 185	128 ±39	82 170	130 ±37
Basal area (m^2 ha^{-1})	12 30	22 ±7	26 36	32 ±4	29 52	38 ±10	27 45	36 ±8	29 43	35 ±6	27 44	36 ±7
Tree count (trees ha^{-1})	728 1576	1245 ±346	181 496	291 ±121	75 160	123 ±40	192 325	248 ±55	235 464	357 ±100	331 763	531 ±186
Mean tree height (m)	8 14	11 ±3	11 20	15 ±3	13 26	22 ± 5	13 21	16 ±4	12 26	18 ±6	14 20	17 ±3
Mean tree DBH (cm)	11 16	14 ±2	20 39	32 ±7	43 85	60 ±16	29 39	36 ±5	20 45	31 ±11	20 30	25 ±4
Tree species richness	1 5	3 ±2	2 3	2 ±1	1 3	2 ±1	2 5	3 ±1	3 8	5 ±2	3 10	5 ±3
Flooding duration (days $year^{-1}$)	6 86	34 ±28	11 59	36 ±18	9 33	22 ±9	0 9	4 ±3	x	x	x	x

2.3.3 Carbon stock estimations

Individual C stocks of trees, shrubs, deadwood, and leaf litter were analyzed in the winter months between January and April of 2018 and 2019. The total C stocks per plot were estimated by averaging the summed values for large trees, shrubs, standing dead trees, downed woody debris, and leaf litter. These values were then scaled to Mg ha^{-1}.

2.3.3.1 Trees

For quantifying C stocks of trees, four 625 m^2 square nested plots (quadrants) were delineated within each of the 30 plots. Within three quadrants for old forests and two quadrants for young plantations, the diameter at breast height (DBH; 1.3 m above ground level) of all trees ≥ 5 cm were measured using a standard diameter tape. Within the same quadrants, the height (H) of all trees with a DBH ≥ 5 cm were measured with a Vertex Laser Geo (Haglöf, Sweden). The species identity of each measured tree was recorded.

Based on the measured variables H and DBH, individual tree stem volumes were calculated with species-specific allometric equations (Table A1) (Zianis et al. 2005a). Aboveground tree biomass was calculated by multiplying estimated tree stem volume by species-specific average wood density (Table A2) taken from the Global Wood Density Database (Zanne et al. 2009b). Finally, a C content (CC) fraction of 0.47 was applied to estimate aboveground tree C stock (UNFCCC 2015b). To estimate the C stocks of tree roots, a root: shoot ratio of 0.3 was applied to the aboveground tree C stock (Mokany et al. 2006).

2.3.3.2 Shrubs

All shrubs with a DBH ≥ 5 cm were inventoried using the line intersect transect method. Each quadrant chosen for the tree inventory was transected diagonally, and the DBH and H of any shrub crossing 1 m from each side of the transect was measured. The allometric volume equation, biomass factor and C factor for *Corylus* (Table A1) was used for all shrubs and the values were scaled to Mg ha^{-1}. The roots of the shrubs were estimated using a root: shoot factor of 0.4 (UNFCCC 2015b).

2.3.3.3 Deadwood

The C stock of deadwood was measured following the methodologies and density reduction factors proposed by the United Nations to measure C stocks (UNFCCC 2015b). Two deadwood pools were measured: large standing dead trees (SDT) and downed woody debris (DWD).

To measure SDT's, the same allometric equations were used as for the estimates of C stocks of large trees, which were then multiplied by density reduction factors depending on the state of decay (sound= 1; intermediate = 0.8; rotten = 0.45). Unlike in the United Nations guidelines (UNFCCC 2015b), if a tree was leaning or newly fallen and lay completely within the study plot, it was included in the SDT pool. The roots of SDTs were measured the same as the live trees, with a root: shoot ratio of 0.3.

Lying downed woody debris (DWD) was measured using transect lines diagonally crossing three quadrants for every plot (with a total length of 106 m per plot). All deadwood with a diameter ≥ 5 cm crossing the transect lines were measured horizontally and vertically at the point of intersect and the state of decay was recorded. Trees already accounted for in the SDT pool were omitted. Equation 2.1 was used to estimate the volume of DWD (Böhl and Brändli 2007). DWD volume estimates were then multiplied by 0.5 to obtain DWD biomass, density reduction factors depending on the state of decay, and finally by 0.5 to estimate C content.

$$\hat{X}_j = \frac{\pi^2}{8L_j} \sum_{i=1}^{N} \left(\frac{d_{1i} + d_{2i}}{2} \right)^2 \tag{1}$$

Equation 2.1 measures the volume of DWD ($\hat{X}$) in m^3 ha^{-1} for the individual sample plots (j). L_j is the horizontal length of the transect lines, while d_{1i} and d_{2i} are the horizontal and vertical diameter measurements (in cm) of individual pieces of dead wood intersected along the transect.

2.3.3.4 Leaf litter

The winter stock of leaf litter was estimated from February to March in 2019. The leaf litter was measured in winter, because the plots are mainly dominated by oak trees, which do not abscise their leaves until late winter to early spring. Within each of the three studied quadrants, a 1 m^2 quadrat frame was randomly placed along the diagonal transect and the dry weight of leaf litter was measured. Subsamples of fresh leaf litter were brought to the lab and air dried until constant weight. The dry: wet weight ratio was applied to the field values, and the average quadrant values were taken as plot values. The biomass values were multiplied by 0.37 to estimate C stock (UNFCCC 2015b).

2.3.4 Forest ages

Forest ages were estimated using annual tree ring measurements (Keeton et al. 2007). Tree cores were taken from four dominant *Q. robur* trees per plot using a 5 mm Mora increment borer. Singular relic trees with an outlying DBH from the other dominant trees from the same plot were not sampled. The surface of each core was carefully scraped with a razor blade to increase the visibility of the tree ring vessel structure. A microscope connected to a LINTAB^{TM} 5 measuring table (RinnTech) and the TSAP-Win^{TM} software program were used to measure tree rings and establish tree ages. When the pith was not present, concentric circles were used to estimate missing rings (Applequist 1958).

2.3.5 Statistical analyses

The C stock data were tested for normality by Shapiro-Wilk test ($p > 0.05$) and a visual inspection of Q-Q plots, box plots, and histograms. Nonparametric independent-samples Kruskall Wallis Tests with pairwise comparisons were conducted to examine the differences in C stock for each C pool according to forest age and structure and for the forests with different hydrological conditions. Different curve estimation models with forest type as the independent variable and total C stocks as the dependent variable were assessed for best fit.

Additionally, a univariate general linear model (GLM) was used to compare C stocks of old, dense forests with different hydrological conditions. The dependent variable was C stocks while the covariate was estimated forest age. Regression curve estimation models were explored to evaluate the best fit relationship between forest age and C stock. All tests were performed using SPSS version 26 (IBM, 2019).

2.4 Results

2.4.1 Carbon stocks related to forest age and structure

On the low active floodplain, the total C stock of young plantations was 50.2 ± 10.8 SE Mg ha^{-1} and thus significantly lower ($H = 10.5$, $p = .005$, $df = 2$) than that of old sparse (180.4 ± 26.6 SE Mg ha^{-1}) and of old dense forests (140.6 ± 11.6 SE Mg ha^{-1}). Pairwise comparisons found no significant difference between old sparse and old dense forests. Young plantations had significantly less C stock in the tree pool than old dense or sparse forests ($H = 10.5$, $p = .005$, $df = 2$). Young plantations also had significantly less DWD than old dense forests ($H = 7.4$, $p = .009$, $df = 1$). No other significant differences comparing C pools between different forest types on the low active floodplain were found. Overall, the most C was stored in the tree C pool than in any other pool (Figure 2.3, Table A3), and the SE of the tree pool was commonly larger than the stock estimated for other C pools. A positive logarithmic relationship ($r^2 = 0.741$, $P < 0.001$) was found between forest age and C stock (Figure 2.4).

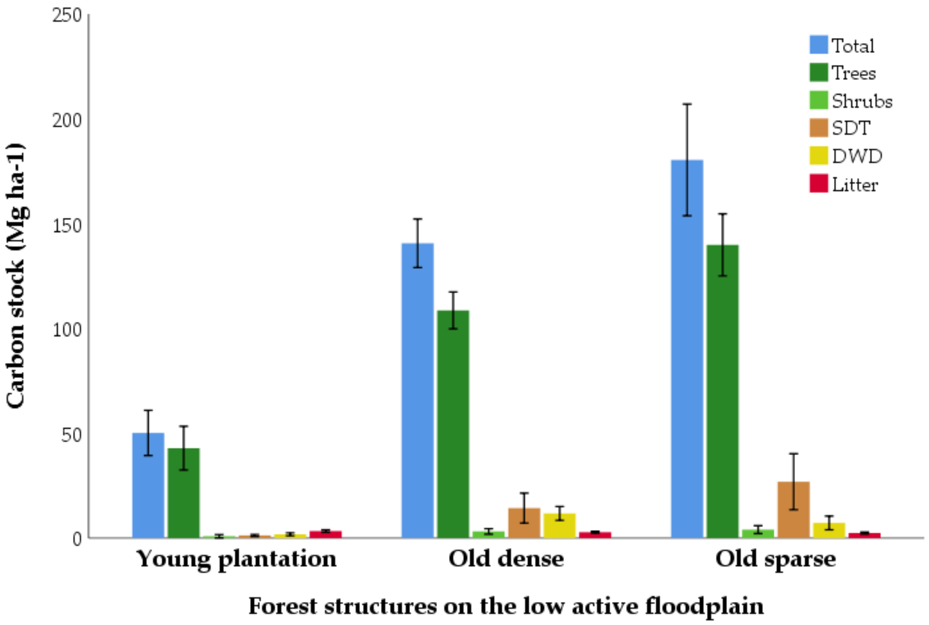

Figure 2.3 Carbon stocks in Mg ha^{-1} of hardwood forests with different ages and structures on the low active floodplain (mean ±SE, *n*=5). Carbon pools include trees, shrubs, standing dead trees (SDT), downed woody debris (DWD), and leaf litter.

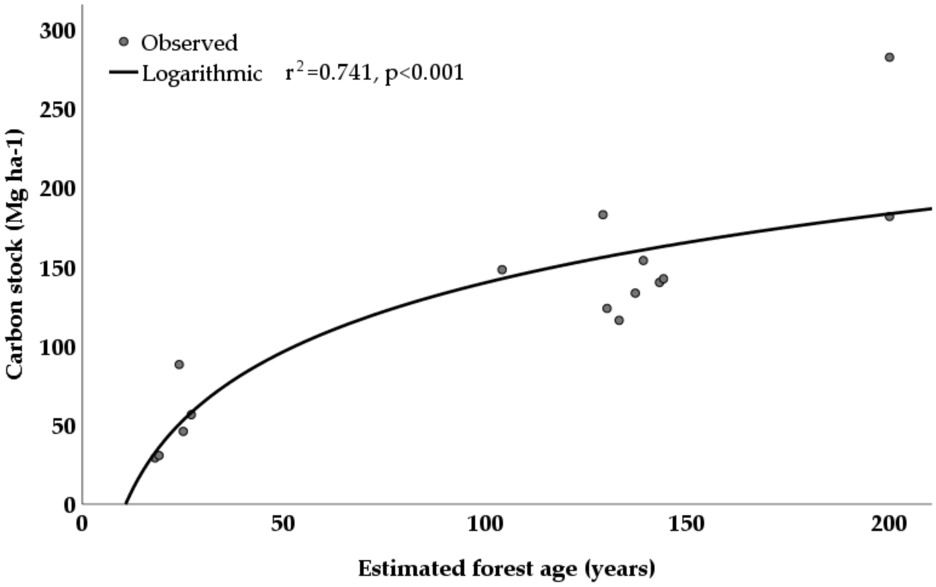

Figure 2.4 Carbon stocks in Mg ha^{-1} of young plantations, old dense, and old sparse hardwood forests on the low active floodplain are plotted against estimated forest age in years. A logarithmic fit curve with the output of the regression is included. Carbon stocks include trees, shrubs, standing dead trees (SDT), downed woody debris (DWD), and leaf litter.

2.4.2 Carbon stocks of old HF forests under different hydrological conditions

C stocks of old dense forests under different hydrological conditions ranged from 140.5 ± 11.6 (low active floodplain) to 163.5 ± 8.3 SE Mg ha^{-1} (high active floodplain) (Figure 2.5, Table A4). Kruskall wallis tests revealed that there were no significant differences between the total C stock or any other C pool of old dense forests with different hydrological conditions. The GLM revealed that the covariate, forest age, was not significantly related to C stock, $F_{1,15} = 0.72$, $p > 0.05$, $r = 0.41$. There was also no significant effect of hydrological conditions on C stocks after controlling for forest age, $F_{3, 26} = 0.54$, $p > 0.05$, partial $\eta^2 = 0.10$.

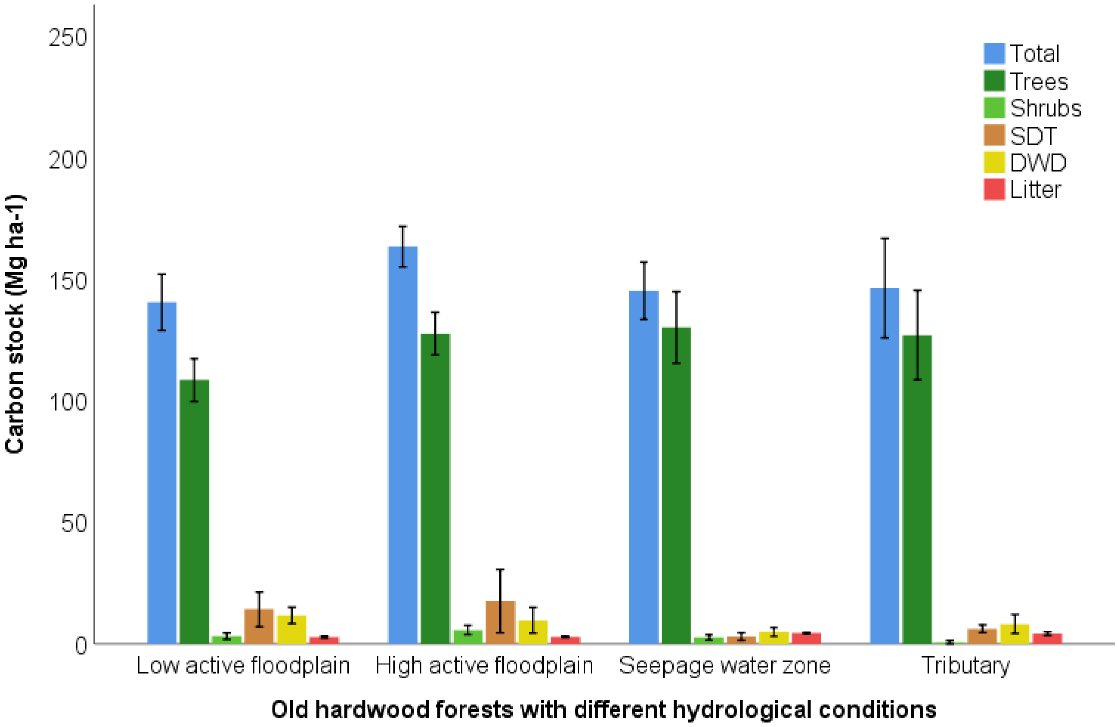

Figure 2.5. Carbon stocks in Mg ha^{-1} of dense hardwood forests with different hydrological conditions (mean ± SE, *n*=5). Carbon pools include trees, shrubs, standing dead trees (SDT), downed woody debris (DWD), and leaf litter.

2.4.3 Carbon stocks by species

Q. robur stored more C than any other species in all hydrological conditions (Figure 2.6). On the active floodplain, *Ulmus* spp. stored the second highest amount of C, whereas in the seepage water zone and on tributary floodplains, *Ulmus* spp. were rare and *C. betulus* stored the second highest amount of C.

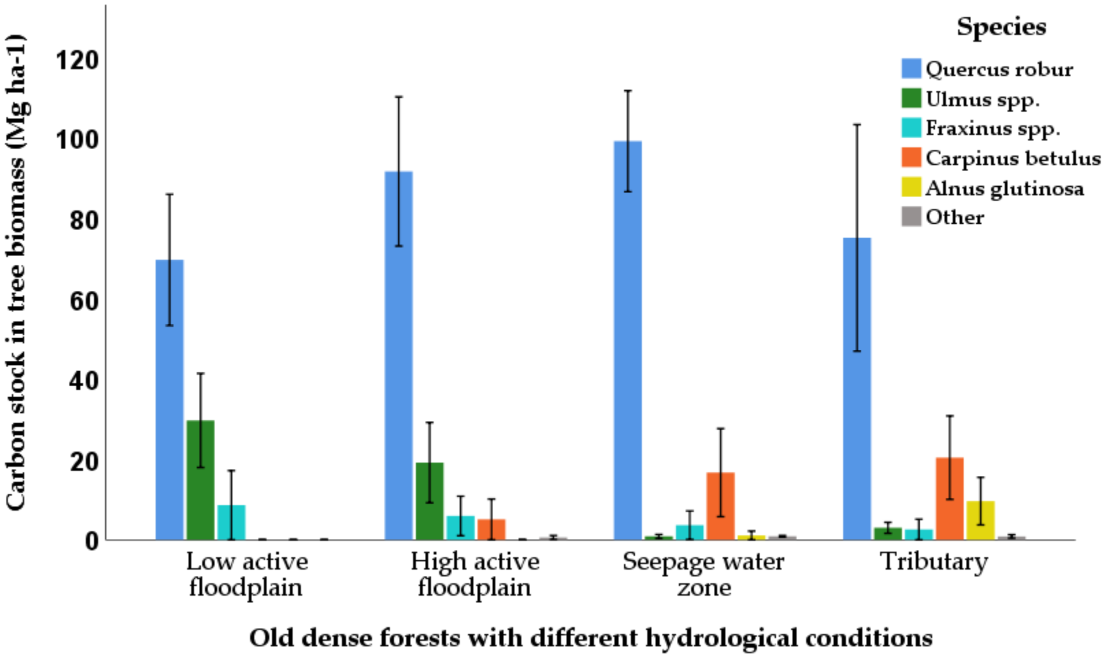

Figure 2.6 Carbon stock of large trees in Mg ha-1 including above- and below-ground biomass by tree species (mean ± SE, n=5). Other tree taxa include *Acer*, *Corylus*, *Fagus*, *Picea*, *Pinus*, *Populus*, *Prunus*, *Salix*, *Sorbus*, and *Tilia* spp.

2.5 Discussion

C stocks positively developed with age, with young plantations storing less C than old forests. This finding supports research in the floodplains of the Danube, where young reforestations also showed significantly lower C stocks than mature HF forests (Cierjacks et al. 2010). Many years are required for young plantations to mature and provide the same ecosystem function as old forests, but from the projected path of the logarithmic age curve, the increase in C stock is greatest in the first fifty years, before the stock slowly begins to taper as the forest matures. This implies that the annual rate at which the young plantations store C, or the C sequestration rate, is larger than that of old forests. The age curve had one major outlier, where the total estimated C stock was 282.4 Mg ha^{-1}. This outlier forest was characterized as sparse, had the highest live tree stock (193.7 Mg ha^{-1}), and had the highest proportion of *U. laevis* trees with large dimensions compared to other studied plots. This forest also had a significantly higher deadwood stock (80.7 Mg ha^{-1}) than any other plot, with large fallen trees and SDTs left to naturally decompose. In most of the other old forest plots, deadwood may have been removed either by management or flooding disturbance. This rare outlier of a forest with ample deadwood suggests that the removal of deadwood decreases the C storage function of HF forests. However, because this is one outlier, more studies should be conducted specifically looking at the potential reduction in C stocks as a consequence of deadwood removal on the floodplains.

On the low active floodplain, sparse forests stored equally as much C as dense forests. While some studies find that thinning of floodplain forests can increase C stocks (Horner et al. 2010), this study suggests that the overall C stock of naturally dense forests are equal to sparse forests. If the only purpose of reforestation is to maximize C storage, then either forest structure would be an appropriate land management target. However, suitable land management decisions rely on the assessment of multiple ecosystem services (Bennett et al. 2009) and must consider potential risks and the preference of local stakeholders. For example, how the different structures contribute to or alleviate flooding should also be quantified and used in the assessment to determine proper floodplain management. The potentially higher roughness of dense forests may increase or decrease flood protection, depending on the location along the river. While flood risk can be reduced downstream from a forest with high roughness through the reduction of flow velocity and peak magnitude at the catchment outflow [11-13], the flood risk upstream from the forest could be increased by the backwater effect (Leyer et al. 2012). Suitable locations for reforestation of either dense or sparse forests is therefore also dependent on the surrounding land use, and considerations should be made to maximize the benefits of reforestation while minimizing potential risks.

The total C stocks and all C pools of old dense HF forests with different hydrological conditions did not significantly differ between each other, which indicates that the C storage function of the HF forests is equal. This finding supports the results of *Rieger et al. (Rieger et al. 2013)*, who observed no significant difference between C stocks of HF forests on the active floodplain and HF forests behind dikes in the seepage water zone. Trees contributed the greatest to the total C stock, and the equal C stocks implies that the trees are well adapted to the different hydrological conditions. Although the dike severs the connection between the forests on the seepage water zone from the flood pulse and the nutrients that come with it (Junk et al. 1989), the trees still grow at a seemingly equal rate. To verify this, quantification of tree growth at an annual scale is needed. Additional research is also needed to assess the effects of climate change on tree vitality and productivity on different elevations of the active floodplain, the seepage water zone, and tributaries. Climate change models project increased temperatures, precipitation, and river discharge at the Elbe (Huang et al. 2015, Hesse and Krysanova 2016), with increasing drought conditions in spring and summer and increased precipitation in autumn and winter (Barkmann et al. 2017). There is some evidence that increased flood frequency may reduce drought effects on the active floodplain (Heklau et al. 2019), but these benefits may not be as pronounced in the seepage water zone behind dikes. If the flooding events occur in winter, drought conditions under high spring and summer temperatures may lead to tree mortality, which will greatly alter the distribution of C within pools, from C-fixing live trees to C-releasing dead trees. The finding that the C storage function of old hardwood forests is nearly equal on the low and high active floodplain, the seepage water zone, and tributaries reveals that all of these sites are potentially suitable for reforestation considering the past climatic conditions, but this may not be the case considering future climate change. Additionally, the other ecosystem services must now be quantified for these forests and stakeholder preferences taken into consideration to determine suitable land management decisions.

