Prospects for climate change mitigation of Scots pine and European beech forests

A comparative study of carbon pools and sequestration in forests of the northern German lowlands

Dissertation

zur Erlangung des mathematisch-naturwissenschaftlichen Doktorgrades

"Doctor rerum naturalium"

der Georg-August-Universität Göttingen

im Promotionsprogramm

Biologische Diversität und Ökologie

der Georg-August University School of Science (GAUSS)

vorgelegt von

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Göttingen, 2021

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Tag der mündlichen Prüfung: 28.09.2021

Summary

The historic large-scale forest conversion in the northern German lowlands resulted in a man-made dominance of Scots pine, in a landscape that would naturally be dominated by forests of European beech. Since drawbacks of pure pine forests such as their susceptibility to calamities have become clear, re-conversion to mixed and broadleaf stands has been promoted. Consequently, the share of pine is progressively declining in German forests. Nevertheless, planting pine is still a popular option from a silvicultural perspective, due to its rapid growth especially at young age, its ability to grow on nutrient-poor and dry sites, and the high demand for its wood. In the face of accelerating climate change, the ability of forests to store and sequester carbon (C) has become a focus in science, politics and forestry. The aboveground biomass represents the largest biomass fraction in the forest and can be modulated directly through management. Fine roots represent only a few percent of the tree´s biomass, but due to their fast turnover as well as through root exudation to the surrounding soil, they are the main source for soil organic carbon.

The presented study therefore compared the C pools and sequestration in the above- and belowground (fine root) biomass in naturally developing, mostly European beech forests (ND) and regularly thinned Scots pine forests (YP), respectively representing the dominant natural and the dominant current forest type of the northern German lowlands. Aboveground biomass C stocks were further determined in pine forests in transition to (mixed) broadleaf stands (OP). The study was conducted in a network of 48 forests at 16 sites, distributed throughout the northern German lowlands, covering a climate continentality gradient from west to east. Aboveground biomass calculations were based on stand structural data and species-specific allometric regressions (live trees, saplings) or volume calculations and species-specific wood density (deadwood). Aboveground net primary production (ANPP) was measured in three consecutive years using permanently attached dendrometer tapes for wood increment, and litter traps for litter production. Two repetitive fine root inventories were conducted, measuring fine root bio- and necromass in the organic layer and the top 20 cm of the mineral soil. Fine root productivity was determined with the ingrowth-core approach in 0–20 cm soil depth, including the organic layer.

Above- and belowground biomass C stocks were significantly higher in beech than in pine forests. A linear mixed-effects model revealed that the tree species was the most important factor in explaining aboveground biomass C stocks. Variation in stand age, with a range of roughly 100 years for both species, was surprisingly not influential. ANPP was higher in beech than in pine forests as well, which was mostly a result of higher litter production, while wood production was similar in the two forest types. Fine root productivity was also higher in beech than in pine forests, but the difference was only significant in 10–20 cm depth. The naturally dominant European beech forests thus have a considerably higher climate change mitigation potential than the Scots pine forests replacing them, although the high share of beech wood used for the production of bioenergy impairs their potential. By

estimating the extent of forest conversion in the northern German lowlands, the significant loss in the C storage and sequestration potential on the landscape-scale was demonstrated. The climatic gradient of the region had only little influence in this study, but performances of beech and pine under future climatic conditions will certainly affect the functioning of the investigated forests. Evidence exists that both tree species will suffer from climate change in the study region, especially from more frequent climatic extremes. In combination with additional negative effects of pine on groundwater recharge, microclimate and soil acidity, the results of this study strongly suggest that Scots pine is not a suitable option in a silviculture focusing on the mitigation of, and the resilience against climate change.

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Chapter 1

General Introduction

1.1 The role of forests in climate change mitigation

1.1.1 Climate change projections

Elevated atmospheric concentrations of carbon dioxide (CO_2) and other green house gases, resulting from human emissions, are the main cause for the global climate change that we currently witness (IPCC 2021). Mean global surface temperature has already risen by 1.09°C in comparison to pre-industrial times, and it is projected to rise by the critical mark of 1.5°C in comparison to pre-industrial times in the next few decades, even if CO_2 emissions would be strongly reduced (IPCC 2021). Summers in central Europe will likely become warmer and drier. At the same time, climate variability is predicted to increase, resulting in more frequent extreme precipitation events, heat waves and probably droughts (Schär et al. 2004, Lindner et al. 2014, IPCC 2021). This agrees with the recently high frequency of severe heat waves and drought spells in Europe, occurring in years 2003, 2015 and 2018-2020 (Büntgen et al. 2021), and which impressively demonstrate the impacts of climate change in Europe that are reality by now.