Our C stock estimates of 50.2 ± 10.8 SE Mg ha^{-1} for young plantations, 140.6 ± 11.6 SE Mg ha^{-1} for old dense forests, and 180.4 ± 26.6 SE Mg ha^{-1} for old sparse forests are within the 7.5-281 Mg ha^{-1} range of previously reviewed HF forests (Sutfin et al. 2016) and are similar to upland forests in Germany. Generally, the C storage in German forests is reported to be 120–190 Mg ha^{-1}, depending on age class and tree species (Dieter and Elsasser 2002). *Quercus petraea* forests in Northern Germany have an estimated C stock of 107.82 ± 7.27 Mg ha^{-1} in aboveground live tree biomass and 9.35 ± 6.51 Mg ha^{-1} in deadwood (Förster et al. 2021). We estimated a C stock in aboveground tree biomass of 33 ± 17.9 SE Mg ha^{-1} for young plantations, 83.6 ± 15.1 SE Mg ha^{-1} for old dense forests, and 107.6 ± 25.5 SE Mg ha^{-1} for old sparse forests. Our C stock estimate for aboveground trees not including roots in old sparse forests is therefore almost identical to the estimate for naturally developed upland forests dominated by *Q. petraea.* Our deadwood estimates for old sparse forests, however, are much higher (26 ± 13.3 Mg ha^{-1} for SDTs with an additional 7.2 ± 3.3 Mg ha^{-1} for DWD). In another study of different forest types in Germany, the average C stocks in aboveground and belowground biomass, deadwood and soils are reported to be 224 Mg ha^{-1} (Wellbrock et al. 2017) It is reported that 46% of C is stored in the aboveground and belowground biomass and 1% of C is stored in deadwood, which would mean a C stock of 105 Mg ha^{-1} in trees and deadwood. This estimate is one third less than in our studied HF forests. The tree pool C stocks calculated in our study are lower than the estimated 281 ± 59 Mg ha^{-1} for HF forests by the Danube River (Cierjacks et al. 2010). The large difference between C stocks estimated along the Danube and those estimated here may be attributed to abiotic and climatic differences, management, forest structures such as number of tree stems, or methodological differences in estimating C stocks. The HF forests along the Danube had a mean tree count of 590 ± 80, while the old forests studied here had a mean tree count ranging from 123 ± 40 to 531 ± 186. However, tree count is not a good indicator to determine C stocks, as shown by young plantations which have a much larger tree count than old forests, but a lower overall C stock. Additionally, a major setback in making accurate comparisons between studies reporting on C stocks of forests is the absence of a universally applied field inventory and C calculation method. There are proposed guidelines, such as the UNFCCC methods (UNFCCC 2015b), however, there are various national inventories (Gschwantner et al. 2016) as well as research papers (Giese et al. 2000, Dieter and Elsasser 2002, Cierjacks et al. 2010, Schöngart et al. 2011, Wellbrock et al. 2017, Förster et al. 2021), which use different field measurements and computational methods to estimate C stocks. Various allometric equations are available, and the choice of the equations can greatly impact the estimated C stock values. Also, many old trees such as oaks and elms become hollow as they mature, and the allometric equations do not take into account this reduction in biomass (Keeton et al. 2011), which may result in an over-estimation of C stock. Although allometric equations provide a non-destructive way of measuring C stocks, there can be large variations depending on the selected equations, which adds great uncertainties to the estimated C distribution in different forest ecosystems worldwide (van Breugel et al. 2011).

Q. robur had a dominating presence in all hydrological conditions compared to other taxa, which may be a consequence of the species' drought and flood tolerance (Parelle et al. 2006) or the fact that forest managers in the past mainly preferred to plant and foster oaks for quality timber harvesting and to provide animal fodder and tanning agents (Glaeser and Schmidt 2006). Today, planting campaigns that include a diversity of species are recommended to increase resilience against biotic stressors and variability in abiotic conditions (Larsen 1995), as well as to enhance productivity and C storage (Pretzsch et al. 2013, Ma et al. 2020). Monoculture planting campaigns should be avoided to minimize pathogens and insect attacks (Guyot et al. 2019). This is especially true in the Middle Elbe region, where outbreaks of oak processionary moth (*Thaumetopoea processionea*) are especially prevalent in plantations with high oak densities. Therefore, although *Q. robur* is a suitable tree species for reforestation under all hydrological conditions, other species should be interspersed. Many elms (mainly *U. laevis*) were found on the active floodplain, while very few elms were growing in the seepage water zone or along the tributaries. Although the results may be interpreted in a way that the hydrological conditions of the seepage water zone are not suitable for elms, the lack of elms behind the dike could also be a consequence of management and the preference of foresters to foster oaks. Compared to oaks and elms, very few ash trees (*F. excelsior*) were observed, except for one plot that had mostly non-native green ash (*F. pennsylvanica*). Although ash dieback caused by the fungus *Hymenoscyphus fraxineus* could be a reason for the low *F. excelsior* numbers (Erfmeier et al. 2019), ash is well adapted to thrive on floodplains but not able to resist this fungal infestation at present, and therefore reforestation of ash may not be suitable. *C. betulus* was numerous in the seepage water zone and tributaries, while the species' presence on the active floodplain was only apparent on the high elevated sites with lower annual flooding duration. This is most likely a consequence of the lower flood tolerance of *C. betulus*, which is not listed as typical species in the NATURA 2000 classification for riparian mixed forests. The exchange of *C. betulus* for *U. laevis* as the second most dominating species in the HF forests on the seepage water zone and tributaries may therefore be a consequence of the different hydrological conditions.

2.6 Conclusions

C stocks developed positively with age and the C storage function of old forests did not significantly vary with forest structure on the low active floodplain or according to different hydrological conditions. Old forests on the low active floodplain, the high active floodplain, the seepage water zone, and tributaries fulfill the same ecosystem function of C storage and the locations are therefore at first glance equally suitable for reforestation campaigns. However, C storage is only one ecosystem service among many that should be quantified and evaluated to provide decisive and suitable land management advice. Additionally, the influence of climate change should also be considered. *Q. robur* is a good candidate for reforestations at all hydrological situations and should be accompanied by other suitable species such as *U. laevis* in all hydrological conditions and *C. betulus* in less frequently flooded conditions. *F. excelsior* is at present not a good candidate for reforestation because of the high risk of dieback.

2.7 Acknowledgments

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3

Chapter 3: Adapting a *Quercus robur* allometric equation to quantify carbon sequestration rates on the Middle Elbe floodplain

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3.1 Abstract

Destructively sampling old Pedunculate oak (*Quercus robur*) trees on the active floodplain of the Middle Elbe to create an allometric equation to estimate carbon stocks (CS) and carbon sequestration rates (CSR) would defeat the purpose of protecting increasingly vulnerable and threatened primeval floodplain forests. To nondestructively estimate CS and CSR, we have adapted a two-parameter allometric equation which uses tree height (H) and diameter at breast height (DBH) (Zianis et al. 2005b) into a 1-parameter equation that requires only DBH to quantify stocks and annual changes in carbon stock (carbon sequestration rates) for individual *Q. robur* trees. The equations have also been adapted to estimate below- and above-ground carbon stocks of individual trees.

The new method has (a) adapted a 2-parameter *Quercus robur* allometric equation which estimates tree volume to a 1-parameter equation which estimates above and below-ground carbon stock, (b) removed the requirement of tree height to reconstruct the carbon stock of trees at an annual timestep and (c) an almost perfect linear relationship (Pearson R^2= 0.998) between carbon sequestration rate and basal area increment (BAI).

3.2 Introduction

Destructively sampling old Pedunculate oak (*Quercus robur*) trees on the active floodplain of the Middle Elbe to create an allometric equation for estimating carbon stocks (CS) and carbon sequestration rates (CSR) is not feasible, because it would require cutting old trees in protected and threatened primeval floodplain forests. To non-destructively estimate CS and CSR, we have adapted a two-parameter allometric equation which uses tree height (H) and diameter at breast height (DBH) (Dik 1984, Zianis et al. 2005b) into a 1-parameter equation that requires only DBH to quantify CS and CSR for individual oak trees (Table 3.1). The original allometric equation by Dik estimates the aboveground volume of tree trunk and bark for *Quercus robur* (Dik 1984). This equation was published in the compilation of allometric equations by Zianis as equation #207 in Appendix C (Zianis et al. 2005b). In this study, we adapt this equation to estimate below- and above-ground carbon stocks of individual trees in Mg tree^{-1}.

Diameter at breast height (DBH) is perceived as the most precise independent variable to estimate tree biomass with allometric equations (Yuste et al. 2005, Cienciala et al. 2008). Past research has estimated CS of trees using allometric equations which require only DBH changes (Köhl et al. 2017). Carbon sequestration rates (CSR) have also been measured using tree cores, allometric equations with DBH, and DBH reconstructions (Rieger et al. 2017). The removal of height from an allometric model to estimate CS and CSR from DBH is therefore feasible.

3.3 Methods

3.3.1 Estimating carbon stock of trees in 2018

We estimated the aboveground volume of 966 *Quercus robur* trees of several community classes using the Dik equation's two input parameters DBH and tree height (Table 3.1). Tree DBH and height were measured in the Middle Elbe study region in winter of 2018/2019 (Shupe et al. 2021). We converted the volume estimates to above- and below-ground CS estimates with three conversion factors (parameters d, e, and f in Table 3.1). For the first conversion factor, we multiplied the volume by a species-specific wood density of 0.56 (Zanne et al. 2009a) to estimate biomass. Secondly, we multiplied the biomass by 0.5 to estimate carbon content (Husmann et al. 2018). Finally, we estimated the total biomass (above- and below-ground biomass) by using a root:shoot ratio of 0.3 (Mokany et al. 2006) and therefore multiplied the above-ground biomass estimate by 1.3.

3.3.2 Creating a one-parameter quadratic equation to estimate carbon stock of *Quercus robur* trees

After applying the modified Dik equation to the individual trees to estimate CS (Shupe 2021 equation in Table 3.1), we plotted CS with DBH (see Figure 3.1) and applied different lines of best fit. The one-parameter quadratic equation to estimate CS with DBH showed a good Pearson R2 of 0.972 and was therefore deemed suitable to reconstruct tree CS at an annual scale without the need to reconstruct tree height back in time.

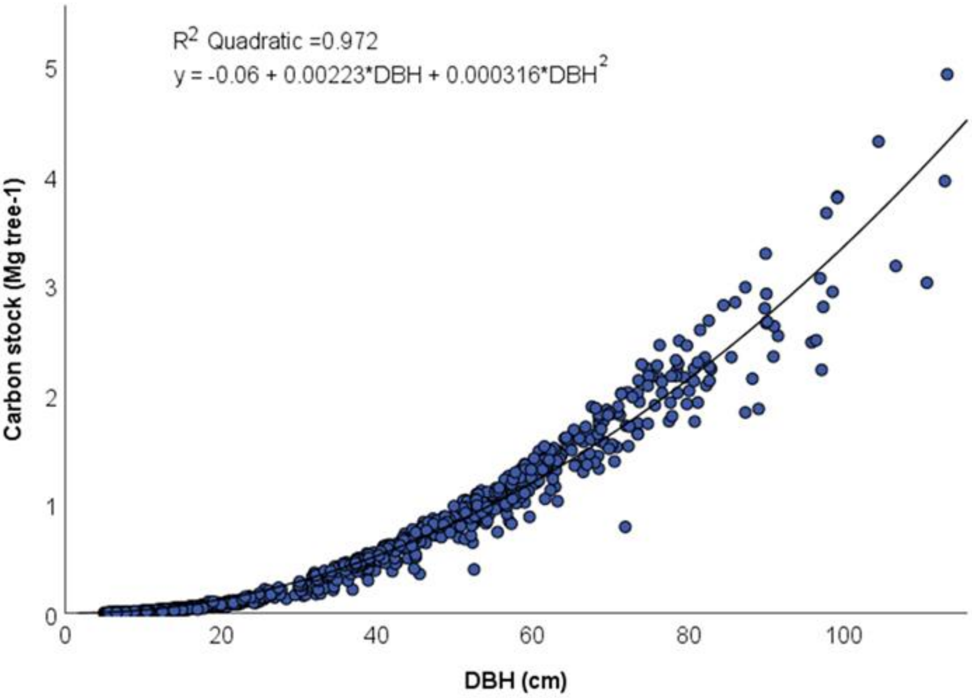

Figure 3.1 Carbon stocks of individual oak trees (*Quercus robur*) are plotted using the allometric equation from Dik 1984 and Ziannis 2005. A quadratic fit ($R^2 = 0.972$) and the developed allometric equation are shown.

3.3.3 Carbon sequestration rate equation

For the purpose of this study, we assume that the carbon sequestration rate (CSR) of an individual tree is the change in CS from one year to the next. Therefore, when we can estimate the change in the DBH from year to year using tree ring increment core widths, we can recreate the CS of the tree at an annual time step using the developed CS equation, and the change in the CS from year (t) to year (t1) is then the CSR (see Table 3.1). The DBH of each tree was reconstructed in an annual step-wise fashion using the measured TRW from increment cores and the conventional DBH reconstruction method (Bakker 2005, Bakker et al. 2008). This method entailed measuring the DBH of each tree at year 2018, subtracting twice the bark width, and incrementally subtracting twice the measured TRW for each year back in time.

Table 3.1 Equations to estimate volume, carbon stocks (CS), and carbon sequestration rates (CSR) of individual *Quercus robur* trees. Diameter at breast height (DBH) is required for all equations and tree height (H) is required only for the Dik (1984) volume and Shupe 2021 CS equation. The Shupe 2021 CS equation estimates below- and above-ground CS by applying three conversion factors to the Dik volume equation. Parameter d is an expansion factor to compute biomass from volume using a species-specific wood density fraction from the Global wood density database (Zanne et al. 2009a). Parameter e is the carbon content (Husmann et al. 2018). Parameter f is the below-ground carbon estimation (Mokany et al. 2006). Shupe 2022 CS and CSR parameters a, b, and c are computed using a quadratic fit equation applied to the Shupe 2021 CS estimates of 966 *Q. robur* trees measured in 2018 in the floodplain forests of the Middle Elbe. DBH_t is the DBH of the tree at the year being analyzed and DBH_{t1} is the DBH of the tree the previous year. Tree ring widths (TRW) of the increment cores are measured at an annual time step and converted into cm.

Source	Output	Units		Equation	Parameters					
		DBH	H		a	b	c	d	e	f
Dik 1984 Zianis 2005	Volume (dm^3)	cm	m	$DBH^a \cdot H^b \cdot \exp(c)$	2.00333	0.85925	-2.86353			
Shupe 2021	CS (Mg $tree^{-1}$)	cm	m	$(DBH^a \cdot H^b \cdot \exp(c))*d*e*f$	2.00333	0.85925	-2.86353	0.56	0.5	1.3
Shupe 2022	CS (Mg $tree^{-1}$)	cm		$a+b*DBH+c*DBH^2$	-0.06	0.00223	0.000316			
Shupe 2022	CSR (Mg tree-1 year-1)	cm		$a+b*DBH_t+c*DBH_t^2$ - $a+b*DBH_{t1}+c*DBH_{t1}^2$	-0.06	0.00223	0.000316			

3.4 Method validation

Using the dataset of 966 *Q. robur* trees to compare the CS estimate with both DBH and H parameters (Shupe 2021) to the CS estimate with only the DBH parameter, we calculated the root mean square error (RMSE) for all trees and for trees in different DBH size classes. Overall, the RMSE was equal to 1. The greater the DBH, the greater we observed the RMSE to be. Trees with a 5cm ≤ DBH < 35cm had a RMSE of 0.12, trees with a 35cm ≤ DBH < 70cm had a RMSE of 0.97, and trees with a 70cm ≤ DBH < 140 cm had a RMSE of 2.6. Therefore, as DBH increases, the variability between the observed and predicted CS values also increases. Overall, the two models were highly correlated ($R^2 = 0.972$).

No destructive sampling of trees was conducted in the protected UNESCO Biosphere Reserve River Landscape Elbe study area. We therefore can validate our CS and CSR equation by comparing the output of the equation with basal area increment (BAI), which is commonly used to compare tree productivity.

Basal area increment (BAI, equation 3.1) and aboveground biomass increment (ABI) have been used in previous dendrochronological studies to compare tree productivity, quantify interannual variability, and improve terrestrial carbon accounting (Klesse et al. 2016). Additionally, the change in carbon stock estimated with allometric equations and increment core measurements has been used to reconstruct carbon accumulation in forest stands (Babst et al. 2014). An allometric equation will never be able to perfectly predict the CS and CSR of every tree because site-specific factors such as competition, soil properties, tree age, and hydrological conditions influence the growth of individual trees (Neumann et al. 2016). However, here we find that the linear relationship between BAI and our estimated CSR is nearly perfect, with a Pearson R^2 of 0.998 (Figure 3.2). This method is therefore assumed to be suitable for the purpose of non-destructively estimating the average CSR of *Quercus robur* trees in the Middle Elbe region.

$$BAI = \pi({r_t}^2 - {r_{t-1}}^2)$$

Equation 3.1 measures basal area increment from the radius (r) of the trees measured at breast height (1.3 m above ground).

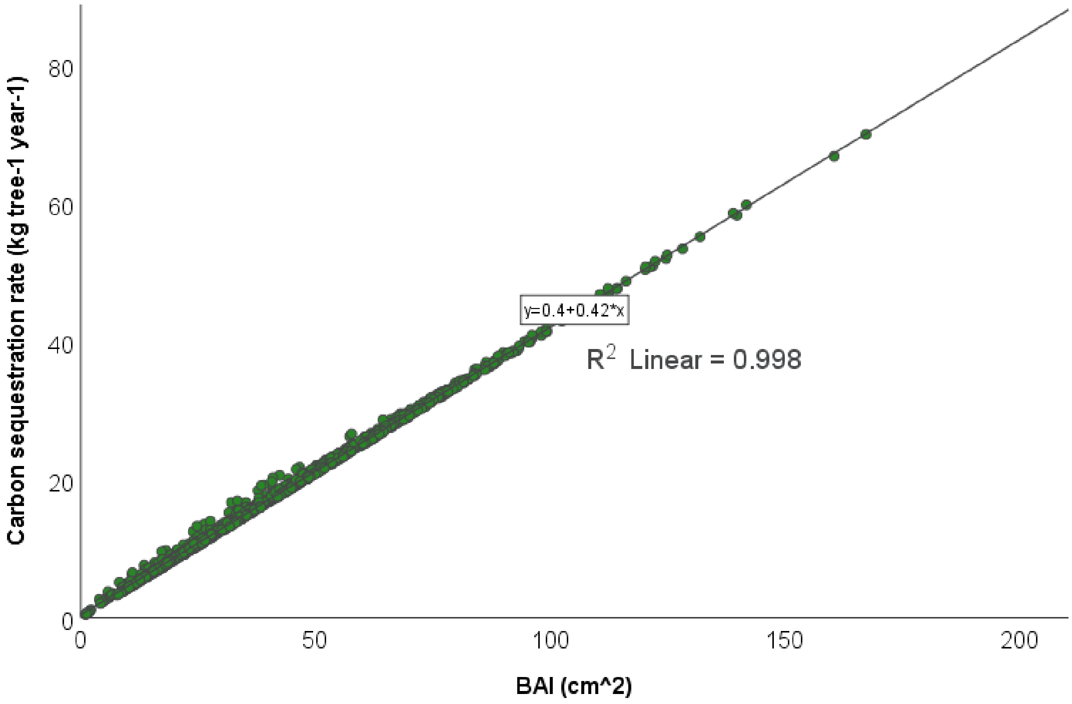

Figure 3.2 Pearson correlation between basal area increment (BAI) and the estimated total (above- plus below-ground) carbon sequestration rate of *Quercus robur* trees in the Middle Elbe area.

The original Dik equation was constructed for *Q. robur* trees in the Netherlands, and we expect that the adapted *Q. robur* equations used here could also be applied to estimate CS and CSR of *Q. robur* in other forests in Northern Europe. However, we do not expect that these equations would be suitable for other tree species, and we would recommend different species-specific equations provided in the literature (Zianis et al. 2005b). There are always going to be differences in forest site factors such as edaphic conditions, hydrological conditions, microclimates, stand management, and stand structure. Climate change can also alter site conditions (IPCC 2021). Although these factors can influence the allometry of individual trees, it is not feasible to create different equations for trees in each of these conditions because it would require destructive sampling of a large number of trees in each condition. In this case, the protected nature of the trees we study prevented this destructive sampling, and we assume that the estimation for the average *Q. robur* tree is suitable for minimizing overall error at the stand or regional level.

3.5 Acknowledgements

This research was conducted within the interdisciplinary project MediAN (Mechanismen der Ökosystemdienstleistungen von Hartholz-Auenwäldern: Wissenschaftliche Analyse sowie Optimierung durch Naturschutzmanagement). This research was funded by the Bundesministerium für Bildung und Forschung (BMBF 01LC1601A). We would like to thank the landowners who participated in this study and the Biosphere reserve Niedersächsische Elbtalaue and Brandenburg Flusslandschaft Elbe with special thanks to Hans-Jürgen Kelm and Torsten Hennig. Additionally, thank you to all MediAN colleagues.

4.

Chapter 4: Droughts decrease and floods increase carbon sequestration rates of *Quercus robur* in hardwood floodplain forests

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4.1 Abstract

Trees can contribute to the reduction of atmospheric CO_2 concentrations, but they do so at varying rates. The carbon sequestration rate (CSR) of trees is influenced by many factors including tree age, forest density, site conditions, and extreme events such as droughts and floods. This research reconstructs past carbon stocks of Pedunculate oak (*Quercus robur*) trees in floodplains with different hydrological conditions (low and high active floodplain, the seepage water zone of the former floodplain, and the tributary floodplain). We used increment tree cores and allometric equations and compared the annual changes in stocks as a way of assessing CSR. Furthermore, we used time series data on floods and droughts to analyze possible effects of extreme events on CSR.

The aims of this study are to (a) compare the CSR of dominant *Q. robur* in young plantations to dominant trees in old forest stands, (b) compare the CSR of old *Q. robur* trees under different hydrological conditions, and (c) analyze how drought and flood events influence the CSR of *Q. robur* in different hydrological conditions.

From 2009-2018, old *Q. robur* trees on the low active floodplain had an average CSR of 18.4 ± 1.1 (SE) Kg tree^{-1} year^{-1}, while young trees had an average CSR of 8.7 ± 0.6 (SE) Kg tree^{-1} year^{-1}. From 1976-2018, the overall CSR of *Q. robur* was highest on the high active floodplain (18.6 ± 1.7 (SE) Kg tree^{-1} year^{-1}) and lowest on the seepage water zone of the former floodplain (13.1 ± 1.1 (SE) Kg tree^{-1} year^{-1}). CSR was higher during flood years in all hydrological conditions, but was significantly reduced by drought only on active floodplains with a comparatively high elevation.

Floodplains are well-suited areas for reforestation as natural climate solutions because the dominant trees in these areas have a high CSR even under severe conditions which are predicted to become more common with climate change in the future.

4.2. Introduction

Human-induced climate change is a pressing global challenge driven by increasing concentrations of atmospheric gases such as CO_2 (IPCC 2021). One solution to reduce atmospheric CO_2 while also providing other benefits to the air, biodiversity, water, and soil is reforestation (Griscom et al. 2017, Bastin et al. 2019). Under the right conditions, terrestrial forests can act as CO_2 sinks by sequestering carbon in woody biomass (Bastin et al. 2019). However, not all areas and not all trees have equal potential to deliver ecosystem services, and appropriate areas for reforestation should be selected carefully (Di Sacco et al. 2021). Under the wrong conditions (e.g. extreme drought events and limited access to water), mortality events can result in the decreased annual uptake of atmospheric CO_2 as well as the emission of CO_2 through biomass decomposition of the deceased trees. Extreme events such as droughts and floods can cause tree mortality and reduce ecosystem services such as the carbon sequestration capacity of the deceased trees. However, higher temperatures in conjunction with high water availability could increase tree productivity and carbon sequestration rates (CSR) of forests (Seppälä 2009, Tatarinov and Cienciala 2009).

Hardwood forests on floodplains with complex geomorphology are known to be biodiversity hotspots and highly productive ecosystems with a great carbon sink potential (Junk et al. 1989, Schnitzler 1994, Giese et al. 2003). Dynamic hydrogeomorphic processes such as flooding, erosion, and sedimentation shape floodplains and interact with biotic processes to create diverse habitats (Steiger et al. 2005). Flooding pulses which bring nutrient-rich sediments to the floodplain can enhance productivity but are limited today by anthropogenic disturbances such as the construction of flood protection dikes (Junk et al. 1989, Steiger et al. 2005). Dike presence reduces the surface area for the deposition of sediments, and results in a more rapid sedimentation between dikes on the active floodplain and a deprivation of sediments on the former floodplains behind the dikes (Schnitzler 1994). In Germany, only around 1% of the floodplains are “very slightly altered” compared to their potential natural state, and two-thirds of historical floodplains are no longer available as retention areas when floods occur (BMU and BfN 2021). Until medieval times, when humans started to build dikes and re-shape floodplain landscapes on larger scales through deforestation, hardwood floodplain (HF) forests were common in Europe (Brown et al. 1997). In Germany, HF forests have now been reduced to 2,500 ha, and a majority of the forests cannot fully fulfil their habitat function for plant and animal species typically thriving on the floodplain (BMU and BfN 2021). Today, European HF forests are severely fragmented and exposed to different hydrological regimes according to their position: on the active floodplain, in the former floodplain behind dikes in the seepage water zone, or on main tributary floodplains. HF forests have a great carbon sink potential, especially when dominated by Pedunculate oak (*Quercus robur*) trees (Kiss et al. 2015), but it is not well known how the influence of dikes and the changes to the hydrological conditions affects the CSR of these trees growing in HF forests.

Irregular floodings and droughts are characteristic features on floodplains, but the frequency and intensity of floods and droughts are expected to change in the future. Drought events have increased since the 1950s and are projected to increase with climate change (IPCC 2021). Decreased precipitation in late summer, decreased snowpack, and rising summer temperatures can decrease soil moisture and result in detrimental drought stress. Northern Hemisphere spring snow cover has decreased since 1950 (IPCC 2021), which can lower river water levels and worsen drought conditions if not offset by precipitation.

Knowledge about how the CSR of *Q. robur* is affected by drought and flooding under different hydrological conditions is vital to the success of future floodplain restoration and ecosystem service provision. *Q. robur* is considered to be a drought-tolerant species because of morphological and physiological adaptations, but higher temperatures and changes in precipitation patterns and river levels can affect tree growth. Depending on the climate scenario, carbon stocks of *Quercus* stands were found to either increase or decrease as an effect of climate change, and progressing drought stress is identified as the most important factor impacting carbon balance changes (Tatarinov and Cienciala 2009). A mass mortality of trees has recently been observed in Europe and connected to drought events, with even *Q. robur* in floodplain forests susceptible to die-back (Colangelo et al. 2018). While drought can have a negative effect on *Q. robur* growth, high temperatures in conjunction with high river water levels and precipitation can be beneficial to the growth of old *Q. robur* trees on the floodplain (Mikac et al. 2018). Although *Q. robur* has an intermediate flooding tolerance because of adaptations such as adventitious roots and lenticels, individual tree response to flooding is complicated (Glenz et al. 2006). A flooding tolerance ranging from 96 to 217 days per year has been estimated for Q. robur, but damage has also been observed after 62 days if the flooding occurs during the physiologically active summer period (Pott 2000, Leuschner and Ellenberg 2017). Flooding can be beneficial to *Q. robur* productivity, as shown by a study that observed an increase in diameter growth after a 120-day flood (Frye and Grosse 1992). Also, *Q. robur* on floodplains near

Kyiv were negatively affected by extreme flooding, but after river regulation, the trees became vulnerable to drought events (Netsvetov et al. 2017). The effects of flooding and drought are context-dependent and must therefore be studied locally.

Reforesting the floodplain is a promising natural climate solution (Griscom et al. 2017), but it is not well understood how tree productivity in floodplains is influenced by the hydrological disconnection from natural river pulses by dike infrastructure, or whether trees on main channel tributaries grow as well as trees on the active floodplain. On floodplains of the Elbe River in Germany, restoration and reforestation projects have been successfully implemented (Damm 2013), but overall survival of planted trees was low. The reason for decreased vitality and high mortality is not known, but it could be a consequence of stress caused by drought and/or extended flooding conditions. In the next decades, it is expected that both drought and flood risk will increase across Europe, and knowledge of how the CSR of HF trees may be affected by these conditions is beneficial to floodplain management. The restoration of HF forests may be able to provide efficient carbon sinks and biodiversity hotspots, and the optimization of ecosystem services can be obtained with local scientifically based, climate-appropriate, and sustainable management decisions.

In this study, we investigate how tree age, hydrological conditions, and flood and drought stress influences dominant *Q. robur* trees. The objectives of this study were to evaluate how tree age influences the CSR of *Q. robur* trees on the active floodplain, how the CSR of old *Q. robur* trees are affected by different hydrological conditions, and how the CSR of *Q. robur* trees in the different hydrological conditions are affected by drought and flood events.

4.3 Materials and Methods

4.3.1 Study area

The study area is located within the UNESCO Biosphere Reserve River Landscape Elbe and the German states Saxony-Anhalt, Brandenburg, and Lower Saxony (Figure 4.1). Spanning approximately 100 km along the lower Middle Elbe River, the study plots are within the European temperate climate region. The climate of the region is characterized by a mean annual precipitation of 615 mm and a mean annual temperature of 9.3°C (1981-2010, Lenzen station, 53.08°N 11.48°E) (DWD 2022). Characteristic soils of the Elbe floodplain include Gleysols, Fluvisols, Arenosols, and Cambisols (Schwartz et al. 2003, Heger et al. 2021). Typically, flooding occurs after snowmelt in the winter and spring and after intense precipitation events in the summer. Drought is particularly prominent in the summer months when the river water level and precipitation is low. Typical species in HF forests include pedunculate oak (*Quercus robur*), European white, field, and wych elm (*Ulmus laevis*, *Ulmus minor*, and *Ulmus glabra*), European hornbeam (*Carpinus betulus*), and European ash (*Fraxinus excelsior*). Typical understory vegetation includes *Crataegus monogyna*, *Cornus sanguinea*, and *Sambucus nigra*.

The floodplain of the Middle Elbe River has been anthropogenically altered since at least the Middle Ages through diking, deforestation, and agricultural use. Hydraulic engineering measures in the 19th and 20th centuries have fundamentally changed the structure of the river and floodplain (BAW 2013). Because of the construction of flood protection dikes, losses of over 80% of the Elbe River floodplain have been recorded (BMU and BfN 2021). In this study, we examine HF forests under different hydrological conditions: the active floodplain, the seepage water zone behind dikes in the former floodplain, and the tributary floodplains. On the active floodplain, plots with lower (low active) and with higher (high active) elevation are differentiated. Diking of the river has greatly reduced the area of the active floodplain, confines river flooding, and prevents natural flood pulses in the former floodplain. The active floodplain, the former floodplain seepage water zone and the tributaries have a history of deforestation and agriculture, which has reduced the connectivity of forests, and has left only small remnants of the former contiguous riparian ecosystem.

On the active floodplain, the geomorphology of the floodplain influences the annual flooding duration of HF forests. Generally, forests with lower elevations on the floodplains (the low active floodplain) are more frequently flooded, while forests on higher elevations (the high active floodplain) are less frequently flooded.

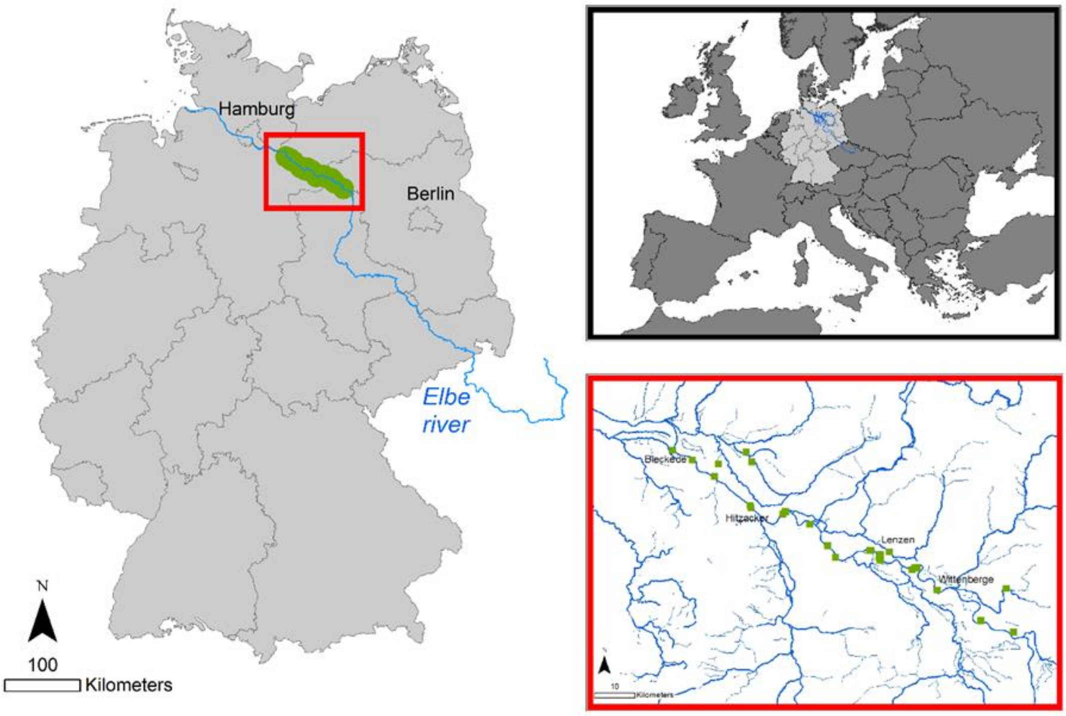

Figure 4.2 Map of the study area along the Elbe River, Germany. The study region is outlined by the red box. Study plots are shown as green squares.

4.3.2 Field measurements and sampling

Five different forest types differentiated by hydrological condition and age were investigated in this study. Forest types include young plantations on the frequently flooded low active floodplain, old forests on the low active floodplain, old forests on the less frequently flooded high active floodplain, old forests in the former floodplain seepage water zone behind the dike, and old forests on the tributaries of the main river channel. For each forest type, five replicate plots (2500 m^2 each) were identified. Plots were spatially distributed throughout the study area to reduce the influences of spatial autocorrelation in further modelling (see section 2.6). Young plantations in this study range in age from 18-27 years and old forests range in age from 81-200 years. See Table 4.1 for other basic plot characteristics.

Each forest plot was inventoried in the winter of 2018 and 2019 (Shupe et al. 2021). Ten dominant trees were selected from five replicate plots per forest type (‘ad-hoc’ sampling according to (Nehrbass-Ahles et al. 2014)). The DBH of the sampled *Q. robur* trees from each forest type, the distribution of all trees according to DBH sizes, and an indication of the different tree densities according to forest type are summarized in the appendix (Figure B1 in appendix). In September 2019, the selected 50 dominant oak trees were cored to the pith at 1.3 m above-ground using a 5 mm wide Mora-Coretax increment borer (Haglöf, Sweden). The cores were dried in an oven at 60° C for 48 hours and stored in paper straws until further analysis.

Table 4.4 Characteristics of hardwood floodplain forest stands classified by floodplain compartment (active floodplain, seepage water zone of the former floodplain, and tributary floodplain), tree age (young vs old) and elevation (low vs high). Mean ± standard deviation (SD) and minimum, maximum value are included. Flooding duration is a 35-year mean (1990–2016) estimate and was only available for the active floodplain.

	Active Floodplain Low Young		Active Floodplain Low Old		Active Floodplain High Old		Seepage water zone Old		Tributary Old	
	Mean ±SD	Min Max	Mean ±SD	Min Max	Mean ±SD	Min Max	Mean ±SD	Min Max	Mean ±SD	Min Max
Forest age (years)	23 ±4	18 27	141 ±36	104 200	134 ±33	81 185	128 ±39	108 186	130 ±37	82 170
Basal area (m^2 ha^{-1})	22 ±7	12 30	32 ±4	26 36	36 ±8	29 43	35 ±6	27 45	36 ±7	27 44
Tree density (trees ha^{-1})	1245 ±346	728 1576	291 ±121	181 496	248 ±55	235 464	357 ±100	192 325	531 ±186	331 763
Mean tree height (m)	11 ±4	3 20	14 ±7	2 30	15 ±9	4 31	17 ±8	3 33	16 ±7	2 32
Mean tree DBH (cm)	14 ±6	5 42	27 ±25	5 140	34 ±27	5 113	28 ±21	5 108	24 ±18	5 99
Tree species richness	3 ±2	1 5	2 ±1	2 3	3 ±1	3 8	5 ±2	2 5	5 ±3	3 10
Flooding duration (days $year^{-1}$)	34 ±28	6 86	36 ±18	11 59	4 ±3	X	X	X	X	X

4.3.3 Increment core processing

After soaking the cores in a warm bath for 30 minutes, the cores were secured in a clamp and the surface of each core was carefully scraped with a razor blade to increase the visibility of the tree ring vessel structure. A microscope connected to a LINTAB^{TM} 5 measuring table (RinnTech) and the TSAP-Win^{TM} software program were used to measure the annual tree ring widths (TRW) from bark to pith. Two researchers measured and visually inspected each core, and the two measurements were then compared. The sampling year (2019) and all years before 1900 were removed. The COFECHA program (Grissino-Mayer 2001) was further used to cross-date samples. Cross-dating was conducted separately for each forest type. If obvious flags were detected, TRW measurements were re-examined and changed accordingly. The mean chronology (Figure B2 in appendix) and the basic chronology statistics (Table B1 in appendix) for ten dominant *Q. robur* trees in each old forest type are included in the appendix. Young plantations on the active floodplain are not included because more measured years would be needed to make a chronology. Basic statistics of the raw series and chronology statistics were performed in R (R Core Team 2019) using the packages dplR (Bunn 2010) and detrendeR (Campelo 2012).

4.3.4 Carbon sequestration rate estimation with a DBH-based allometric equation

The DBH of each tree was reconstructed in an annual step-wise fashion using the measured TRW from increment cores and the conventional DBH reconstruction method (Bakker 2005, Bakker et al. 2008). This method entailed measuring the DBH of each tree at year 2018 and incrementally subtracting twice the measured TRW for each year back in time. A one-parameter allometric equation to estimate tree carbon stock using only DBH was created (Shupe et al. 2022) and the carbon stock of the tree was reconstructed at an annual scale using the annual DBH change estimates. The CSR of each tree was then estimated as the change in carbon stock from one year to the next (Shupe et al. 2022). This method is based on the assumption that the same allometric equation is applicable to both young and old trees and that there is a constant root:shoot ratio. For the purpose of this study, CSR is a measure of the rate at which atmospheric carbon is taken in and stored as biomass within a year's time in kilograms of carbon per tree (Kg tree^{-1}). Because this study reconstructs CSR for the year according to the growth of the trees, the "year" begins and ends in what would be the early spring of the Gregorian calendar. The beginning of the year is marked on the tree cores as the emergence of early wood vessels and terminates with the end of the latewood vessels and the beginning of the next year's early wood vessels. To avoid pseudoreplication, average CSRs were calculated per plot.

4.3.5 Drought, flood and control years

To analyze the effects of flood and drought events on CSR, flood and drought years were determined. To determine drought years, we used the Standardized Precipitation Evaporation Index (SPEI_12) for the study region [52.75, 10.75], [53.25, 11.75] (Vicente-Serrano et al. 2010b). If average seasonal (spring or summer) SPEI_12 values were below -1, the year was considered to be a drought year (Figure 4.2).

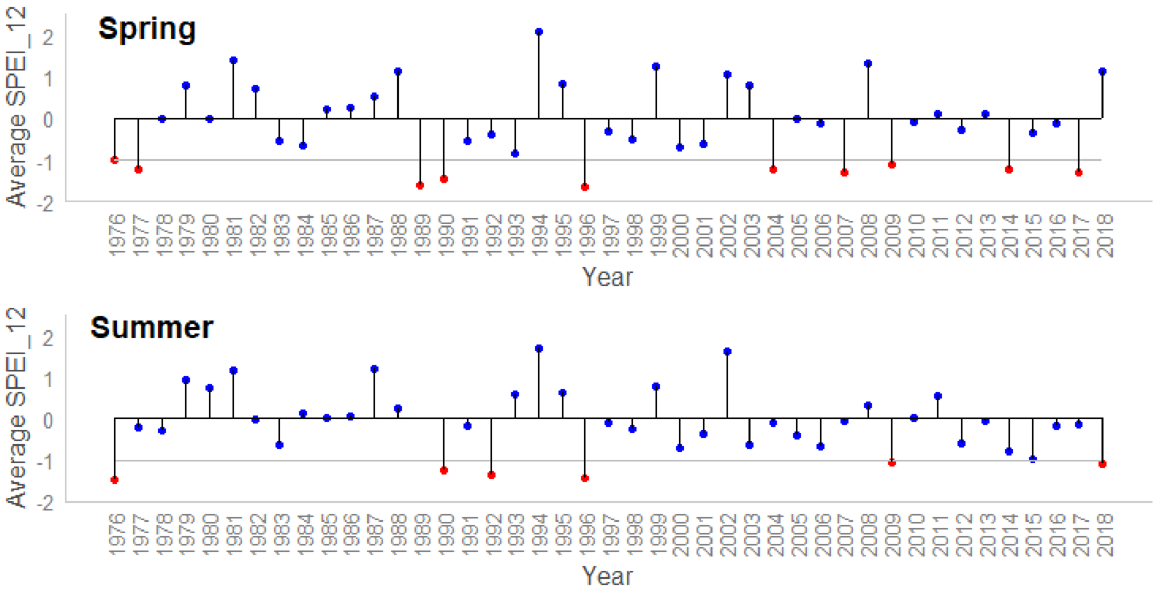

Figure 4.2 Standardized Precipitation Evaporation Index (SPEI_12) values extracted for the study region [52.75, 10.75], [53.25, 11.75] at an annual scale (Vicente-Serrano et al. 2010b). Mean spring and summer values are plotted separately. All drought years with an SPEI ≤ -1 are colored red.

Flood years were identified using the Elbe River water level measurements from the Lenzen gauge station (BfG 2021). The year was considered to be a flood year if at least one mean seasonal river water level was above 16.7 NHN (Normalhöhennull: German Height Reference System), as this is the measured elevation of our study plots at Lenzen (Figure 4.3). Extreme floods with a short duration are not included in this analysis. All years which were not considered a flood or a drought year were taken as control years. The classification of the years into year types can be seen in the appendix (Table B2 in Appendix).

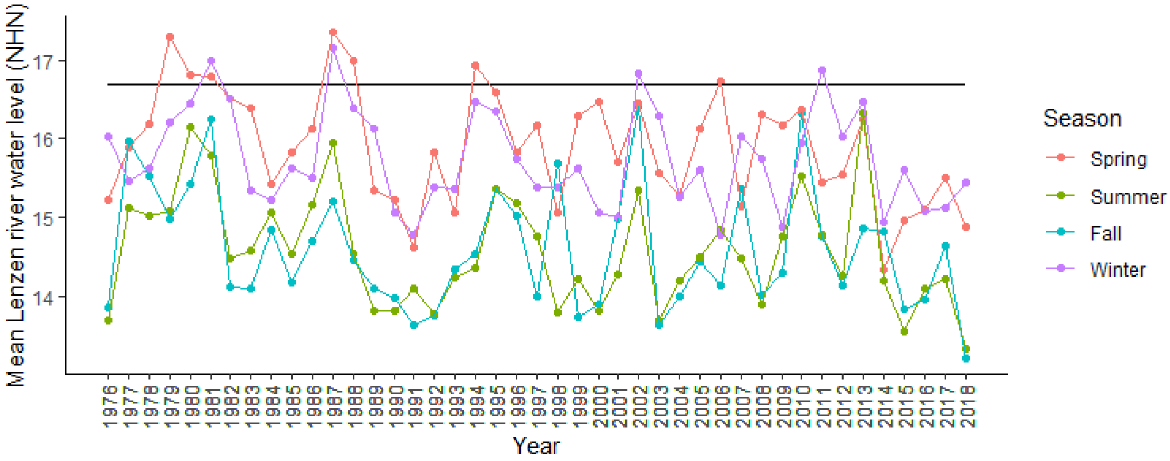

Figure 4.3 Seasonal mean Elbe River water levels at the Lenzen gauge from 1976-2018 in Normalhöhennull (NHN). The black line at 16.7 NHN is the elevation of the forest plot nearby and was used as the threshold value to determine flood years. All years with at least one mean seasonal river water level ≥16.7 NHN are considered flood years.

4.3.6 Statistical analysis

To compare the CSR of different forest ages, the CSR data was tested for normality with a Shapiro-Wilk test ($p > 0.05$) and a visual inspection of Q-Q plots, box plots, and histograms. Residuals were inspected for homoscedasticity. Because non-normality and homoscedasticity were observed for the response variable, a pairwise Wilcoxon Rank Sum Test with a Bonferroni-Holm correction was used.

Before comparing the CSR of old forests in different hydrological conditions, data exploration was carried out following a recommended protocol (Zuur et al. 2010). Scatterplots for each independent variable versus CSR were inspected and Pearson correlations among all independent variables were checked to ensure no multicollinearity.

To model the CSR of dominant *Q. robur* trees in different hydrological conditions while accounting for covariates, a generalized linear mixed effect model (GLMM) with a gamma log link transformation was used (Equation 4.1). The gamma log link function was chosen because the data was only positive and showed positively-skewed errors. Fixed effects included the hydrological condition (categorical with four levels: low active floodplain, high active floodplain, seepage water zone, and tributary), stand age (continuous), and stand density (continuous). We plotted residuals and assessed for temporal and spatial dependency. Temporal autocorrelation was observed, and was strongly reduced with an AR1 correlation structure.

$$\begin{aligned}&glmmTMB(CSR \sim Hydrological\_condition \ + stand\_age \ + stand\_density \\ &\quad + ar1(Year \ + 0|Plot), \quad data = All\_hydrological\_conditions, \\ &\quad family \ = \ Gamma(link = "log"))\end{aligned}$$

Equation 4.1 Generalized linear mixed effect model to estimate the carbon sequestration rate (CSR) of dominant *Quercurs robur* trees in different hydrological conditions. The mean CSR data per plot (n=5 per plot) was used.