1.1.2 Forest ecosystem services in a changing climate

Following Brockerhoff et al. (2017), ecosystem functions are defined as the ecological mechanisms that support the integrity or maintenance of an ecosystem. Ecosystem services are those functions with a direct or indirect benefit for human well-being and from which ecosystem goods with direct market value can be obtained. Forests provide a variety of ecosystem services that include, but are not limited to carbon (C) sequestration, water supply and purification, provision of timber, nutritional plants and game, protection against storms, soil formation and composition, pest control, provision of habitats, pollination, or simply the enjoyment of wilderness (Haines-Young & Potschin 2018, Bowditch et al. 2020). While some ecosystem services are positively related, there are trade-offs between others. For example, timber is an important ecosystem good and its production is probably the most acknowledged provisioning service of forests. In Europe, more than 2.6 million people are employed in the forest sector and Europe's forests produce roundwood with an annual market value of about EUR 21,000 million (Forest Europe 2020). However, by increasing the amount of wood extracted from the forests, remaining C stocks decrease, as well as the

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amount of deadwood serving as habitats and the recreational value of the forests (Verkerk et al. 2014).

The forest carbon cycle and climate change

Forests cover about one third of the Earth's land area, but they store about 45 % of terrestrial carbon (Bonan 2008). Forests bind C through photosynthesis and store it in the above- and belowground bio- and necromass and the soil. Through decomposition and fire events, C is released from the forests into the atmosphere. Harvested wood and the products made thereof represent an additional C pool, but the lifespan of these products is critical for their influence on the C balance (WBAE & WBW 2016). Wood can furthermore substitute fossil fuels and energy-intensive materials such as concrete or steel, thereby increasing the climate change mitigation effect (Bösch et al. 2019). In the face of accelerating climate change, the ability of forests to store and sequester C and thus their potential to mitigate climate warming has become a key focus of scientists and policy-makers (e.g. Nabuurs et al. 2015). European forests annually sequester about 100 Tg C more than they release (1990 – 2005, Luyssaert et al. 2010), which makes them an important carbon sink. The forests of Germany alone annually sequester ~15.8 Tg C. Additionally, the annual material substitution effect accounts for ~8.2 Tg C, the annual energy substitution effect for ~9.8 Tg C and the annual fixation in the wood product pool for ~0.8 Tg C, contributing to the positive carbon balance of German forests (WBAE & WBW 2016).

In the temperate forest zone, the highest amount of C is stored in the soil, but the biomass represents the largest carbon sink (Lal 2005, Luyssaert et al. 2010). With increasing stand age, the biomass of a forest accumulates (Pregitzer & Euskirchen 2004), and thus in mature temperate forests, the biomass generally represents the largest C pool (e.g. Knohl et al. 2003, Seedre et al. 2015). The rate of C accumulation depends on site characteristics such as climate or soil fertility and moisture (Oren et al. 2001, Babst et al. 2013, Gustafson et al. 2017). Further key factors for the forest biomass C storage and sequestration are the tree species and the stand structure (Wördehoff et al. 2011, Leuschner & Ellenberg 2017, Glatthorn et al. 2018), and in production forests, these are strongly determined by management decisions.

The major part of the biomass C in forests is stored aboveground (e.g. Wördehoff et al. 2011), while fine roots (≤2 mm in diameter) represent only a few percent of the tree's biomass (Vogt et al. 1996, Kalyn & Van Rees 2006). Nevertheless, it has been estimated that fine roots contribute as much as 22 – 33 % to global terrestrial net primary production (Jackson 1997, McCormack et al. 2015). Due to their fast turnover as well as through root exudation to the surrounding soil, they represent the main source for soil organic carbon (Ashton et al. 2012, Clemmensen et al. 2013). The study of fine roots and especially their dynamics is labor-intensive and, despite much progress made in recent time, knowledge about their functioning is scarce when compared to the aboveground parts of a tree (Weemstra et al. 2016, Meier et al. 2019).