To model the CSR of dominant *Q. robur* trees during different year types by different hydrological conditions while accounting for covariates, a GLMM with a gamma log link transformation was used separately for each hydrological condition (Equation 4.2). Fixed effects included the year type (categorical with three levels: drought, flood, or control year), stand age (continuous), and stand density (continuous).

$$\begin{aligned}&glmmTMB(CSR \sim year\_type \ + stand\_age \ + stand\_density \ + ar1(Year \\ &\quad + 0|Plot), \quad data = Hydrological\_condition, \\ &\quad family \ = \ Gamma(link = "log"))\end{aligned}$$

Equation 4.2 Generalized linear mixed effect model to estimate the carbon sequestration rate (CSR) of dominant *Quercus robur* trees during different year types. This equation was used separately for each hydrological condition and included the mean CSR data per plot (n=5 per plot).

All tests were performed using R (R Core Team 2019). Main packages included glmmTMB (Brooks et al. 2017), emmeans (Lenth 2020), visreg (Breheny and Burchett 2017), and ggplot2 (Wickham 2016).

4.5 Results

4.5.1 CSR and tree age

On the low active floodplain, dominant *Q. robur* trees in old forests sequestered an average of 18.4 ± 1.1 (SE) Kg tree^{-1} year^{-1}, which was significantly more carbon ($p < 0.01$, Wilcoxon ranksum test) than the average 8.7 ± 0.6 (SE) Kg tree^{-1} year^{-1} sequestered by dominant trees in young plantations (Figure 4.4).

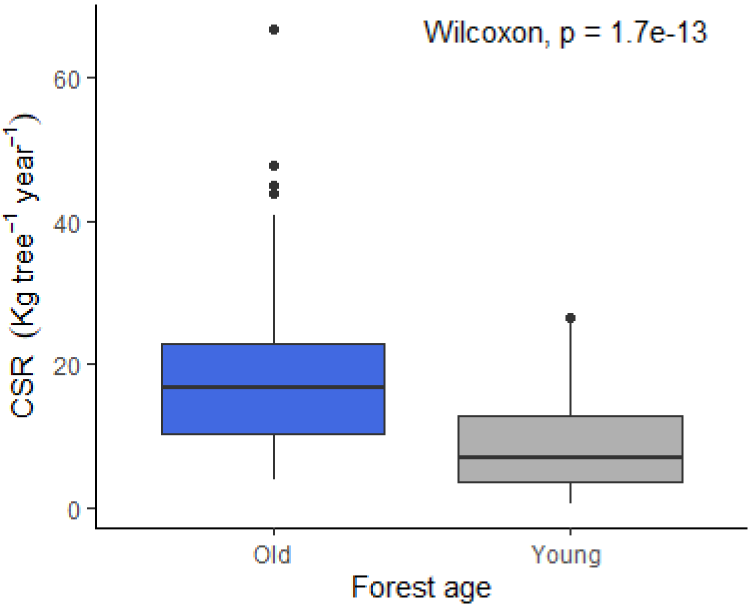

Figure 4.4 Carbon sequestration rates (CSR) of dominant *Quercus robur* trees in old and young hardwood forests on the low active floodplain of the Middle Elbe River. Boxes represent 25–75% of values, black strips medians, whiskers 1.5 interquartile ranges, and black dots outliers.

4.5.2 CSR and hydrological conditions

There was a high variation in the CSRs of the old forests in each hydrological condition over the years (Figure 4.5). There was also a high variability between the ten replicate trees measured in each hydrological condition per year. The lowest average CSR (9.3 Kg tree^{-1} year^{-1}) was recorded in the seepage water zone in the drought year of 1996, while the highest average CSR (28.6 Kg tree^{-1} year^{-1}) was recorded on the high active floodplain in the flood year of 1994.

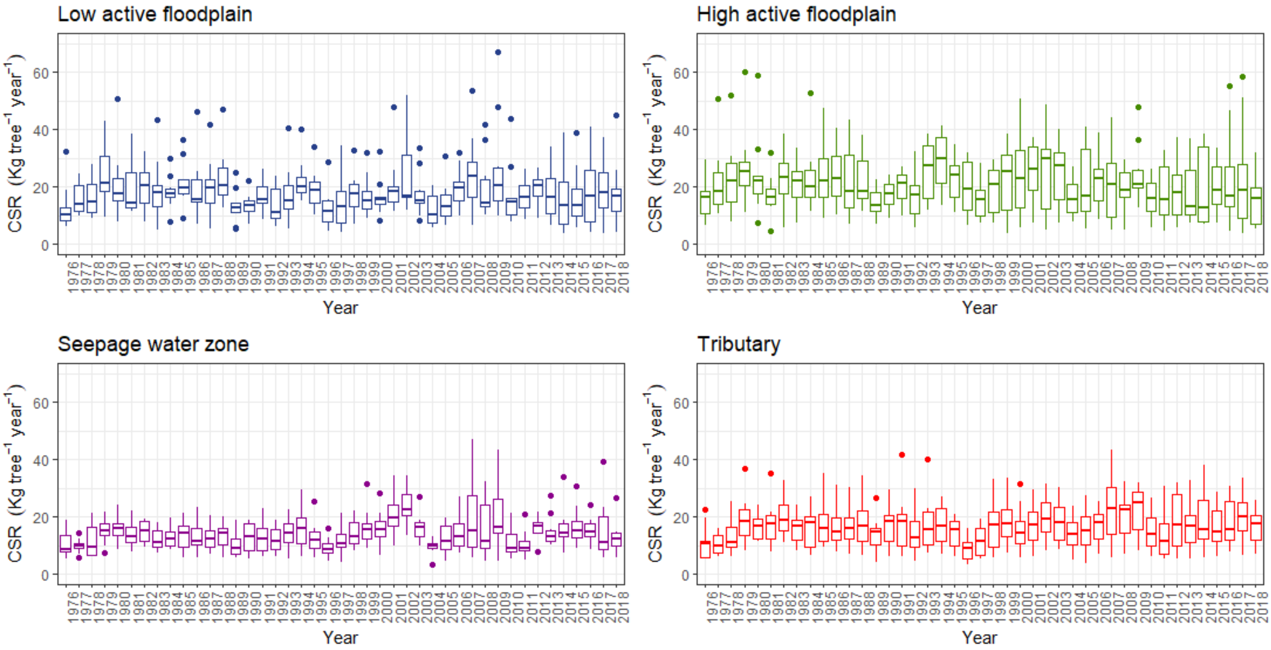

Figure 4.5 Temporal variation of the carbon sequestration rate (CSR) of dominant *Quercus robur* trees within old forests between 1976 and 2018. Dominant *Quercus robur* trees were analyzed in old forests of the low active floodplain, high active floodplain, seepage water zone, and along tributary floodplains of the Middle Elbe River (n=10 for each hydrological condition). Boxes represent 25–75% of values, strips medians, whiskers 1.5 interquartile ranges, and dots outliers.

The CSR of dominant *Q. robur* trees significantly differed between the high active floodplain and the seepage water zone (Figure 4.6). The highest CSR was observed in trees on the high active floodplain, which showed an average CSR of 18.6 ± 1.7 (SE) Kg tree^{-1} year^{-1}. The individual trees in the seepage water zone showed the lowest overall CSR, with an average CSR of 13.1 ± 1.1 (SE) Kg tree^{-1} year^{-1}. *Q. robur* trees on the low active floodplain and on tributary floodplains showed a similar average CSR of 16 ± 1.4 (SE) Kg tree^{-1} year^{-1} and 16.2 ± 1.7 (SE) Kg tree^{-1} year^{-1}, respectively.

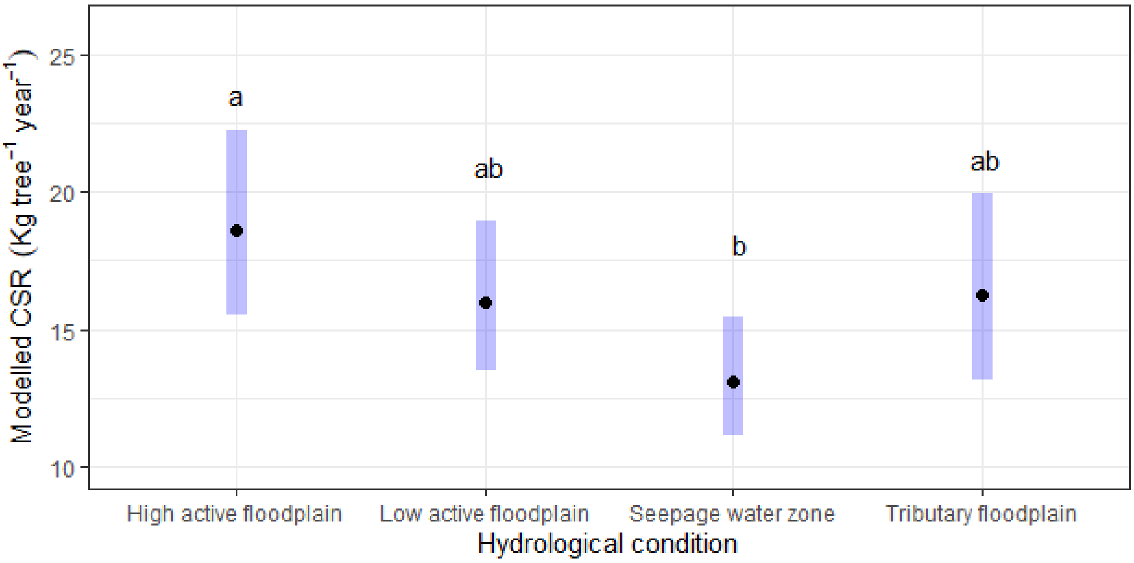

Figure 4.6 Modelled carbon sequestration rate (CSR) of 10 dominant Quercus robur trees per hydrological condition: high active floodplain, low active floodplain, seepage water zone and Tributary. Blue boxes outline confidence intervals (confidence level of 0.95). Intervals are back-transformed from the log scale. P value adjustment: Tukey method for comparing a family of 4 estimates. Tests were performed on the log scale. Significance levels indicated with letters (alpha = 0.05).

4.5.3 Effects of drought and flooding on CSR in different hydrological conditions

The CSR of dominant *Q. robur* trees was significantly greater ($p \leq 0.05$) during flood years than during drought years on the low active floodplain, the high active floodplain and the seepage water zone (Figure 4.7). On the low active floodplain, the CSR of *Q. robur* trees was not significantly lower during drought years than during control years ($p > 0.05$). In contrast to this, the CSR was significantly lower during drought years than during control years ($p \leq 0.05$) on the high active floodplain. In the seepage water zone, the CSR of the individual trees was not significantly different between control and drought years. On the tributary, CSRs of the individual tress did not differ between drought, flood, or control years.

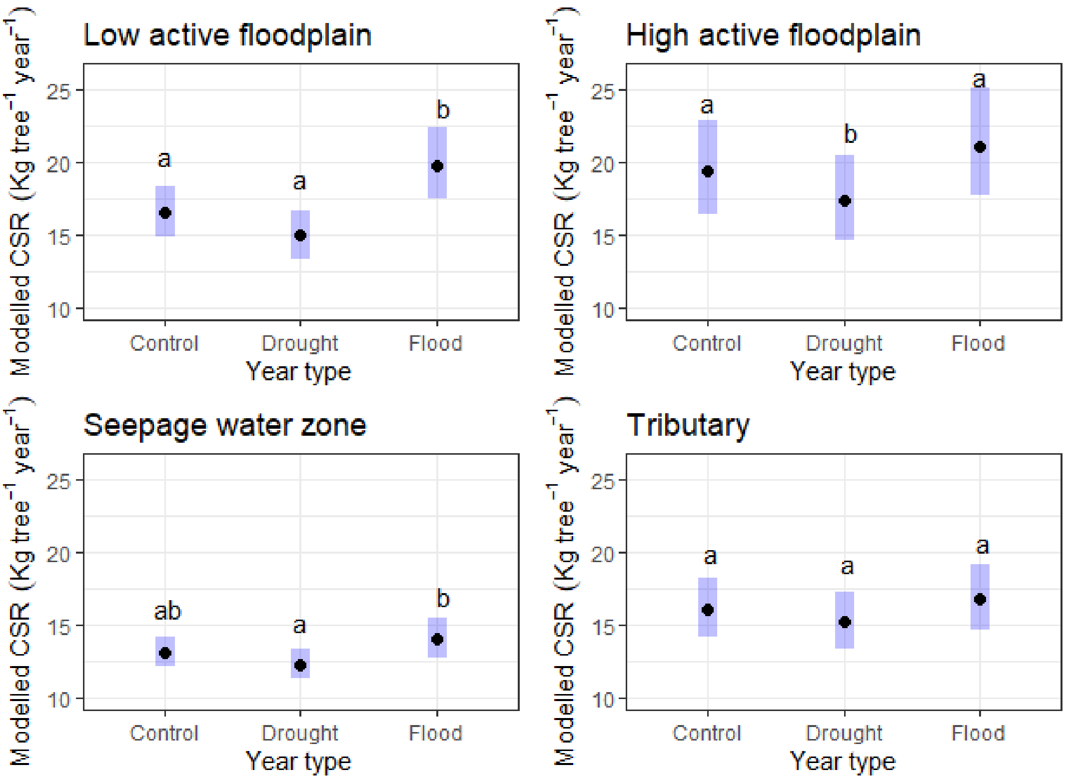

Figure 4.7 Modelled carbon sequestration rate (CSR) of dominant *Quercus robur* for drought, flood and control years (year type) by hydrological condition. Blue boxes outline confidence intervals (confidence level of 0.95). Intervals are back-transformed from the log scale. P value adjustment: Tukey method for comparing a family of 3 estimates. Tests are performed on the log scale. Significance levels indicated with letters (alpha = 0.05).

4.6 Discussion

4.6.1 Tree age and carbon sequestration rate in floodplain forests

The comparison of *Q. robur* trees in this study shows that dominant old trees can sequester over twice as much carbon per year than dominant young trees and therefore provide a substantially higher carbon sequestration service than young trees at the individual tree scale. This result is supported by the findings that the rate of carbon accumulation increases with tree size (Stephenson et al. 2014). Because the allometric equation used here is dependent on DBH (Shupe et al. 2022), the increase in the young tree’s height is not considered, which may underestimate the CSR of the young trees and overestimate the CSR of older trees with greater DBH. The limitations of allometric equations are commonly discussed in literature (Paul et al. 2013, Duncanson et al. 2015, Vorster et al. 2020), but the equations are nonetheless widely developed and used in biomass estimations and carbon accounting (Forrester et al. 2017, Martin-Benito et al. 2021). It should be emphasized that throughout this study, we refer to the CSRs of individual dominant *Q. robur* trees which were vital at the time of coring, and we do not estimate CSRs at a stand or hectare level. In our study, young plantations have more individual trees (ranging from 728-1576 individual trees per hectare) than old forests (ranging from 181-763 individual trees per hectare), but a majority of the young trees would not be classified as dominant because they are suppressed by the dominant competitors. Suppressed trees grow slower because they lack access to vital resources such as sunlight, and are thus not able to sequester as much carbon as dominant trees. Any estimation of CSR at the stand or hectare level would require a sampling of all species present in the HF forests as well as all tree community classes of each species. This was not possible because of the difficulty in reconstructing annual CSRs of other species (e.g. *Ulmus laevis* trees which were mostly hollow), trees of other community classes (e.g. suppressed trees with no discernible annual rings), deceased trees, and harvested trees.

4.6.2 Hydrological conditions and carbon sequestration rate in floodplain forests

Humans have changed the hydrological conditions of floodplains along large rivers in Europe for centuries, mainly by building dikes along the river shores resulting in a clear separation between active and former floodplains (Naiman et al. 2005). In the Danube, Rhine, Elbe and Oder River basins, 59% to 85% of the former floodplains are no longer flooded, and these areas are dominated by agriculture today (BMU and BfN 2021). Former floodplains may be well-suited for dike relocations and large-scale reforestation measures aiming to mitigate climate change by increasing the carbon sequestration potential of the floodplain ecosystems. As we found a 42% (high active floodplain) and 22% (low active) higher CSR of *Q. robur* in the active floodplain compared to the seepage water zone of the former floodplain, our study for the first time provides evidence that CSR in the seepage water zone of former floodplains is lower than on the active floodplain. This indicates that the dike presence negatively affects tree growth and thus carbon sequestration. This result contrasts with results from the Danube River in Austria, where no differences in carbon sequestration of forests in the active and the former floodplain were observed (Rieger et al. 2017). The significantly lower CSR of *Q. robur* in the seepage water zone found in our study may be a result of the disconnection from nutrient-rich flooding pulses. Nutrients associated with sediments can boost tree productivity (Marks et al. 2020) and the loss of these nutrients may limit growth. For instance, the plant available phosphorus concentration is significantly lower in the former floodplains which are disconnected from river pulses by dikes than on the active floodplain of the Middle Elbe (Vásconez Navas et al. 2022). In addition, soil organic carbon content in the seepage water zone is 30% lower than on the active floodplain (Heger et al. 2021). Taken together, these results indicate that the seepage water zone of the former floodplain is not as efficient of a carbon sink as the active floodplain for individual dominant *Q. robur* trees, and that a reconnection to river pulses may boost carbon sequestration.

Average growth rates (AGR) of trees are commonly reported as average tree ring widths. For dominant *Q. robur* trees on the Middle Elbe floodplains, the average annual AGR is 2.2 mm year^{-1} for the low active floodplain, the seepage water zone and the tributary, while the AGR in the high active floodplain is 2.8 mm year^{-1}. This is very similar to the 2.1 to 3.0 mm year^{-1} AGRs of *Q. robur* in floodplain forests in the Czech Republic (Tumajer and Treml 2016) and slightly more than AGRs of 1.7 to 2.5 mm year^{-1} on hydromorphic soils in north-east Germany (Scharnweber et al., 2013). Both in upland forests and in parks in north-east Germany, *Q. robur* had overall lower AGRs of 1.4 to 1.8 mm year^{-1} and 1.1 to 2.0 mm year^{-1} (Scharnweber et al. 2011).

4.6.3 Flooding, drought, and carbon sequestration rates in floodplain forests

We found that dominant *Q. robur* trees in all hydrological conditions had the highest CSR during flood years (Figure 4.7). This indicates that the flooding observed in our study sites is not detrimental to *Q. robur*, but rather beneficial. This increase in productivity could be due to higher nutrient availability as a consequence of flooding pulses (Junk et al. 1989) and/or an increase of soil water availability which may be especially beneficial early in the growing season. In our study, all nine flood years between 1976 and 2018 had either flooding in winter or in spring, but not in summer or autumn (see Figure 4.3). Because the flood years are selected based on the Elbe River water level, the seepage water zone may not be flooded to the same extent as the active floodplain. *Q. robur* seems to benefit from these flood pulses both when the trees are dormant in winter and in spring when the trees are beginning to produce their leaves. Flooding associated with soil hypoxia can also decrease vitality and CSR in *Q. robur* as it negatively affects earlywood development in roots, causes root dieback, and strongly reduces hydraulic conductivity (Copini et al. 2016). However, on hydromorphic soils in northeast Germany, no reductions in radial growth of *Q. robur* was found under extremely wet spring conditions (Scharnweber et al. 2013). Overall, our study confirms a high tolerance of adult *Q. robur* to flooded conditions and shows that flooding increases carbon sequestration of dominant *Q. robur* trees.

CSRs of dominant old *Q. robur* trees were only significantly negatively affected by drought in the active high floodplains, but not in active low sites, in the seepage water zone of the former floodplain, or in tributary floodplains. This indicates that *Q. robur* is rather resilient to drought events when located in most of the hydrological conditions studied here. Sufficient groundwater availability during drought events and the deep rooting trait of *Q. robur* may explain the lack of drought effects. Drought may affect the high active sites more than the low sites because of the soil properties, where high sites are predominantly sandy and low sites are loamy (Heger et al. 2021). The water holding capacity of the sandy sites is lower than loamy sites, and thus may dry out more quickly. At the same time, the water level is higher on the low sites longer than it is on the high sites, delaying the drought conditions. Radial growth of *Q. robur* on floodplains in the Czech section of the Elbe River was also not negatively affected by drought due to sufficient groundwater availability (Tumajer and Treml 2016). The relatively high resilience of *Q. robur* to drought in floodplains indicates that HF forests may maintain high CSRs also in the future with an expected higher frequency of European droughts (IPCC, 2021).

4.7 Conclusions

We conclude that individual dominant old *Q. robur* trees on the active floodplain can sequester over twice as much carbon as individual dominant young trees and are therefore important CO_2 sinks. Dominant old *Q. robur* trees on the active floodplain and tributaries have a higher CSR than dominant old *Q. robur* in the seepage water zone, so planting trees on the active floodplain and tributaries may provide a higher ecosystem service in terms of carbon sequestration than planting trees in the seepage water zone. This also implies that de-embankments and dike relocations may increase the potential CSR of individual *Q. robur* trees by between 20 and 40%. This is a clear co-benefit of de-embankments which nowadays are carried out to increase the area of active floodplains and to decrease the risks of catastrophic floodings to human societies (Damm 2013, BMU and BfN 2021). Additionally, winter and spring flooding is shown to be beneficial to the radial growth of *Q. robur*, which implies that these older trees are well adapted to the flooded conditions. Drought was shown to decrease CSR significantly on the high active floodplain, but old trees were resilient to drought in all other hydrological conditions. We conclude that floodplains are well-suited areas for reforestation as natural climate solutions because trees in these areas have a high CSR even under severe conditions which are predicted to become more common with climate change in the future.

4.8 Acknowledgments

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5.

Chapter 5: Leaf litter decomposition of *Quercus robur* and *Ulmus laevis* in hardwood forests on the Middle Elbe floodplain

In Prep.

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5.1 Abstract

Carbon storage in the leaf litter pool of forests is affected by both organic carbon (C) input from primary production and by C output due to decomposition. This study was conducted in hardwood forests on the floodplain of the Middle Elbe River, Germany, to determine how leaf litter decomposition rates may be affected by two main types (*Quercus robur* and *Ulmus laevis*) in old forests with different flooding durations as well as to determine the influence of forest age on decomposition rates. In addition, leaf litter quality (C%, N%, C:N ratio, NDF%, ADF%, ADL%, and ADL:N) of the two species was analyzed.

The C content of *Q. robur* leaf litter was estimated to be higher (48 - 49% C) than that of *U. laevis* (41 – 45% C). Over two years of field incubation, leaf litter decomposition was significantly faster in *U. laevis* compared to *Q. robur*. After two years, 95% of the *U. laevis* leaf litter and 53% of the *Q. robur* leaf litter was decomposed. By assuming an exponential rate of leaf litter decomposition and excluding macrofauna decomposers, it is estimated that it would take a total of 7.9 years for 95% of *Q. robur* leaf litter to be decomposed. No significant effects of hydrology (the low- compared to the high-active floodplain sites) on the decomposition of *Q. robur* or *U. laevis* were detected. Also, no significant effects of forest age (old forests compared to young plantations) on the decomposition of *Q. robur* leaf litter were detected.

These findings imply that the hydrological conditions and forest ages do not play a significant role in leaf litter decomposition, but the tree species do affect decomposition rates. The leaf litter of *Q. robur* can store more C than *U. laevis* for longer periods of time, but may provide less fodder and nutrition to decomposer communities. Therefore, for the maximization of ecosystem services to promote both C storage and biodiversity, a mixture of both species is recommended for floodplain reforestation.

5.2 Introduction

Temperate forests are important sinks for atmospheric carbon dioxide (CO_2), but local conditions and tree species may affect the rate of exchange between carbon pools (Dixon et al. 1994, Martin et al. 2001, Sedjo and Sohngen 2012). A tree assimilates inorganic CO_2 through photosynthesis and stores organic carbon (C) as biomass until decomposition begins. After growing every year, leaves from broadleaf trees are abscised, fall to the forest floor, and this leaf litter begins to decompose. Many abiotic and biotic factors can influence the rate of leaf litter decomposition, the residence time the C remains in leaf form, and C storage (Sierra et al. 2017). The amount of C that can be stored in the leaf litter C pool is dependent on the amount of input (how much leaf litter is produced by the trees in a year) and decomposition rates. Since the 1960s, decomposition constants known as *k* values are typically used in research on decomposition to compare the effect of different factors on decomposition (Prescott 2010). These rates are also required as input for C budget modelling of forests (e.g. the Carbon Budget Model of the Canadian Forest Sector CBM-CFS3) (Kurz et al. 2009). The hydrological conditions of the forest floor and the colonization and activity of decomposer communities, the tree species and quality of the leaf litter, soil characteristics, and many other factors can influence leaf litter decomposition rates (Mcclaugherty et al. 1985, Molles et al. 1995, Langhans et al. 2008, Ágoston-Szabó et al. 2015).

Complex topography and wet and cold conditions are ideal for C accumulation and storage (Sutfin et al. 2016), but hydrological conditions within

HF forests can vary and potentially affect decomposition. HF forests develop on recent alluvial deposits which are liable to flooding and the soil may be well drained between inundations or remain wet. On floodplains, the flooding regime is a primary driver of decomposition processes. The geomorphological differences on the floodplain can alter leaf litter, the duration of flooding, nutrient inputs, and drying and wetting processes of leaf litter (Molles et al. 1995, Andersen et al. 2003, Langhans and Tockner 2006, Sarneel and Veen 2017). Flood pulses and drying and wetting cycles can alter the quality of leaf litter (Harner and Stanford 2003) as well as nutrient conditions (Junk et al. 1989, Robertson et al. 1999, Heffernan and Sponseller 2004) and decomposer communities (Fierer et al. 2003). Decomposition can be accelerated by conditions that benefit the growth and productivity of decomposers (Mcclaugherty et al. 1985), however, different decomposers thrive in different environments. Water can solubilize substrates and increase availability to decomposers by diffusion (Kirschbaum 1995). Flooding duration can affect the availability of oxygen in the soil and by this alter decomposer communities and their activity. In the soil, increasing moisture content can increase microbial respiration until saturated conditions limit aerobic respiration and C metabolism. While flooding can promote leaf litter decomposition under aerobic conditions (Day 1983), anaerobic conditions slow decomposition (Williams and Gray 1983). While microbial growth and C-use-efficiency strongly decreases under high moisture content (Zheng et al. 2019), hydrological conditions which do not limit aqueous diffusion, gaseous diffusion, or water potential can maximize decomposition rates (Ghezzehei et al. 2019). The many ways that hydrological conditions can influence decomposition requires further research at local scales, and an investigation into the effect of flooding duration is therefore warranted to better understand the effects of different hydrological conditions in HF forests along the Middle Elbe floodplain (Germany).

The quality of leaf litter can vary by tree species and is among the most important factors regulating decomposition processes (Ágoston-Szabó et al. 2015). Leaf litter production and decomposition is an important part of the C cycle, foodwebs, and nutrient cycling in floodplain ecosystems (Sutfin et al. 2016). On the Middle Elbe floodplain, the two main tree species which store the greatest amount of C are Pedunculate oak (*Quercus robur*) and European white elm (*Ulmus laevis*) (Shupe et al. 2021). Soluble carbohydrates, hemicellulose, cellulose, lignin, and recalcitrant materials present in the leaf litter can require different decomposers and time to decompose. Different percentages of fiber types such as neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid determined lignin (ADL) can influence the decomposition of leaf litter (Melillo et al. 1989, Gholz et al. 2000). Decomposition rates have been negatively correlated with carbon to nitrogen ratios (C:N) (Edmonds 1980). However, high N concentrations and a lower C:N ratio have also been found to slow lignin degradation (Berg 2000). The reason for why N has different effects on leaf litter decomposition may be explained by the leaf litter quality and the ADL:N ratio, and decomposition rate *k*-values are known to decrease with increasing ADL:N ratios (Aerts 1997, Carreiro et al. 2000, Zhang et al. 2008, Prescott 2010). N has different effects on microbial enzymes, and while higher N has been observed to stimulate cellulases, it also suppresses lignolytic enzymes and reduces the efficiency of microbes and fungi responsible for the decomposition of leaf litter with a high lignin content (Carreiro et al. 2000). Therefore, it is expected that different species with different leaf litter qualities will also have different *k*-values and C storage potential within the leaf litter pool. The different effects of N on leaf litter decomposition are still poorly understood (Prescott 2010), which is why the measurement of leaf litter quality is important in any research conducted on leaf litter decomposition.

Forest age and structure may also play a role in decomposition, because the input and quality of leaf litter, the decomposer communities, soil respiration, and abiotic conditions such as temperature may differ. As forests develop, structural and physiological changes occur. Natural forests with a mixture of species are fundamentally different than monoculture plantations, providing a mixture of leaf litter from different species to the forest floor. It has been observed that tree species diversity is not as important to decomposition as the presence and abundance of individual tree species (Jacob et al. 2009), with high quality leaf litter having higher decomposition rates (Setiawan et al. 2016). Forest age has been found to affect fungal communities and soil physiochemical properties such as C:N ratios (He et al. 2016). Soil respiration has been found to decline with stand age, and changes in temperature may effect the soil respiration in mature stands less than in young stands (Tedeschi et al. 2006). Higher temperatures can increase decomposition if enough moisture is present. However, leaf litter decomposition was found to decrease more strongly during summer in a young plantation than in an old stand on a floodplain in Italy (Gioacchini et al. 2006). If soil respiration and decomposition in mature forests is less sensitive to temperature changes than young forests, the different forest ages could therefore affect decomposition rates.

In hardwood forests on the active floodplain of the Middle Elbe River, we ask (a) how does leaf litter decomposition differ between tree species, (b) how is leaf litter decomposition of *Q. robur* and *U. laevis* affected by hydrological conditions, and (c) how does stand age affect the decomposition rates of *Q. robur* leaves?

5.3 Methods

5.3.1 Study area

The study area is within the UNESCO-biosphere reserve Flusslandschaft Elbe and includes the German states Saxony-Anhalt, Brandenburg, and Lower Saxony (Figure 5.1). Located in the central European temperate climate region, the study area records a mean annual temperature of 9.8° C and a mean annual precipitation of 600.6 mm (means from 1991-2020, Lenzen/Elbe station 2951: 53.1° N, 11.5° E) (DWD 2022). Characteristic soils of the Middle Elbe floodplain include Gleysols, Fluvisols, and Cambisols (Heger et al. 2021).

5.3.2 Study sites

The study investigates three different forest types: old forests on the low active floodplain, old forests on the high active floodplain, and young plantations on the low active floodplain (*n* = 5 per type). A total of 15 plots (2500 m^2 each) representing typical temperate HF forests were studied. Five replicate plots of each forest type were selected based on the modelled mean annual flooding duration (mean of 1990-2016) (Weber in prep). Young plantations on the low active floodplain have an estimated mean annual flooding duration of 34 ± 28 SD days per year, while old forests on the low active floodplain are flooded 36 ± 18 SD days per year, and old forests on the high active floodplain are flooded 4 ± 3 SD days per year. It should be noted that these flooding durations were estimated for the 25 years prior to 2017, and these conditions were not the same during our leaf litterbag study period which took place from December 2018-January 2021. Using the Standardized Precipitation-Evapotranspiration Index (SPEI) for the study region [52.75, 10.75], [53.25, 11.75], we find that the drought conditions were greater during our study period than from 1990-2016 (Vicente-Serrano et al. 2010a). While the average SPEI 12 drought index value for 2019-2016 was -0.1 ± 0.8 SD, the average SPEI 12 value for December 2018-January 2021 was -1.30. Because the SPEI 12 values are considerably lower during our study period, we can assume that the flooding durations of our plots were also less than the 25-year average that we based our plot selection on.

The main tree species in the forests include Pedunculate oak (*Quercus robur)*, European white, field, and wych elm (*Ulmus laevis, Ulmus minor,* and *Ulmus glabra)*, European hornbeam (*Carpinus betulus)*, European ash (*Fraxinus excelsior).* Typical understory vegetation include *Crataegus monogyna*, *Sambucus nigra*, and *Cornus sanguinea*.

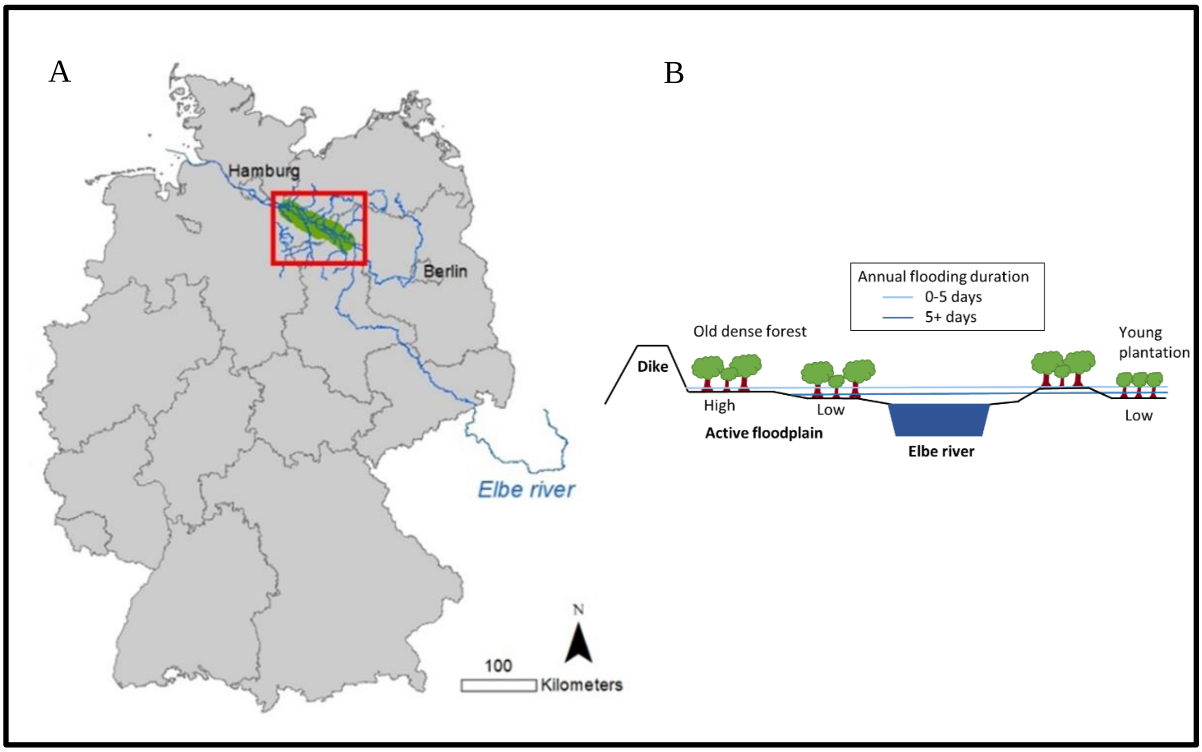

Figure 5.1 Map of the study area within Germany outlined in red (A) and the three different forest types on the Middle Elbe floodpain: old dense forests on the high and low active floodplain and young plantations on the low active floodpain (B).

5.3.3 Leaf litterbags

Mixed leaf litter from the 15 plots along the Middle Elbe floodplain was collected from the ground surface in the second week of November, 2018. Leaf litter was oven-dried at 25° C for a minimum of 24 hours, air-dried to constant mass, and then sorted by species (*Q. robur* and *U. laevis*). Additional leaf litter from both species was oven-dried at 105° C to establish a correction factor for air-dry to oven-dry weight. 306 leaf litterbags were constructed from vinyl-coated fiberglass (15 x 15 cm with a 1.6mm x 1.8mm mesh size), filled with 5 g of species-specific dried leaf litter, and closed with plastic clips (see Figure 5.2). In some cases, not enough *U. laevis* leaf litter was available per old forest plot, and was supplemented by *U. laevis* leaf litter from another plot in the same hydrological condition class (high or low active floodplain).

Within each of the 15 study sites, three replicate leaf litterbags were deployed for four incubation periods (3, 6, 9, and 12 months). After collection and weighing of the 3- and 6-month leaf litterbags, the leaf litterbags were again deployed to incubate for a total of 18- and 24-months in order to extend the total investigation time to two years. *Q. robur* and *U. laevis* replicates were deployed in the study sites representing old forests on low active, and high active floodplains, while only *Q. robur* was deployed in young plantations (which were mainly dominated by *Q. robur*). Each leaf litterbag was secured to a pole using fishing wire (Figure 2). Six control leaf litterbags were transported and dried along with the field leaf litterbags to estimate mass loss in transport. A transport correction factor of 0.07 g was applied to all leaf litterbags.

Figure 5.2 Leaf litterbags attached and arranged around a pole in the old sparse forest site LS1 (53°05'16.8"N 11°17'37.9"E) on the low active floodplain of the Middle Elbe. Photo taken by H.A. Shupe in December, 2018.

5.3.4 Leaf litter quality analysis

5.3.4.1 C%, N%, and C:N ratio

Dried samples of the leaf litter that was used in the leaf litterbags were finely ground in a steel ball mill and analyzed for mass percentages of C and N using an element analyzer (EURO-EA 3000, Euro Vector, Pavia, Italy). Approximately 2 mg of each type of leaf litter (*Q. robur* and *U. laevis*) per plot was weighed to the nearest 0.001 and secured tightly in 3.5mm x 5mm tin capsules (Hekatech GmbH) before being analyzed next to approximately 1 g of the appropriate pure chemical standard (2.5-Bisthiopene (BBOT)).

5.3.4.2 Other leaf litter properties

Using the ANKOM protocol and an Ankom 200 Fiber analyzer (ANKOM Technology, NY), leaf litter of Q. robur and of U. laevis from the different plots were extracted for neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid determined lignin (ADL). Dried leaf litter was ground using a 40 mm screen. Filter bags were dried at 105° C for 24 hours and weighed before filling each filter bag with 0.5 g of sample leaf litter. Three replicate filter bags per leaf litter species per plot were weighed after drying for at least 24 hours at 105° C before and after each extraction. Two empty filter bags were also included in each extraction to apply a filter bag correction factor. We used a neutral detergent solution for the NDF extraction, a H_2SO_4 and CTAB acid detergent solution for the ADF extraction, and a 72% H_2S0_4 with a specific gravity of 1.638 for the ADL extraction.

5.3.5 Statistical analysis

All data were tested for normality by Shapiro-Wilk test ($p > 0.05$) and a visual inspection of Q-Q plots, box plots, and histograms. Nonparametric Independent-Samples Kruskal-Wallis Tests were conducted to examine the differences in leaf litter properties for each leaf litter type (*Q. robur* and *U. laevis*) and according to forest type (young plantation, low active floodplain, and high active floodplain).

To compare the mass loss of the different leaf litter types in the different forest types over the months of field incubation, Wilcox tests with Bonferroni corrections were conducted.

To be comparable to other leaf litter decomposition studies, the commonly used mean decomposition constant (*k*) of leaf litter was calculated using the negative exponential decay model (Equation 5.1) (Olson 1963) where W_0 is the initial weight (5 g of dry leaf litter) and W_t is the weight remaining after time period t (the end of the experiment: two years). The time (in years) for 95% loss of material to occur in *Q. robur* was estimated by dividing 3 by *k*, assuming an exponential rate of decomposition for a range of leaf litters (Olson 1963, Newsham et al. 1999).

$$W_t = W_0 e^{-kt}$$

Equation 5.1 negative exponential decay model (Olson 1963). W_0 is the initial weight and W_t is the weight remaining after time period t.

5.4 Results

5.4.1 Leaf litter properties

For the different forest types, no significant differences ($p > 0.05$) in the C%, N%, C:N ratio, NDF%, ADF%, ADL%, or ADL:N of *Q. robur* or *U. laevis* leaves were observed (Table 5.1). On average, the leaf litter of *Q. robur* had a higher C content (48 – 49%) than that of *U. laevis* (41 -45%) The only significant difference detected between the tree species' leaf litter properties was for C%, where *Q. robur* leaves are higher ($p \leq 0.05$) than *U. laevis*.

Table 5.1 Leaf litter properties according to species and forest type. Carbon (C), Nitrogen (N), neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid determined lignin (ADL) are shown in percent of dry mass.

	Quercus robur						*Ulmus laevis*			
	High active floodplain		Low active floodplain		Young plantation		High active floodplain		Low active floodplain	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
C (%)	48.4	1.0	48.1	0.9	48.5	1	41.1	4.2	45.0	0.2
N (%)	1.4	0.6	1.2	0.3	1.0	0.2	0.9	0.6	1.5	0.4
C:N	38.8	11.6	44.1	10.8	48.9	11.1	54.9	32.5	31.6	8.2
NDF (%)	50.3	3.6	48.7	4.5	49.0	4.0	56.5	8.6	50.2	6.2
ADF (%)	33.6	3.3	32.9	5.2	32.9	4.0	28.2	0.9	26.8	6.8
ADL (%)	16.4	2.9	15.6	4.5	15.5	3.2	12.1	1.5	10.4	5.8
ADL:N	13.1	3.8	13.6	0.7	15.3	2.9	17.6	9.8	6.7	2.0

5.4.2 Leaf litter decomposition of different tree species

The mass loss of *U. laevis* leaf litter was significantly ($p \leq 0.001$) greater than *Q. robur* leaf litter at every collection time over the two years of field incubation except for month three (Figure 5.3). Although not significantly different, the mass loss of *U. laevis* leaf litter was still greater (18% ± 9% SD) than *Q. robur* (9% ± 3% SD) after three months of field incubation. After two years, the mass loss of *U. laevis* leaf litter was 95 ± 3% SD while the mass loss of *Q. robur* leaf litter was only 53% ± 6%SD. Over the two years, *Q. robur* leaf litter had an estimated *k*-value of 0.38 while *U. laevis* leaf litter had an estimated *k*-value of 1.47. It would take an estimated 7.9 years for 95% of *Q. robur* leaf litter to decompose.

Out of the 450 leaf litterbags deployed, 37 leaf litterbags were either lost or damaged by animals and excluded from the analysis. Fortunately, there was always at least one replicate per plot per collection to be included in the analysis.

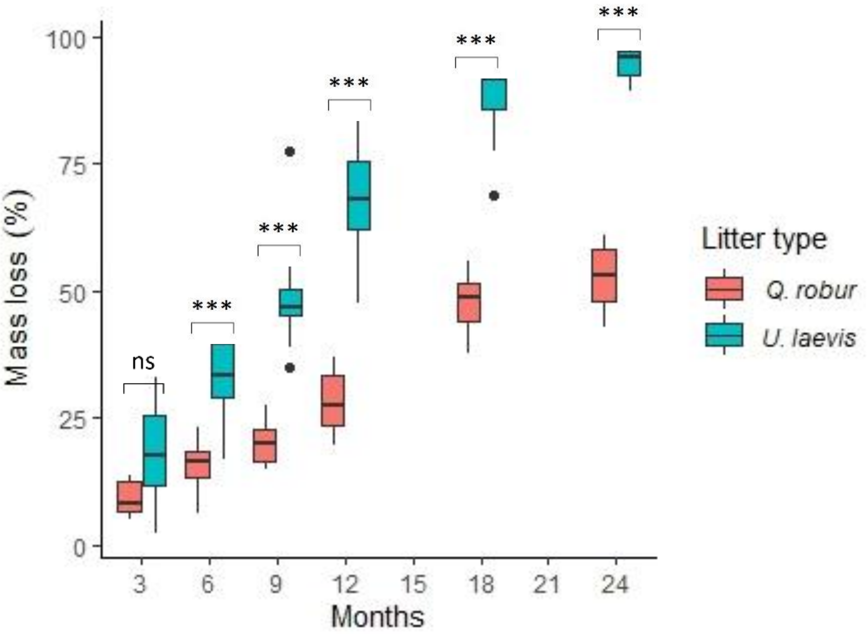

Figure 5.3 Leaf litter mass loss of *Q. robur* (n=10) and *U. laevis* (n=10) after 3, 6, 9, 12, 18, and 24 months of field incubation. Boxes represent 25–75% of values, black strips medians, whiskers 1.5 interquartile ranges, and black dots outliers. P-values of Wilcox test for differences between species per sampling month with Bonferroni correction are shown (ns= not significant, *** p ≤ 0.001).

5.4.3 Leaf litter decomposition of different tree species under different hydrological conditions

No significant differences were observed for *Q. robur* (Figure 5.4) or *U. laevis* (Figure 5.5) leaf litter under different hydrological conditions on the active floodplain. Although not significantly different, the mass loss of *Q. robur* leaf litter was higher in the low active floodplain than the high active floodplain for every three-month timestep over the first year of field incubation. For *U. laevis* leaf litter, the mass loss was higher in the low active floodplain for the first six months of field incubation. After two years, the average mass loss of *Q. robur* leaf litter on the low active floodplain (53% ± 7% SD) was slightly higher than on the high active floodplain (52% ± 5% SD). After two years, the average mass loss of *U. laevis* leaf litter on the low active floodplain (95% ± 2% SD) was also slightly higher than on the high active floodplain (94% ± 4% SD).