Increasing atmospheric CO_2-concentrations since the beginning of industrialization, responsible for human-induced climate change, have positively affected gross primary production, terrestrial ecosystem carbon stocks and water use efficiency of trees, but also increased tree mortality due to climate change-induced droughts (Walker et al. 2020). Soil C stocks could either rise as a consequence of increased plant-derived carbon input into the soil, or decrease due to accelerated decomposition (Davidson & Janssens 2006, Walker et al. 2020). Rising temperatures can stimulate tree growth where water and nutrients are not limiting (Lindner et al. 2010). On the other hand, climate change already has and will further promote the risk of wildfires and possibly storms, both causing large carbon releases into the atmosphere (Lindroth et al. 2009, Vautard et al. 2019, Jones et al. 2020).

The forest hydrological cycle and climate change

The effect forests have on water yield is intensively debated (Ellison et al. 2012). While some emphasize the role of trees as water consumers, others stress the importance of forests as suppliers of water to the atmosphere through transpiration. In forests, precipitation reaches the floor as direct throughfall, stemflow or crowndrip. The vegetation absorbs water that infiltrates the soil, which subsequently is returned to the atmosphere through transpiration. Evapotranspiration is defined as the sum of transpiration and water that evaporates either after its interception from the crown and stem, or from litter and soil. The streamflow from the forest and thus its water balance is determined by the precipitation amount, the loss through evapotranspiration and the change in water storage (Roberts 2009, Creed & van Noordwijk 2018).

Altering rainfall patterns and rising temperatures in the course of climate change will affect the water regime of forests. Among the projected impacts are an increasing risk of floods, lower soil moisture or reduced groundwater recharge and streamflow in summer (Eckhardt & Ulrich 2003, Fuhrer et al. 2006, Luo et al. 2018). However, there are large differences between individual sites, depending not only on current and projected climate, but also on forest disturbance or management regimes (Creed & van Noordwijk 2018).

Further forest functions and services related to climate change

Besides carbon storage and sequestration, and the maintenance of hydrological cycles, diverse other forest functions and services, partially related to these, are likely to be affected by climate change. Some examples that are relevant in the context of this study will be mentioned here.

Biodiversity has strongly decreased in the past decades and centuries, in response to a variety of human-induced stressors, on which climate change adds up (Mooney et al. 2009). Biodiversity is positively related to many ecosystem services, through mechanisms such as niche and trait complementarity (Brockerhoff et al. 2017). Species distributions, including that of trees, shift in response to climate change, moving to higher elevations and higher latitudes where possible (Chen et al. 2011, Boisvert-Marsh et al. 2014). While some species suffer from climate warming, other species benefit. For example, accelerated development

and higher population sizes of insect herbivores, caused by warmer temperatures, could lead to more frequent pest outbreaks (Westgarth-Smith et al. 2007), with subsequent higher tree mortality and reduced C stocks.

Forest productivity and thus timber yield in the temperate European region are expected to increase under future climatic conditions where water is not limited (Lindner et al. 2010, Gutsch et al. 2016). Carbon and nutrient dynamics of soils depend on climate, because the decomposition of organic matter is limited by temperature and water availability (Davidson & Janssens 2006). Furthermore, soils will be affected in case of increased streamflow and floodings that cause erosion (Fuhrer et al. 2006).

The microclimate under forest canopies is characterized by buffered extremes of temperature and humidity compared to the macroclimate in open landscapes (von Arx et al. 2013, De Frenne et al. 2019). This buffering effect is probably an important factor for determining the impact of climate warming on forest-dwelling biota and their distributions (Lenoir et al. 2017). Microclimatic conditions in forests vary with tree species and the canopy structure and affect ecosystem functions such as primary production or soil decomposition (von Arx et al. 2013, De Frenne et al. 2021). There are complex interrelationships between micro- and macroclimate, which are hitherto poorly understood (De Frenne et al. 2021)

1.2 Forest management and ecosystems services

1.2.1 Primary forests and their ecological relevance

Primary forests are defined as "naturally regenerated forests of native tree species, where there are no clearly visible indications of human activities and ecological processes are not significantly disturbed" (FAO 2020). Due to growing impact by humans, primary forests have become rare around the globe. While more undisturbed forest areas are left in the boreal and tropical zones, temperate broadleaf forests are barely represented among them (Watson et al. 2016, Potapov et al. 2017). In Europe, less than 1 % of the current forest area can be attributed to primary forests and most of these remnants are small and fragmented (Sabatini et al. 2018). This is alarming, considering the outstanding value that primary forests have for biodiversity and ecosystem services (Watson et al. 2018).