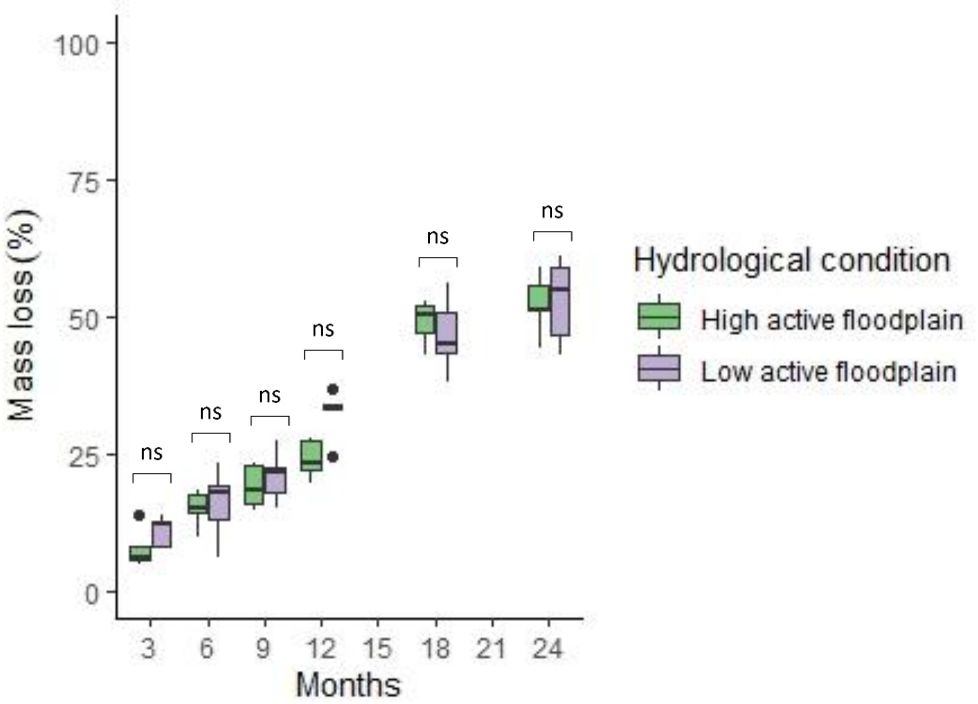

Figure 5.4 Leaf litter mass loss of *Q. robur* leaves measured under different hydrological conditions after 3, 6, 9, 12, 18, and 24 months of field incubation. Boxes represent 25–75% of values, black strips medians, whiskers 1.5 interquartile ranges, and black dots outliers. P-values of all Wilcox tests with Bonferroni correction for pairwise differences in mass loss between high active and low active floodplains are not significant (ns).

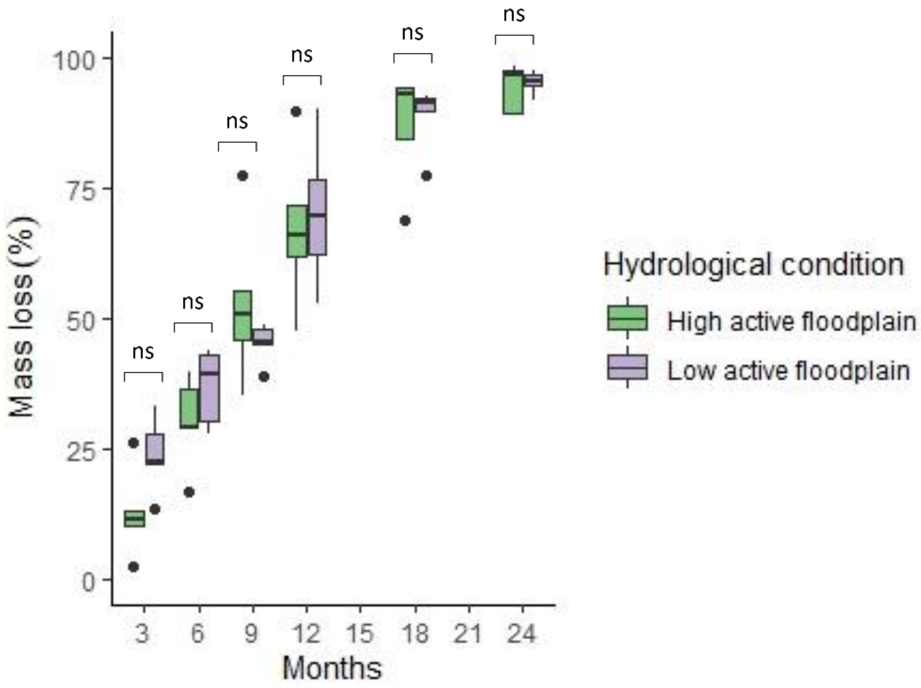

Figure 5.5 Leaf litter mass loss of *U. laevis* leaves measured under different hydrological conditions after 3, 6, 9, 12, 18, and 24 months of field incubation. Boxes represent 25–75% of values, black strips medians, whiskers 1.5 interquartile ranges, and black dots outliers. P-values of all Wilcox tests for pairwise differences in mass loss between high active and low active floodplains with Bonferroni correction are not significant (ns).

5.4.4 *Q. robur* decomposition and stand age

No significant differences were detected between the mass loss of *Q. robur* leaf litter in old forests or young plantations (Figure 5.6). Although not significant, the average mass loss of *Q. robur* leaf litter was higher in old forests (11% ± 3% SD) than young plantations (10% ± 3% SD) for the first three months. After two years, the mass loss of leaf litter in young plantations (56% ± 4% SD) was higher than the average mass loss of leaf litter in old forests (53% ± 7% SD).

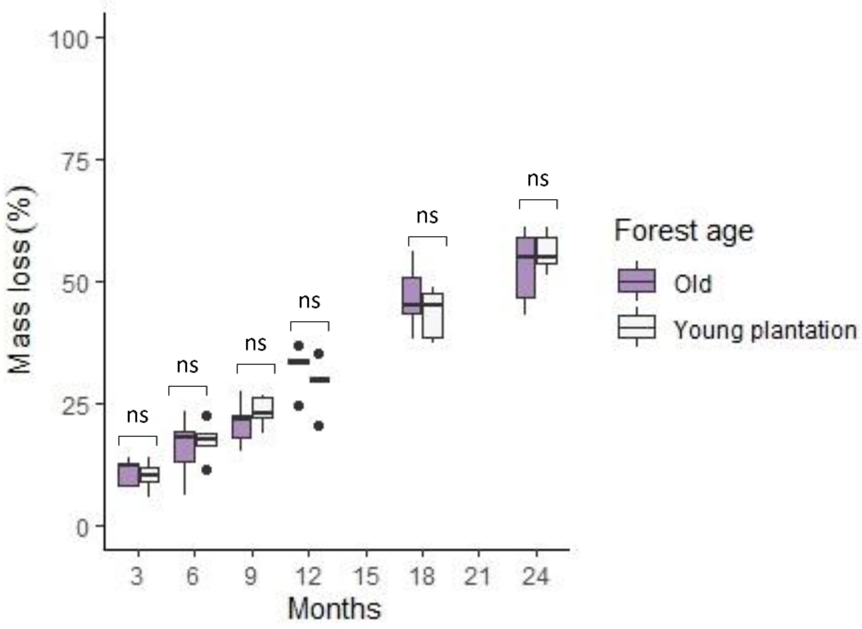

Figure 5.6 Leaf litter mass loss of *Q. robur* leaves measured in old forests and young plantations on the low active floodplain after 3, 6, 9, 12, 18, and 24 months of field incubation. Boxes represent 25–75% of values, black strips medians, whiskers 1.5 interquartile ranges, and black dots outliers. P-values of all Wilcox tests for pairwise differences in mass loss between old forests and young plantations with Bonferroni correction are not significant (ns).

5.5 Discussion

Interestingly, except for the C%, leaf litter properties of *Q. robur* and *U. laevis* did not show any significant differences. European studies on leaf litter decomposition have recorded a C content of 46 - 62% and an N content of 1 – 3% for *Q. robur* leaf litter (Davey et al. 2007, Ágoston-Szabó et al. 2017, Jurkšienė et al. 2017, Horodecki et al. 2019). Meanwhile, *U. laevis* leaf litter in the literature has a C content of 41 – 52% and an N content of 1 – 2% (Ágoston-Szabó et al. 2017, Horodecki et al. 2019). Our average values of 48 - 49% C and 1% N for *Q. robur* and 41 – 45% C and 1 – 2% N for *U. laevis* are thus within the expected range. Although not specifically *U. laevis*, elm leaves have a recorded ADL content of 15% (Taurbekov et al. 2021), which is similar to the ADL content range we measured for *U. laevis* (10 – 12% ADL). *Q. robur* leaf litter in the literature has an ADL content of 31 – 44% (Davey et al. 2007, Graca and Poquet 2014, Jurkšienė et al. 2017), however, our study observed an ADL content below the expected range (16%).

Although the mean ADL% is higher for *Q. robur* than *U. laevis* in our study, it is unexpected that the ADL values would not be significantly higher for *Q. robur* than for *U. laevis* leaves, because *Q. robur* is known to have a high ADL content and there should be some significant differences in properties between *U. laevis* and *Q. robur* to explain the differences in decomposition rates. These differences may be biophysical properties which are not measured in this study, but the large difference between our measured ADL% and that in the literature for *Q. robur* leads us to advise a repeated ADL extraction.

The mass loss results indicate that C can be stored longer in *Q. robur* leaves than in *U. laevis* leaves. Not only was the C% of *Q. robur* leaves greater than *U. laevis* leaves, the decomposition rate was also slower. After two years, only 53% of the *Q. robur* leaf litter was decomposed, while 95% of the *U. laevis* leaf litter was decomposed. It would take 7.9 years for the *Q. robur* leaf litter to be 95% decomposed, which is four times longer than it took the *U. laevis* leaf litter. These estimates assume an exponential rate of decomposition for leaf litter within leaf litterbags with a 1.6 mm x 1.8 mm mesh size and excludes macrofauna decomposers. Although a mesh size of 1-2 mm is most common in leaf litterbag studies, a mesh size greater than 2 mm is needed to allow for macrofauna decomposers (Karberg et al. 2008). Because our leaf litterbags have a mesh size smaller than 2 mm, the true decomposition rate of the leaf litter in the field without the influence of the leaf litterbags is likely higher. Further investigation into effects of macrofauna decomposers is thus recommended.

In a *Quercus-Fraxinus* woodland in the UK, the mass loss of *Q. robur* sapling leaf litter was approximately 35% after 16 months (Newsham et al. 1999), which is in between the amount measured for month 12 and 18 in our study. The study also estimated it would take up to 9.9 years for 95% of the leaf litter to decompose, which is 1.8 years more than we estimated. The *k*-values of *Q. robur* and *U. laevis* leaves in a postmining spoil heap in Poland were estimated to be 0.22 and 0.73 and respectively (Horodecki et al. 2019). In our study, *Q. robur* leaf liter had a faster rate at $k = 0.37$ and *U. laevis* leaf litter had a much faster rate at $k = 1.47$. If we calculate our decomposition *k*-rate with days instead of years, we estimate *Q.*

robur leaf litter *k* = 0.001 and *U. laevis* leaf litter *k* = 0.004. Decomposition rates of *Q. robur* and *U. laevis* leaf litter (calculated using days) in a forest with lotic conditions on a side arm of the Danube River were 0.005-0.007 and 0.013-0.020 for the respective species (Ágoston-Szabó et al. 2015). The range of *k* was dependent on mesh sizes of leaf litterbags, with decomposition rates being lower for leaf litterbags with a smaller mesh size of 0.04 mm compared to leaf litter bags with a larger mesh size of 1 mm. Decomposition rates of *Q. robur* and *U. laevis* leaf litter (calculated using days) in lentic conditions were 0.001 and 0.0063, respectively (Ágoston-Szabó et al. 2017). While our *Q. robur* leaf litter decomposition rates are the same as Ágoston-Szabó et al. 2017, they are lower than Ágoston-Szabó et al. 2015. The *U. laevis* leaf litter *k*-rates in our study are much lower than those reported in by Ágoston-Szabó et al. Differences in *k*-rates, especially for *U. laevis*, may be explained by potential differences in decomposer communities which might be influenced by different hydrological conditions. However, it is hard to conclude without further research into the decomposer communities present in the different locations.

A partial explanation for why no significant differences in leaf litter decomposition were detected between low and high active floodplain sites may be related to the environmental and site conditions during the study period. It should be noted that during the time of this study (December 2018-January 2021), drought conditions and low river water levels decreased the overall mean flooding days in most plots. While some of the low active floodplain plots were flooded, others were not. If flooding durations during the study period had been similar to the 35-year average amounts that we based our site selections on, perhaps the results of this study could have been different. The data we have collected, however, leads us to conclude that because there is no difference between the litter decomposition rates of *Q. robur* on the high or low active floodplain, no change to the decomposition rate in carbon cycle modeling of the leaf litter C pools in these forests with different hydrological conditions is required.

Leaf litter in young plantations and old forests in our study may have had no differences in decomposition rates, because the microclimates under the forest canopy could be similar. Most of the young plantations were dense and some had tall trees dispersed throughout the plots, which could affect temperature and water moisture and temperature.

The leaf litterbag method was developed in the 1960s in order to estimate mass loss and decomposition rates (Prescott 2010), however, the use of leaf litterbags has weaknesses in determining true decomposition amounts (Karberg et al. 2008). Leaf litterbag studies can tell how much C is lost from the leaf litterbags, but cannot give an indication of where the C goes in the ecosystem. In order to trace the C pathways (i.e. respiration back into the atmosphere by decomposers or humification and sequestration into the soil C pool), further analyses such as C isotope labelling could be undertaken (Steffens et al. 2015). Although the mass of the *U. laevis* leaf litter was greatly reduced in the leaf litter C pool, it is not known how much C still remains as biomass in decomposers or was sequestered into the soil C pool. More easily digestible plant material is important for the diverse decomposers that live in the forest. Not only the C storage, but also the promotion of biodiversity, should be considered during ecosystem service accounting. Therefore, both tree species and their leaf litters are beneficial to promoting ecosystem services on the floodplain.

5.6 Conclusions

These findings show that *Q. robur* leaf litter can store more C for longer periods of time than *U. laevis* leaf litter. However, lower decomposition rates also imply that *Q. robur* provides less fodder and nutrients to decomposer communities. Therefore, for the maximization of ecosystem services to promote both C storage and biodiversity, a mixture of both species is recommended for floodplain reforestation.

The decomposition of leaf litter in the HF forests studied here does not differ by flooding duration on the active floodplain or forest age, so from an ecosystem service accounting perspective, the low and high floodplain and young plantations or old forests provide an equal C cycling service in the leaf litter pool, and the decomposition rate in carbon budget modelling can be left constant for *Q. robur* in the different forest types.

5.7 Acknowledgements

This research was conducted within the interdisciplinary project MediAN (Mechanismen der Ökosystemdienstleistungen von Hartholz-Auenwäldern: Wissenschaftliche Analyse sowie Optimierung durch Naturschutzmanagement). This research was funded by the Bundesministerium für Bildung und Forschung (BMBF 01LC1601A). We would like to thank the landowners who participated in this study and the Biosphere reserve Niedersächsische Elbtalaue and Brandenburg Flusslandschaft Elbe. Thank you to Matilda J. Nicolaus and Lilli Hamm who helped with field work and lab work and Irene Tomaschewski who helped with lab work. Additionally, thank you to all MediAN colleagues.

6.

Chapter 6: Synthesis

The aim of this thesis was to estimate carbon stocks and sequestration rates of the vegetation of HF forests along the Middle Elbe, Germany, and to determine if different ecosystem services are provided by different forest types based on hydrological conditions, stand age, or stand structure. Carbon stocks of trees, shrubs, deadwood and leaf litter were all estimated in 2018/2019, thus setting a baseline stock for these carbon pools in HF forests of the Middle Elbe (Chapter 2). The highest carbon stock was estimated in the tree pool, specifically for the species *Q. robur*, which is why the carbon sequestration rates of *Q. robur* trees was the main focus of Chapter 3 and Chapter 4. In Chapter 5, we focused on the decomposition of leaf litter of the two dominant tree species (*Q. robur* and *U. laevis*) to look more deeply into carbon cycling rates.

6.1 Key findings

6.1.1 Carbon stocks of hardwood floodplain forests along the Middle Elbe: the influence of forest age, structure, species, and hydrological conditions (Chapter 2)

On the low active floodplain, the total carbon stock of the vegetation of young plantations was 50.2 ± 10.8 SE Mg ha^{-1} and thus significantly lower ($H = 10.5$, $p = .005$, $df = 2$) than that of old sparse (180.4 ± 26.6 SE Mg ha^{-1}) and of old dense forests (140.6 ± 11.6 SE Mg ha^{-1}). Pairwise comparisons found no significant difference between old sparse and old dense forests. Overall, the most carbon was stored in the tree carbon pool compared to the other carbon pools studied here. Young plantations had significantly less carbon stock in the tree pool than old dense or sparse forests ($H = 10.5$, $p = .005$, $df = 2$). Young plantations also had significantly less DWD than old dense forests ($H = 7.4$, $p = .009$, $df = 1$). No other significant differences comparing carbon pools between different forest types on the low active floodplain were found. A positive logarithmic relationship (r^2 = 0.741, $P < 0.001$) was found between forest age and carbon stock.

Carbon stocks of the vegetation in old dense forests under different hydrological conditions ranged from 140.5 ± 11.6 (low active floodplain) to 163.5 ± 8.3 SE Mg ha^{-1} (high active floodplain). No significant differences between the total carbon stock or any other carbon pool of old dense forests with different hydrological conditions were found. There was no significant effect of hydrological conditions on carbon stocks of old forests after controlling for forest age, $F_{3, 26}$ = 0.54, $p > 0.05$, partial η^2 = 0.10.

Q. robur stored more carbon than any other species in all hydrological conditions. On the active floodplain, *Ulmus* spp. stored the second highest amount of carbon, whereas in the seepage water zone and on tributary floodplains, *Ulmus* spp. were rare and *Carpinus betulus* stored the second highest amount of carbon.

carbon stocks developed positively with age and the carbon storage function of old forests did not significantly vary with forest structure on the low active floodplain or according to different hydrological conditions. Old forests on the low active floodplain, the high active floodplain, the seepage water zone, and tributaries fulfill the same ecosystem function of carbon storage of the vegetation, and the locations are therefore at first glance equally suitable for reforestation campaigns.

6.1.2 Adapting a *Quercus robur* allometric equation to quantify carbon sequestration rates on the Middle Elbe floodplain (Chapter 3)

The adaptation of a 2-parameter *Q. robur* allometric equation (based on tree height and DBH) which estimates tree volume to a 1-parameter equation (based only on DBH) which estimates above- and below-ground carbon stock was deemed suitable for reconstructing CSRs of *Q. robur* back in time without the need for past tree height measurements.

An almost perfect linear relationship (Pearson $R^2 = 0.998$) was observed between CSR and basal area increment (BAI). Using a dataset of 966 *Q. robur* trees to compare carbon stock estimates with both DBH and H parameters to the carbon stock estimate with only the DBH parameter, we calculated the root mean square error (RMSE) for all trees and for trees in different DBH size classes. Overall, the RMSE was equal to 1. The greater the DBH, the greater we observed the RMSE to be. Trees with a 5cm ≤ DBH < 35cm had a RMSE of 0.12, trees with a 35cm ≤ DBH < 70cm had a RMSE of 0.97, and trees with a 70cm ≤ DBH < 140 cm had a RMSE of 2.6. Therefore, as DBH increases, the variability between the observed and predicted carbon stock values also increases. Overall, the two models were highly correlated ($R^2 = 0.972$). We conclude that the developed 1-parameter equation is highly suitable for estimating CSRs based on DBH only.

6.1.3 Droughts decrease and floods increase carbon sequestration rates of *Quercus robur* in hardwood floodplain forests (Chapter 4)

On the low active floodplain, dominant *Q. robur* trees in old forests sequestered an average of 18.4 ± 1.1 (SE) Kg tree^{-1} year^{-1}, which was significantly more carbon ($p < 0.01$, Wilcoxon ranksum test) than the average 8.7 ± 0.6 (SE) Kg tree^{-1} year^{-1} sequestered by dominant trees in young plantations.

There was a high variation in the CSRs of the old forests in each hydrological condition over the years. There was also a high variability between the ten replicate trees measured in each hydrological condition per year. The lowest average CSR (9.3 Kg tree^{-1} year^{-1}) was recorded in the seepage water zone in the drought year of 1996, while the highest average CSR (28.6 Kg tree^{-1} year^{-1}) was recorded on the high active floodplain in the flood year of 1994.

The CSR of dominant *Q. robur* trees of old forests significantly differed between the high active floodplain and the seepage water zone. The highest CSR was observed in trees on the high active floodplain, which showed an average CSR of 18.6 ± 1.7 (SE) Kg tree^{-1} year^{-1}. The individual trees in the seepage water zone showed the lowest overall CSR, with an average CSR of 13.1 ± 1.1 (SE) Kg tree^{-1} year^{-1}. *Q. robur* trees on the low active floodplain and on tributary floodplains showed a similar average CSR of 16 ± 1.4 (SE) Kg tree^{-1} year^{-1} and 16.2 ± 1.7 (SE) Kg tree^{-1} year^{-1}, respectively.

The CSR of dominant *Q. robur* trees was significantly greater ($p \leq 0.05$) during flood years than during drought years on the low active floodplain, the high active floodplain and the seepage water zone. On the low active floodplain, the CSR of *Q. robur* trees was not significantly lower during drought years than during control years ($p > 0.05$). In contrast to this, the CSR was significantly lower during drought years than during control years ($p \leq 0.05$) on the high active floodplain. In the seepage water zone, the CSR of the individual trees was not significantly different between control and drought years. On the tributary, CSRs of the individual trees did not differ between drought, flood, and control years.

We conclude that individual dominant old *Q. robur* trees on the active floodplain can sequester over twice as much carbon as individual dominant young trees and are therefore important CO_2 sinks. Dominant old *Q. robur* trees on the active floodplain and tributaries have a higher CSR than dominant old *Q. robur* in the seepage water zone, so planting trees on the active floodplain and tributaries may provide a higher ecosystem service in terms of carbon sequestration than planting trees in the seepage water zone. This also implies that de-embankments and dike relocations may increase the potential CSR of individual *Q. robur* trees by between 20 and 40%. This is a clear co-benefit of de-embankments which nowadays are carried out to increase the area of active floodplains and to decrease the risks of catastrophic floodings to human societies (Damm 2013, BMU and BfN 2021). Additionally, winter and spring flooding is shown to be beneficial to the radial growth of *Q. robur*, which implies that these older trees are well adapted to and even benefit from the flooded conditions. Drought was shown to decrease CSR significantly on the high active floodplain, but old trees were resistant to drought in all other hydrological conditions. We conclude that floodplains are well-suited areas for reforestation to aid in the reduction of atmospheric $C0_2$ because trees in these areas have a high CSR even under severe conditions which are predicted to become more common with climate change in the future.

6.1.4 Leaf litter decomposition of *Quercus robur* and *Ulmus laevis* in hardwood floodplain forests on the Middle Elbe floodplain (Chapter 5)

For the different forest types, no significant differences ($p > 0.05$) in the C%, N%, C:N ratio, NDF%, ADF%, ADL%, or ADL:N of *Q. robur* or *U. laevis* leaves were observed. On average, the leaf litter of *Q. robur* had a higher carbon content (48 – 49%) than that of *U. laevis* (41 – 45%) The only significant difference detected between the tree species' leaf litter properties was for C%, where *Q. robur* leaves are higher ($p \leq 0.05$) than *U. laevis*.

The mass loss of *U. laevis* was significantly ($p \leq 0.001$) greater than *Q. robur* at every collection time over the two years of field incubation except for month three. Although not significantly different, the mass loss of *U. laevis* was still greater (18% ± 9% SD) than *Q. robur* (9% ± 3% SD) after three months of field incubation. After two years, the mass loss of *U. laevis* leaf litter was 95 ± 3% SD while the mass loss of *Q. robur* leaf litter was only 53% ± 6% SD. Over the two years, *Q. robur* leaf litter had an estimated *k*-value of 0.38 while *U. laevis* leaf litter had an estimated *k*-value of 1.47. It would take an estimated 7.9 years for 95% of *Q. robur* leaf litter to decompose.

No significant differences were observed for *Q. robur* or *U. laevis* leaf litter under different hydrological conditions on the active floodplain. Although not significantly different, the mass loss of *Q. robur* was higher in the low active floodplain than the high active floodplain for every three-month timestep over the first year of field incubation. For *U. laevis*, the mass loss was higher in the low active floodplain for the first six months of field incubation. After two years, the average mass loss of *Q. robur* on the low active floodplain (53% ± 7% SD) was slightly higher than on the high active floodplain (52% ± 5% SD). After two years, the average mass loss of *U. laevis* on the low active floodplain (95% ± 2% SD) was also slightly higher than on the high active floodplain (94% ± 4% SD).

No significant differences were detected between the mass loss of *Q. robur* leaf litter in old forests or young plantations. Although not significant, the average mass loss of *Q. robur* leaf litter was higher in old forests (11% ± 3% SD) than young plantations (10% ± 3% SD) for the first three months. After two years, the mass loss of leaf litter in young plantations (56% ± 4% SD) was higher than the average mass loss of leaf litter in old forests (53% ± 7% SD).

These findings show that *Q. robur* leaf litter can store more carbon for longer periods of time than *U. laevis* leaf litter. However, lower decomposition rates also imply that *Q. robur* provides less fodder and nutrients to decomposer communities. Therefore, for the maximization of ecosystem services to promote both carbon storage and biodiversity, a mixture of both species is recommended for floodplain reforestation. The decomposition of leaf litter in the HF forests studied here does not differ by flooding duration on the active floodplain or forest age, so from an ecosystem service accounting perspective, the low and high floodplain and young plantations or old forests provide an equal carbon cycling service in the leaf litter pool. The data collected here also implies that the decomposition rate of *Q. robur* leaf litter in these different forest types can remain constant in carbon budget models.

6.2 Challenges, limitations, and recommendations for future research

6.2.1 Upscaling carbon sequestration rates

Fulfilling the MediAN project task of providing a CSR estimate for all forest types in Megagrams (equivalent to metric tons) of carbon per hectare per year (Mg ha^{-1} year^{-1}) was challenging. Our method to use tree cores to estimate CSRs of *Q. robur* limited our ability to upscale to the hectare level for all strata classes researched within the MediAN project. In order to upscale properly with this method, we would need multiple tree cores from every tree species (*Quercus*, *Ulmus*, *Fraxinus*, *Carpinus*, *Acer*, *Corylus*, *Fagus*, *Picea*, *Pinus*, *Populus*, *Prunus*, *Salix*, *Sorbus*, and *Tilia spp.*) in every tree social class (either pre-dominant, dominant, co-dominant, dominated, and overshadowed (Kraft 1884) or dominant, co-dominant, dominated, and suppressed (Klesse et al. 2016)), within every forest strata class replicate plot (at least five different plot replicates within seven different strata classes were defined for the MediAN project). While tree rings from *Q. robur* are more easily discernible and thus measurable, other species such as *U. laevis* are more difficult to measure considering their irregular growth at 1.3 m above ground level (where DBH is measured) and internal vessel structure. Tree cores from dominant and suppressed *U. laevis* were analyzed during the course of this thesis, however, especially for suppressed trees, annual rings were largely indistinguishable and thus not able to be properly cross-dated. The quality of annual reconstructions of other tree species besides *Q. robur* is questionable and was thus omitted here.

With the data collected in this body of research, we can estimate the CSRs of the different forest types by dividing the carbon stock estimated in 2018/2019 by the estimated age of the forests. Upscaling CSRs to the hectare scale for the Middle Elbe region in every forest type we studied has been conducted (Figure 6.1 and Figure 6.2). Using this method, the CSR of trees in young plantations is 167% higher than the estimate for old forests on the high active floodplain (the highest CSR estimated for old forests). For forests of different developmental stages on the low active floodplain, we estimate a significantly ($p \leq 0.05$) higher average CSR of 2.17 Mg ha^{-1} year^{-1} ± 0.86 SD for young plantations, than either old dense (1.03 Mg ha^{-1} year^{-1} ± 0.2 SD) or old sparse (1.18 Mg ha^{-1} year^{-1} ± 0.22 SD) forests on the low active floodplain. The CSR of old dense forests differing in hydrological conditions do not significantly differ ($p \geq 0.05$), and we estimate a CSR of 1.3 Mg ha^{-1} year^{-1} ± 0.39 SD on the high active floodplain, 1.21 Mg ha^{-1} year^{-1} ± 0.36 SD on the seepage water zone, and 1.16 Mg ha^{-1} year^{-1} ± 0.35 SD on tributaries. The average range of 1.03-2.17 Mg ha^{-1} year^{-1} is within the 0.15-4 Mg ha^{-1} year^{-1} range estimated for HF forests in Europe (Vila et al. 2013, Rieger et al. 2017).

However, there are some shortcomings of this CSR estimation approach to be aware of. First, not all of the trees which have grown in the forests and the deadwood which could have accumulated over the years may be included in the old forest CSR estimates. Stumps from large harvested trees and the stacking and removal of deadwood was observed during fieldwork campaigns. The removal of trees and deadwood from the forest plots could greatly decrease the carbon stock estimated in 2018/2019, and therefore the CSR estimate. If no anthropogenic intervention occurred and the HF forests were left in a natural state, we can assume that older forests would have an overall higher CSR than what we present here. A second potential downfall of this method is that the CSR of the young plantations is not likely to continue for long as the stand ages, because many of the trees growing will be shaded by the dominant competitors. Competition from herbaceous and woody vegetation can reduce tree stem diameter and height growth as well as decrease the survival rates of *Q. robur* in plantations (Jensen and Löf 2017), thus potentially reducing CSRs.

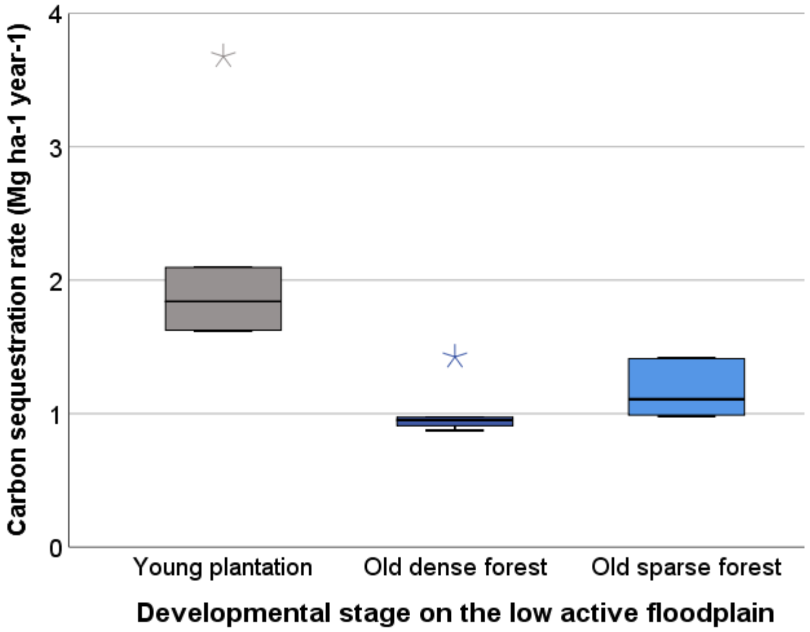

Figure 6.1 Carbon sequestration rates estimated for forests of different developmental stages on the low active floodplain of the Middle Elbe River. Boxes represent 25–75% of values, black strips medians, whiskers 1.5 interquartile ranges, and asterisks outliers.

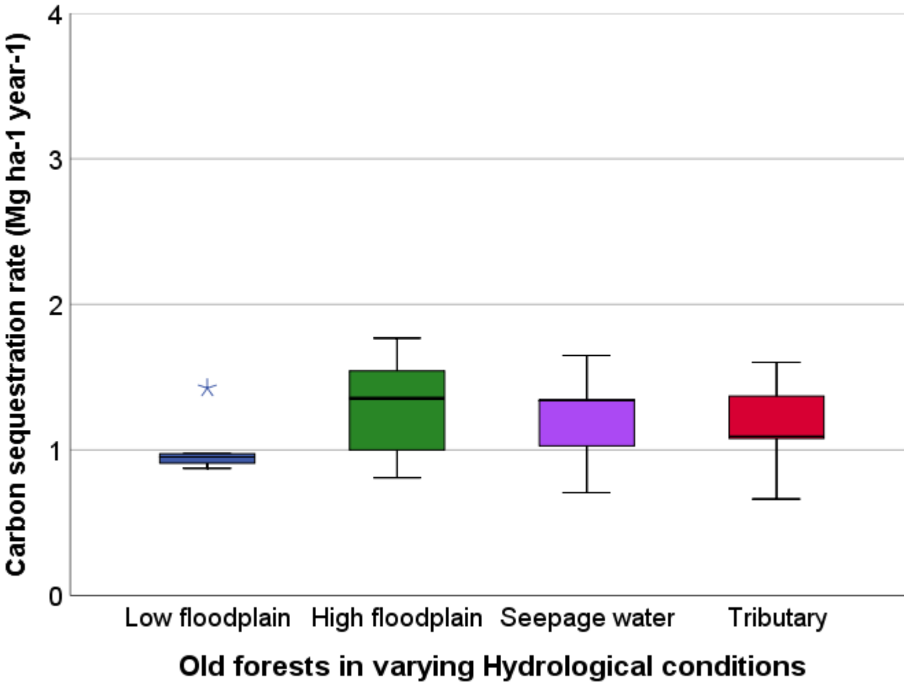

Figure 6.2 Carbon sequestration rates estimated for old forests in different hydrological conditions along the Middle Elbe River. Boxes represent 25–75% of values, black strips medians, whiskers 1.5 interquartile ranges, and asterisks outliers.

Long-term forest studies which estimate CSRs at the hectare level mainly rely on at least two inventory campaigns: the first to establish a baseline carbon stock and the second to estimate the carbon stock after a certain amount of years have passed (UNFCCC 2015a). The change in the carbon stock divided by the surpassed years is thus the average CSR. Within this body of research, we have established a baseline carbon stock of the forests in each strata class, and we therefore recommend a second inventory of the same plots to be conducted in the future. Because we conducted the inventory in 2018/2019, we recommend a second carbon stock inventory campaign following the same methods established here in Chapter 2 to be conducted in 2028/2029. CSRs are not a constant, especially with changing environmental conditions and extreme events such as floods and droughts. Continued monitoring of the plots established during this research can provide valuable insight into how the trees react to changing climatic and hydrological conditions. The assimilation of repeated biomass observations can also decrease uncertainty and bias in all ecosystem carbon pools (Smallman et al. 2017).

Another approach to quantifying carbon stocks and CSRs is to use remote sensing techniques. Advancements in the field of remote sensing make it possible to estimate tree and deadwood volumes above- and below-canopy. Carbon stock estimates can then be calculated from the volume estimates. Terrestrial laser scanning using light detection and ranging (LiDAR) as well as the development of unmanned aerial vehicles (UAVs) may increase the efficiency of field campaigns to measure large forest areas (Dassot et al. 2011, Wallace et al. 2014). Combining 3D point clouds with optical data such as hyperspectral imagery can also improve forest analysis and carbon stock estimation by allowing for the differentiation between different species and between vital and dead trees, as well as allowing for the visualization of the structural complexity of forests (Camarretta et al. 2019). Remote sensing techniques, however, require ground-truthing to analyze any potential error or bias (Camarretta et al. 2019). The carbon stock data presented in this dissertation (Chapter 2) can be used as ground-truth data for a future remote sensing approach to estimate carbon stocks and sequestration rates of HF forests.

6.2.2 Carbon cycling models

We have estimated carbon stocks, have provided preliminary estimates of CSRs, and investigated decomposition of leaf litter, however, a holistic understanding of carbon cycling pathways in HF forests is still open to further research. To trace carbon pathways, various models such as the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3) (Kurz et al. 2009) and CO2FIX V.2 (Masera et al. 2003) have been developed. These models can separate different carbon pools and estimate the stocks and flows between the pools based on different decomposition rates. Input data of decomposition rates for all carbon pools included in the models are thus required. Our research provides decomposition rates of the leaf litter of *Q. robur* and *U. laevis* (excluding decomposition by macrofauna), but decomposition rates of other tree species and mixtures of tree species as well as the change of the decomposition rate if macrofauna were included should also be quantified. Also, the decomposition rate of other carbon pools such as deadwood needs to be quantified. The carbon budget models can also account for forest management such as the harvesting of trees and traces the pathways the carbon after removal from the forest (e.g. combusted and released into the atmosphere or stored for a longer time period in products such as boards for construction). This is valuable information for understanding how long the carbon sequestered by the forest remains out of the atmosphere and allows for the proper quantification of the ecosystem service of climate mitigation (Pilli et al. 2013).

6.2.3 Plot variability

Although we have attempted to remove the variability of the plots in each forest type class by choosing similar replicates, some variations could still exist that may interfere with and therefore limit the full validity of our conclusions. All forest stands are not alike because they can have different species compositions, tree densities, structures, harvesting amounts, flooding durations, edaphic conditions, and other abiotic and biotic conditions and interactions. Although we have chosen strata class replicates based on floodplain compartments and developmental stages, other variations in the site conditions of the replicates may also influence carbon stocks, CSRs, and leaf litter decomposition processes. Harvesting schemes and management, for instance, could have a great impact on carbon storage and the sequestration rates of dominant trees left in the plots. These plot variations are thus important to be aware of when drawing conclusions from the data we have collected.

6.2.4 Oak Processionary Moth outbreak

A great challenge during tree inventory was the presence of Oak Processionary Moths (*T. processionea*) and their toxic hairs which caused histamine reactions. In some plots, such as in the young plantations in Lenzen, nests were observed on most trees, and many of the nests were at breast height, which made measuring DBH a challenge. We do not know how much of an impact the presence of defoliators, such as *T. processionea*, have on the CSRs of forests, however defoliation can weaken trees and leave them vulnerable to other stressors and further attacks (Tomlinson et al. 2015). Also, defoliation in combination with drought stress increases the risk of desiccation damage to *Quercus* trees by increasing water loss and reducing water uptake capacity, thus intensifying the negative effects of drought on tree growth (Gieger and Thomas 2002). The overall photosynthetic capacity of trees is thus likely to decrease in response to defoliation and stress, which would also mean a decrease in the CSR of the affected trees. Further investigations into how defoliation in combination with drought stress on the floodplains is therefore recommended.

6.3 Recommendations for reforestation of floodplains

All floodplain compartments studied here (the low and high active floodplain, the seepage water zone, and tributary floodplains) provide a high carbon storage function and are suitable for reforestations. While plantations may have higher CSRs than older forests, we observed that the carbon storage function increases with forest age until at least 200 years old (the oldest forest we studied here), while at the same time providing habitat to a high diversity of biota that only thrive in old forests (Ónodi et al. 2021). Although a higher CSR may provide a higher service in terms of climate mitigation, it is not the only ecosystem service to be factored into management decisions. This is especially true for endangered habitats such as HF forests. Therefore, allowing the plantations to age on the floodplain rather than harvesting and replanting when the CSR is at a maximum is highly recommended.

Q. robur, the dominant species in HF forests of the Middle Elbe, can provide a higher carbon sequestration service on the active floodplain, and thus reforestation of the active floodplain with this species is preferred. However, monoculture *Q. robur* plantations are not recommended because they are more susceptible to insect infestations such as *T. processionea*. It is highly recommended that measures are taken to control the current *T. processionea* infestations, and that future *Q. robur* saplings are checked for any signs of infestation before planting. The inclusion of more flood-tolerant species such as *Ulmus laevis* are also recommended on low active floodplain sites. While *Fraxinus excelsior* is a typical HF species, it may not be recommendable to plant considering the consequences of Dutch Elm disease. *Fraxinus pennsylvanica* seems to be more tolerant to the disease and was observed to thrive on the low active floodplain of the Middle Elbe, but it is not a native species in Europe and therefore the benefits of planting this species must be weighed against the risks (Pötzelsberger et al. 2020). *Carpinus betulus*, which is less tolerant to flooding, is recommended in the seepage water zone and less frequently flooded areas of tributary floodplains. Species mixtures are recommended over monocultures because they can increase productivity and ecosystem stability and are more resistant to defoliation during insect outbreaks (Larsen 1995, Pretzsch et al. 2013, Guyot et al. 2019).

Tree age can play a role in how well individual trees respond to flooded conditions, and thus impact tree vitality and the CSR potential of HF forests. Although we observed that flooding increases the CSR of established old *Q. robur* trees, the same beneficial growth may not be observed for young trees, especially saplings. In a comparison between flooded and unflooded hardwood forests, the density of saplings was higher in unflooded forests (Tremolieres et al. 1998), indicating that saplings prefer less flooded conditions. The presence of hardwood saplings also has been observed to decrease with increasing inundation duration, with an inundation duration limit of 30 days for *Q. robur* saplings (Vreugdenhil et al. 2006). This must be taken into account during reforestation planting campaigns which plant saplings in frequently flooded areas. Also, the encouragement of natural succession and the implementation of protection measures against herbivory are recommended (Schindler et al. 2021).

6.4 Conclusions and Outlook

By quantifying carbon stocks, sequestration rates, and leaf litter decomposition in HF forests along the Middle Elbe River, Germany, we conclude that HF forests provide the valuable ecosystem services of carbon storage and sequestration in all floodplain compartments. Old forests provide a higher carbon storage function than young plantations, while young plantations may provide higher CSRs than old forests. In terms of carbon storage, old forests on the low and high active floodplain as well as in the seepage water zone and tributaries provide the same service. In terms of carbon sequestration of *Q. robur* (the tree species responsible for the highest amount of carbon storage in HF forests), dominant trees on the active floodplain provide a higher service than trees in the seepage water zone. Also considering climate change projections, HF forests with ample access to water and flooding can provide a higher CSR service than forests located behind dikes in the seepage water zone. Therefore, reforesting the current active floodplain and increasing the active floodplain area through dike relocations may provide a higher CSR service in the future. Although we have now quantified carbon stocks of HF forests in 2018/2019 and set suitable baselines, another carbon stock inventory in the future is recommended to estimate CSRs in Mg ha^{-1} $year^{-1}$.

This research increases the understanding of how HF forests may act as carbon sinks and contribute to atmospheric $C0_2$ reductions. Reforestation to increase terrestrial carbon sinks can act as a natural climate solution to help reduce atmospheric carbon, however, when compared to gross CO_2 emissions, it is not a feasible climate solution on its own. If we put the calculated carbon sequestered in the vegetation of HF forests into perspective by comparing it with annual $C0_2$ emissions in Germany, the ability of HF forest vegetation to offset emissions and reduce atmospheric $C0_2$ is minor. Germany reported 163.5 million Mg of CO_2 emissions from the transportation sector alone in 2019 (EEA 2021). This is equivalent to 44.6 million Mg of carbon (the molar mass of one carbon atom is 12 while the molar mass of two oxygen atoms is 32). If the vegetation in one hectare of old HF forest sequesters an estimated 1.3 Mg $year^{-1}$, this would mean that 34.3 million hectares (343,000 km^2) worth of HF forest vegetation would be needed to offset Germany's annual transport-related emissions. It should be kept in mind that the carbon sequestered by the soil would also have to be factored in and reduce the total area of HF forests needed. However, considering Germany is 357,588 km^2 and only 4.5% of the land (16,092 km^2) is classified as floodplain (BMU and BfN 2021), it is impossible for Germany to offset emissions at the 2019 level through reforestation alone. To prevent excess accumulation of CO_2 in the atmosphere and potential catastrophic destabilization of the earth system, a reduction of fossil fuel use as well as an increase in other carbon sinks is imperative.

HF forests are valuable not only for their carbon sink potential, but also for other ecosystem services they provide. Along with carbon storage and sequestration, enlargement and reforestation of the floodplain can provide other important services which should be taken into account while determining suitable floodplain management measures. HF forests provide habitat, flood control, reduce erosion, alleviate air and soil pollution, remove excessive nutrients from agricultural runoff, and improve water quality (Dixon et al. 2016, Hornung et al. 2019). Data that was collected by the MediAN project partners in each HF site is being compiled and the analysis of other ecosystem services of HF forests is currently in progress.

7. Appendices

7.1 Appendix A: Chapter 2

Table A1. Tree stem volume equations for all species inventoried in the Middle Elbe study area are shown, taken from Zianis et. al., 2005 (Appendix C). The country where the equation originates from and the units for volume (V), diameter at breast height (D), and the height (H) of individual trees are shown.

Tree		Unit			Equation	Parameters					
species		V	D	H		a	b	c	d	e	f
Acer spp.	NT	dm^3	cm	m	$D^a \cdot H^b \cdot \exp(c)$	1.89756	0.97716	-2.94253			
Alnus glutinosa	NT	dm^3	cm	m	$D^a \cdot H^b \cdot \exp(c)$	1.85749	0.88675	-2.5222			
Betula pendula	NT	dm^3	cm	m	$D^a \cdot H^b \cdot \exp(c)$	1.8906	0.26595	-1.07055			
Carpinus spp.	NT	dm^3	mm	m	$a \cdot D^{(b+c)} \cdot H^d$	0.00021491	2.258957614	0.001411006	0.60291075		
Corylus avellana	NO	dm^3	cm	m	$a+b \cdot D^2+c \cdot D^2 \cdot H+d \cdot D \cdot H^2+e \cdot H^2$	-1.86827	0.21461	0.01283	0.0138	-0.06311	
Fagus sylvatica	NT	dm^3	cm	m	$D^a \cdot H^b \cdot \exp(c)$	1.55448	1.5588	-3.57875			
Fraxinus excelsior	NT	dm^3	cm	m	$D^a \cdot H^b \cdot \exp(c)$	1.95277	0.77206	-2.48079			
	GER	m^3	m	m	$a \cdot H \cdot D^2$	0.502					

Picea abies											
Pinus sylvestris	GER	m^3	cm	m	$a*D^b*H^c$	0.000056537	1.960466	0.894433			
Populus spp.	NT	dm^3	mm	m	$a \cdot D^{(b+c)} \cdot H^d$	0.0009507	1.895629295	0.001650837	0.8392146		
Prunus avium	BE	m^3	cm	m	$a+b \cdot D+c \cdot D^2+d \cdot D^3 +e \cdot H+f \cdot D^2 \cdot H$	-0.002311	-0.00117728	0.000149061	-7.8058E-06	0.00033282	0.000031526
Quercus robur	NT	dm^3	cm	m	$D^a \cdot H^b \cdot \exp(c)$	2.00333	0.85925	-2.86353			
Ulmus spp.	NT	dm^3	cm	m	$D^a \cdot H^b \cdot \exp(c)$	1.942950	1.292290	-4.200640			

Table A2. Specific wood densities for tree species inventoried in the HF forests of the Middle Elbe and sourced from the global wood density database (Zanne et. al 2009).

Tree species	Specific wood density (g cm^{-3})
Acer spp.	0.525
Alnus glutinosa	0.439
Betula pendula	0.525
Carpinus betulus	0.706
Corylus avellana	0.517
Fagus sylvatica	0.585
Fraxinus excelsior	0.560
Picea abies	0.370
Pinus sylvestris	0.422
Populus alba	0.353
Prunus avium	0.474
Quercus robur	0.560
Ulmus spp.	0.551

Table A3 Mean (± SE, *n*=5), minimum and maximum carbon stocks of old hardwood floodplain forests on the active floodplain with different ages and forest structures. The total carbon stock combines five carbon pools: The above-and belowground carbon stocks (AGC and BGC) of trees, shrubs, and standing dead trees (SDT) ≥ 5 cm diameter at breast height, as well as downed woody debris (DWD) and leaf litter. The mean, standard error of the mean (SE), minimum (min), and maximum (max) values are shown for the five replicate plots per forest type. All carbon stocks are presented in Megagrams carbon per hectare (Mg ha^{-1}).

Forest age and structure		Total C stock	Tree	Shrub	SDT	DWD	Leaf litter
Young plantation	Mean	50.2	42.9	0.9	1.3	1.8	3.3
	SE	10.8	10.4	0.8	0.5	0.7	0.6
	Min	29.2	19.6	0.0	0.0	0.4	1.9
	Max	88.2	77.7	4.0	2.8	3.6	5.0
Old dense	Mean	140.6	108.6	3.2	14.3	11.8	2.8
	SE	11.6	8.8	1.3	7.1	3.3	0.4
	Min	116.2	82.6	0.8	0.0	5.6	1.8
	Max	181.8	133.6	7.9	32.9	22.1	4.0
Old sparse	Mean	180.4	139.9	4.0	26.9	7.2	2.4
	SE	26.6	14.8	1.9	13.3	3.3	0.5
	Min	140.1	109.0	0.0	3.4	1.7	1.5
	Max	282.4	193.7	9.7	77.5	19.3	4.0

Table A4 Mean (± SE, n=5), minimum and maximum carbon stocks of old hardwood floodplain forests at different hydrological conditions. The total carbon stock combines five carbon pools: The above-and belowground carbon stocks (AGC and BGC) of trees, shrubs, and standing dead trees ≥ 5 cm diameter at breast height, as well as dead woody debris and leaf litter. The mean, standard error of the mean (SE), minimum (min), and maximum (max) values are shown for the five replicate plots per hydrological condition. All carbon stocks are presented in Megagrams carbon per hectare (Mg ha^{-1}).

Hydrological condition		Total C stock	Tree	Shrub	SDT	DWD	Leaf litter
Low active floodplain	Mean	140.6	108.6	3.2	14.3	11.8	2.8
	SE	11.6	8.8	1.3	7.1	3.3	0.4
	Min	116.2	82.6	0.8	0.0	5.6	1.8
	Max	181.8	133.6	7.9	32.9	22.1	4.0
High active floodplain	Mean	163.5	127.7	5.7	17.6	9.7	2.8
	SE	8.3	8.7	2.0	13.0	5.3	0.3
	Min	140.0	104.4	2.6	0.0	0.8	2.4
	Max	185.1	151.8	12.6	68.2	29.7	3.8
Seepage water zone	Mean	145.3	130.3	2.6	3.0	5.0	4.4
	SE	11.8	14.7	1.1	1.6	1.9	0.3
	Min	124.4	104.5	0.0	0.0	0.4	3.9
	Max	190.0	184.1	5.5	8.7	10.9	5.5
Tributary	Mean	146.5	127.1	0.7	6.3	8.2	4.2
	SE	20.4	18.4	0.7	1.6	3.9	0.8
	Min	88.5	78.1	0.0	0.4	2.3	2.2
	Max	189.0	168.4	3.4	10.4	23.4	6.0

7.2 Appendix B: Chapter 4

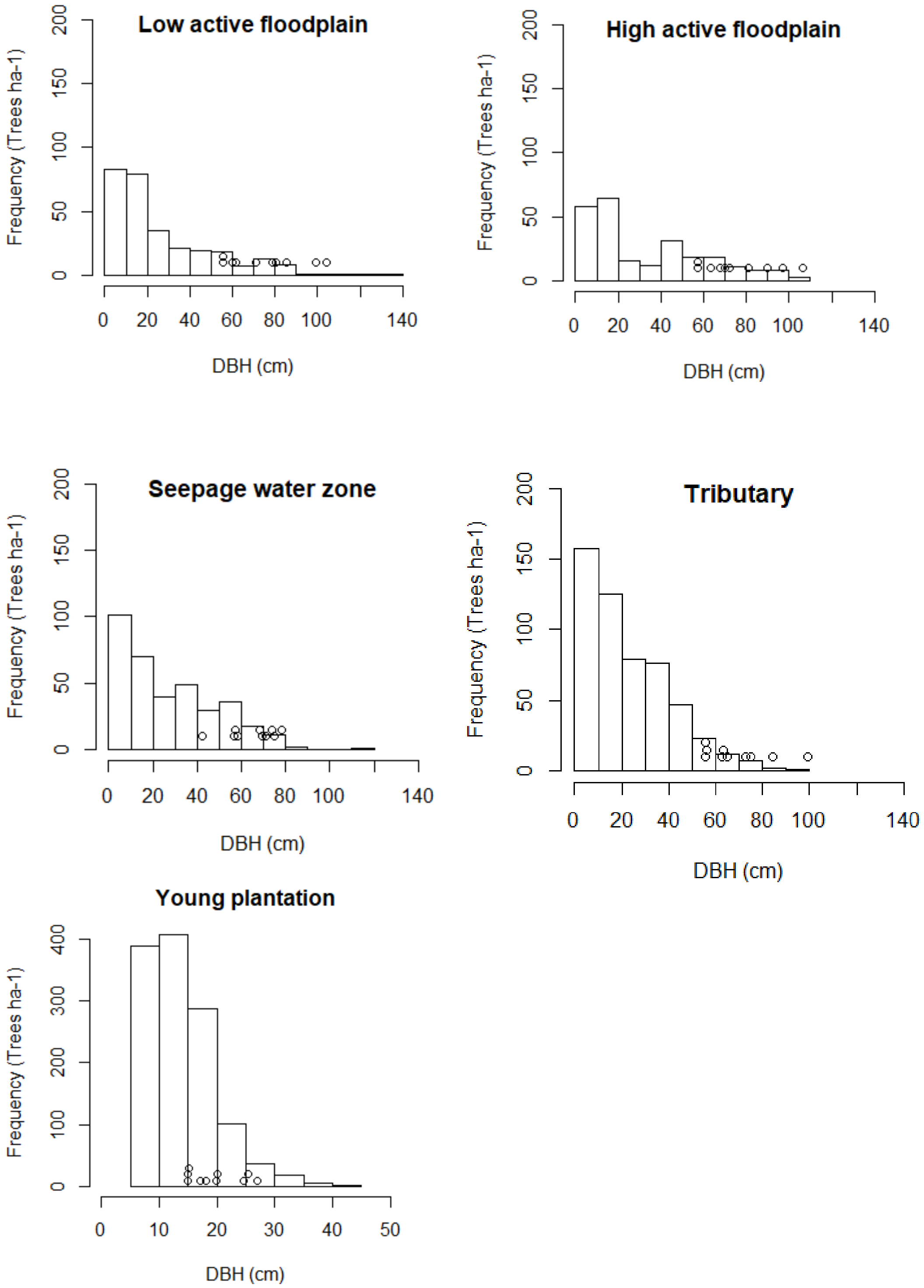

Figure B1 Frequency distributions of the diameter at breast height (DBH) of all trees in each forest type. Ten dominant *Quercus robur* trees per hydrological condition were selected for coring. Circles indicate the DBH of each sampled tree.

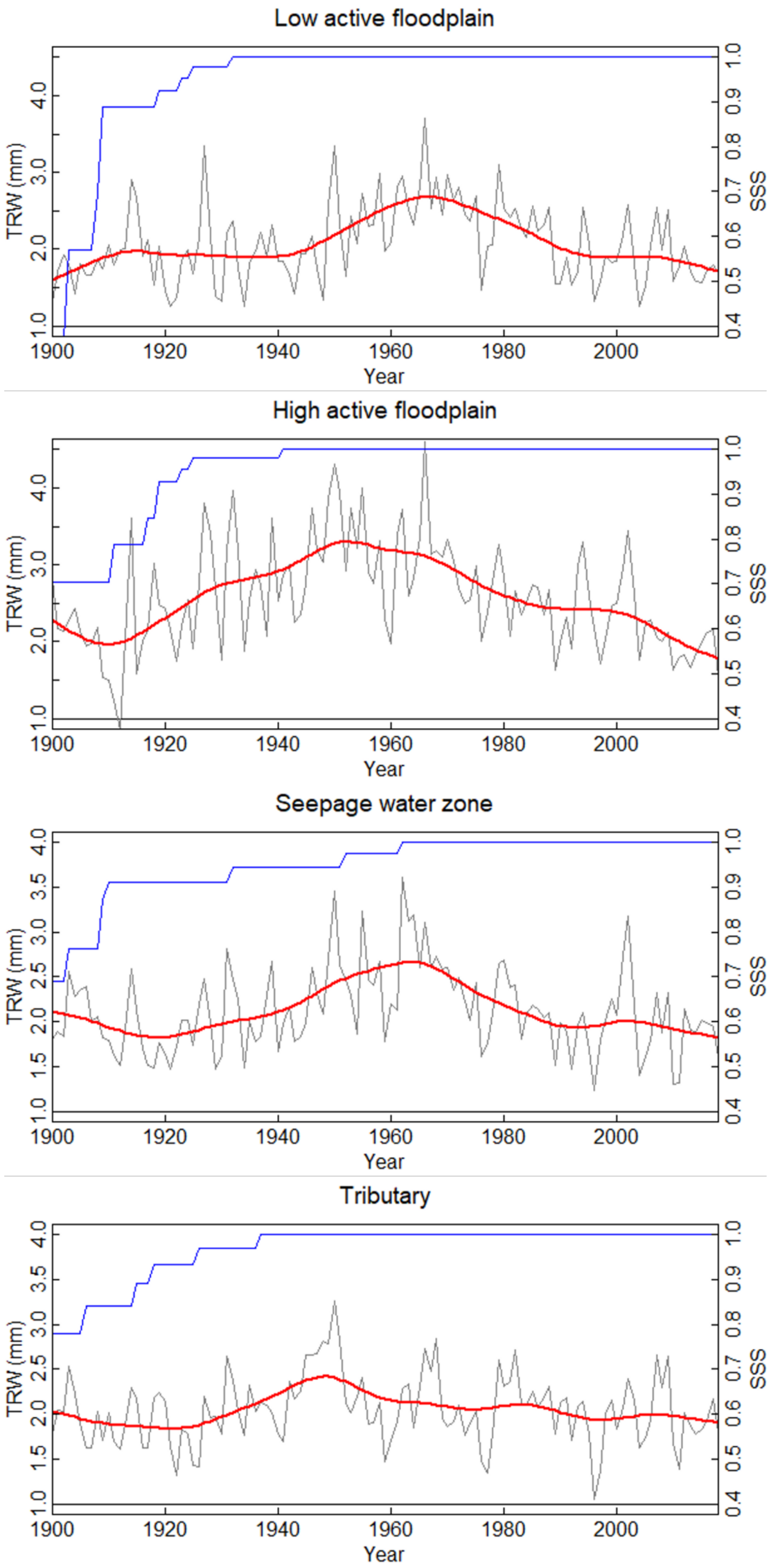

Figure B2 Mean tree ring width (TRW) chronology shown in red and subsample signal strength (SSS) shown in blue for ten dominant *Quercus robur* trees per hydrological condition.

Table B1 Characteristics of sampled trees. Each hydrological condition includes five replicate plots along the Middle Elbe River. DBH – diameter at breast height, AGR – annual growth rate, EPS – expressed population signal, Rbar-average correlation between individual series.

Hydrological condition	Mean tree age	Tree number	DBH (cm) ± SD in 2018	Mean annual AGR ± SD (mm year-1)	EPS	Rbar
Low active floodplain	141	10	58 ± 17	2.18 ± 0.47	0.85	0.35
High active floodplain	134	10	60 ± 18	2.75 ± 0.70	0.90	0.48
Seepage water zone	128	10	45 ± 15	2.24 ± 0.57	0.75	0.23
Tributary	130	10	60 ± 14	2.17 ± 0.52	0.75	0.23

Table B2. Year types include control, drought, and flood. Years are considered drought years if the mean spring or summer SPEI_12 is ≤ -1. Years are considered flood years if the Elbe River water level is ≥16.7 NHN for any season. Years are considered control years if not already classified as a flood or drought year.

Control	Drought	Flood
2016	2018	2011
2015	2017	2006
2013	2014	2002
2012	2009	1994
2010	2007	1988
2008	2004	1987
2005	1996	1981
2003	1990	1980
2001	1989	1979
2000	1977	
1999	1976	
1998		
1997		
1995		
1993		
1992		
1991		
1986		
1985		
1984		
1983		
1982		
1978		

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Summary

Hardwood floodplain (HF) forests are biodiversity hotspots that provide valuable ecosystem services such as carbon storage and sequestration, habitat provision, and nutrient cycling. Despite their high value, HF forests are listed as Endangered on the European Red List of Habitats and are threatened by river modifications (e.g. dikes), climate change, and agriculture and other anthropogenic land use on the floodplain. Although some European floodplain re-naturalization and reforestation measures have been undertaken in recent years, targets have not been met and more potential exists to increase HF forest area and improve ecosystem services of the floodplain.

Before this research, the quantification of ecosystem services such as carbon stocks and sequestration rates of *Quercus robur* was unknown for HF forests differing in age, structure, and hydrological conditions along the Middle Elbe River. This research provides a baseline quantification of the carbon stocks of trees, shrubs, deadwood, and leaf litter (Chapter 2), a method for estimating carbon sequestration rates of *Q. robur* trees (Chapter 3), an estimation of the carbon sequestration rates (CSR) of dominant *Q. robur* trees in forests differing in age, hydrological conditions, and during flood and drought years (Chapter 4), as well as a quantification of the decomposition of *Q. robur* and *Ulmus laevis* leaf litter in different forest types on the active floodplain (Chapter 5).

This research found that old forests provide a higher carbon storage function than young plantations, while young plantations may provide higher CSRs than old forests. In terms of carbon storage, old forests on the low and high active floodplain as well as in the seepage water zone and tributaries provide the same service. In terms of carbon sequestration of *Q. robur* (the tree species responsible for the highest amount of carbon storage in HF forests), dominant trees on the active floodplain provide a higher service than trees in the seepage water zone behind dikes. Also considering climate change projections, HF forests with ample access to water and flooding can provide a higher CSR service than forests located

behind dikes in the seepage water zone. Therefore, afforesting the current active floodplain and increasing the active floodplain area through dike relocations may provide a higher CSR service in the future.

Zusammenfassung

Hartholz-Auenwälder sind Hotspots der Biodiversität, die wertvolle Ökosystemleistungen, wie die Kohlenstoffspeicherung, die Bereitstellung von Lebensräumen erbringen und eine wichtige Rolle in funktionierenden Nährstoffkreisläufen spielen. Trotz ihres hohen Wertes sind Hartholz-Auenwälder auf der Europäischen Roten Liste der Lebensräume als gefährdet aufgeführt und durch Flussveränderungen (z. B. Deiche), Klimawandel, und Landwirtschaft und andere anthropogene Landnutzung in der Aue bedroht. Obwohl in den letzten Jahren einige europäische Maßnahmen zur Renaturierung und Wiederaufforstung von Überschwemmungsgebieten durchgeführt wurden, wurden die beabsichtigten Ziele nicht erreicht, und es besteht weiterhin Potenzial, die Hartholz-Auenwaldfläche zu vergrößern und die Ökosystemleistungen der Überschwemmungsgebiete zu verbessern.

Vor dieser Untersuchung bestanden große Wissenslücken bezüglich der Quantifizierung von Ökosystemleistungen wie Kohlenstoffvorräte und Sequestrationsraten von *Quercus robur* für Hartholz-Auenwälder unterschiedlichen Alters, Struktur und hydrologischer Bedingungen entlang der Mittleren Elbe. Die vorliegende Untersuchung liefert eine grundlegende Quantifizierung der Kohlenstoffvorräte von Bäumen, Sträuchern, Totholz und Laub (Kapitel 2), eine Methode zur Schätzung der Kohlenstoffbindungsraten von *Q. robur*-Bäumen (Kapitel 3), eine Schätzung der Kohlenstoffbindungsraten (CSR) von dominanten *Q. robur*-Bäumen in Wäldern unterschiedlichen Alters, unterschiedlicher hydrologischer Bedingungen und während Flut- und Dürrejahren (Kapitel 4), sowie eine Quantifizierung des Abbaus von *Q. robur*- und *Ulmus laevis*-Blattstreu in verschiedenen Waldtypen der aktiven Aue (Kapitel 5).

In der vorliegenden Arbeit wurde herausgefunden, dass alte Wälder eine höhere Kohlenstoffspeicherfunktion bieten als junge Plantagen, während junge Plantagen höhere CSRs liefern können als alte Wälder. In Bezug auf die Kohlenstoffspeicherung leisten alte Wälder in der niedriger und höher liegenden aktiven Aue sowie in der Qualmwasserzone und an den Nebenflüssen die gleiche

Menge Kohlenstoff pro ha. Hinsichtlich der Kohlenstoffspeicherung von *Q. robur* (der Baumart, die für die höchste Kohlenstoffspeicherung in Hartholz-Auenwälder verantwortlich ist) speichern dominante Bäume in der aktiven Aue mehr Kohlenstoff als Bäume in der Qualmwasserzone hinter dem Deich. Unter Berücksichtigung von Prognosen zum Klimawandel können Hartholz-Auenwälder bei ausreichender Wasserversorgung eine höhere CSR-Leistung erbringen als Wälder hinter dem Deich in der Qualmwasserzone. Daher kann die Wiederaufforstung der aktuellen aktiven Auenbereiche und die Vergrößerung des aktiven Überschwemmungsgebiets durch Deichrückverlegungen in Zukunft einen höheren CSR-Service ermöglichen.

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Contributors:

All articles were conceptualized by Dr. Kristin Ludewig, Kai Jensen, Annette Eschenbach and Heather A. Shupe. Heather A. Shupe had the main responsibility for fieldwork, labwork, data analysis and evaluation, and paper writing. All co-authors helped to edit and provide feedback to improve the articles. All work was done within study areas selected by colleagues in the MediAN project (Adrian Heger, Lizeth Vásconez Navas, Anastasia Leonova, Timo Hartmann, Mathias Scholz, Simon Thomsen, Kai Jensen, Annette Eschenbach, and Kristin Ludewig).

In the first manuscript (Chapter 2), Timo Hartmann and Mathias Scholz helped with conceptualization. Fernanda Chavez and Timo Hartmann helped with fieldwork.

In the second manuscript (Chapter 3), Stefan Klesse provided valuable insight into methods.

In the third manuscript (Chapter 4), Matilda J. Nicolaus helped with fieldwork and labwork. Sabine Kruse helped with labwork. Jens Oldeland helped with statistical analysis. Stefan Klesse and Jan Altman provided insight into methods.

In the fourth manuscript (Chapter 5), Matilda J. Nicolaus and Lilli Hamm helped with field work and lab work and Irene Tomaschewski helped with labwork.

Author’s contribution

Chapter 2

Carbon stocks of hardwood floodplain forests along the Middle Elbe: the influence of forest age, structure, species, and hydrological conditions

Authors: Heather A. Shupe, Timo Hartmann, Mathias Scholz, Kai Jensen, and Kristin Ludewig

Published in: Water (Special Issue Hydrology-Shaped Plant Communities: Diversity and Ecological Function)

Publisher: MDPI

Year: 2021

DOI: 10.3390/w13050670

Heather A. Shupe contributed to the design and conducted field work to measure trees, deadwood, and leaf litter in all forest plots. Heather A. Shupe analyzed the data and wrote the first draft of the manuscript.

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Prof. Dr. Kai Jensen

Author's contribution

Chapter 3

Adapting a *Quercus robur* allometric equation to quantify carbon sequestration rates on the Middle Elbe floodplain

Authors: Heather Alyson Shupe, Kai Jensen, Kristin Ludewig

Under review in: MethodsX

Publisher: Elsevier

Year: 2022

Heather A. Shupe contributed to the design and conducted field work to obtain data used in the model. Heather A. Shupe analyzed the data and wrote the first draft of the manuscript.

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Prof. Dr. Kai Jensen

Author’s contribution

Chapter 4

Droughts decrease and floods increase carbon sequestration rates of *Quercus robur* in hardwood floodplain forests

Authors: Heather Alyson Shupe, Kai Jensen, Jens Oldeland, Kristin Ludewig

Accepted by: Trees, Forests, People

Publisher: Elsevier

Year: 2022

Heather A. Shupe contributed to the design and conducted fieldwork to core the trees and labwork to measure the annual tree ring widths. Heather A. Shupe analyzed the data and wrote the first draft of the manuscript.

Prof. Dr. Kai Jensen

Author’s contribution

Chapter 5

Leaf litter decomposition of *Quercus robur* and *Ulmus laevis* in hardwood forests on the Middle Elbe floodplain

Authors: Heather Alyson Shupe, Kai Jensen, Kristin Ludewig

In prep.

Heather A. Shupe contributed to the design and conducted labwork to prepare and analyze samples and fieldwork to install and remove leaf litterbags. Heather A. Shupe analyzed the data and wrote the first draft of the manuscript.

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Prof. Dr. Kai Jensen

Declaration of Identical Dissertations

Ich versichere, dass dieses gebundene Exemplar der Dissertation und das in elektronischer Form eingereichte Dissertationsexemplar (über den Docata-Upload) und das bei der Fakultät Biologie Studienbüro zur Archivierung eingereichte gedruckte gebundene Exemplar der Dissertationsschrift identisch sind.

Hamburg, Germany **Heather Alyson Shupe**

04.07.2022

I, the undersigned, declare that this bound copy of the dissertation and the dissertation submitted in electronic form (via the Docata upload) and the printed bound copy of the dissertation submitted to the faculty of Biology Academic Office for archiving are identical.

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I hereby declare, on oath, that I have written the present dissertation by my own and have not used other than the acknowledged resources and aids.

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04.07.2022