Even though species numbers at a given location (α-diversity) in managed forests can exceed those of primary forests, this picture seems to reverse when similarity between locations (β-diversity) or diversity on the landscape-scale (γ-diversity) are considered (Kaufmann et al. 2017). It is not only via the positive relation between biodiversity and ecosystem functioning, that primary forests have a high ability to provide numerous ecosystem services (Brockerhoff et al. 2017, Watson et al. 2018). For instance, primary forests store large amounts of carbon above- and belowground, and contrary to former beliefs, old-growth forests remain carbon sinks, rather than reaching an equilibrium state (Luyssaert et al. 2008, Glatthorn et al. 2018). Intact forests can stabilize the groundwater-

table and reduce run-off, which can help to limit the impact of extreme precipitation events (Watson et al. 2018). Last, but not least, primary forests are an irreplaceable opportunity to understand and evaluate the human impact in managed forest ecosystems, as they allow us to study their natural functioning in the absence of direct human intervention.

1.2.2 Multifunctional forestry

In Germany, more than 90 % of the forest area is used unrestrictedly for timber production (TI 2014). The silvicultural management has great influence on the appearance of a forest, most obviously through determination of the tree species composition and the age structure, and it represents part of the local disturbance regime (Bartsch et al. 2020). Thereby, the decisions of the forester strongly affect also the functioning of the forest ecosystem. One simple example is the availability of habitats for species that depend on deadwood, which is directly determined by the decision to extract or retain deadwood in the stand. Thinning intensity can affect numerous ecosystem services, such as carbon storage, forest stability, soil retention, downstream water quality or nutrient cycles (Blanco et al. 2005, Fukuyama et al. 2010, Verkerk et al. 2014, Marchi et al. 2018).

Common clearcut systems that focused solely on timber production were increasingly scrutinized, when ecological problems emerged in the forests in the second half of the 20th century (Çolak et al. 2003, Bauhus et al. 2013). As knowledge and awareness of the diverse functions of the forest ecosystem have grown, societal demands on silviculture augmented as well (Schmithüsen 2007). In consequence, silvicultural concepts developed that focus not only on a sustainable use of forests, but attempt to integrate various forest functions besides productivity into the management concept (e.g. Gustafsson et al. 2012, Bauhus et al. 2013, Brang et al. 2014). Under the impression of urgent need for climate action, climate-smart-forestry (CSF) recently emerged, a sustainable management concept that focuses on the ability of forests to adapt to, resist and mitigate climate change (Verkerk et al. 2020). CSF aims to create forests that sustainably provide ecosystem goods and services in a changing environment and that minimize the impact of climate change (Bowditch et al. 2020). Even though the carbon storage and sequestration are key functions for climate change mitigation, the multifunctionality of forests is an inherent and essential part of CSF (Bowditch et al. 2020).

1.3 Forests of the northern German lowlands

1.3.1 Soils and climate of the study region

The here presented study was conducted in the northern German lowlands that extent from the Netherlands in the west to the Polish border in the east, and from the North Sea and the Baltic Sea coasts to the lower mountain ranges of Central Germany in the south (Fig. 1.1). The northern German lowlands were mainly formed by glacial processes during the Pleistocene, that shaped moraine landscapes with mostly flat or undulating reliefs (Böse et al. 2018). Soils are characterized by sandy deposits, originating from the last (Saalian-) and

the penultimate (Weichselian-) glacial periods. The climate in the study region is cool-temperate, with a climate continentality gradient from west to east that manifests in lower mean annual precipitation (MAP, range: 555–908 mm), slightly higher summer temperatures (range: 16.6–18.0°C) but lower winter temperatures (range: 0.5–2.9°C) in the east. Mean annual temperature (MAT) ranges from 8.6–10.3°C (multi-annual means 1981–2010, DWD CDC 2019).
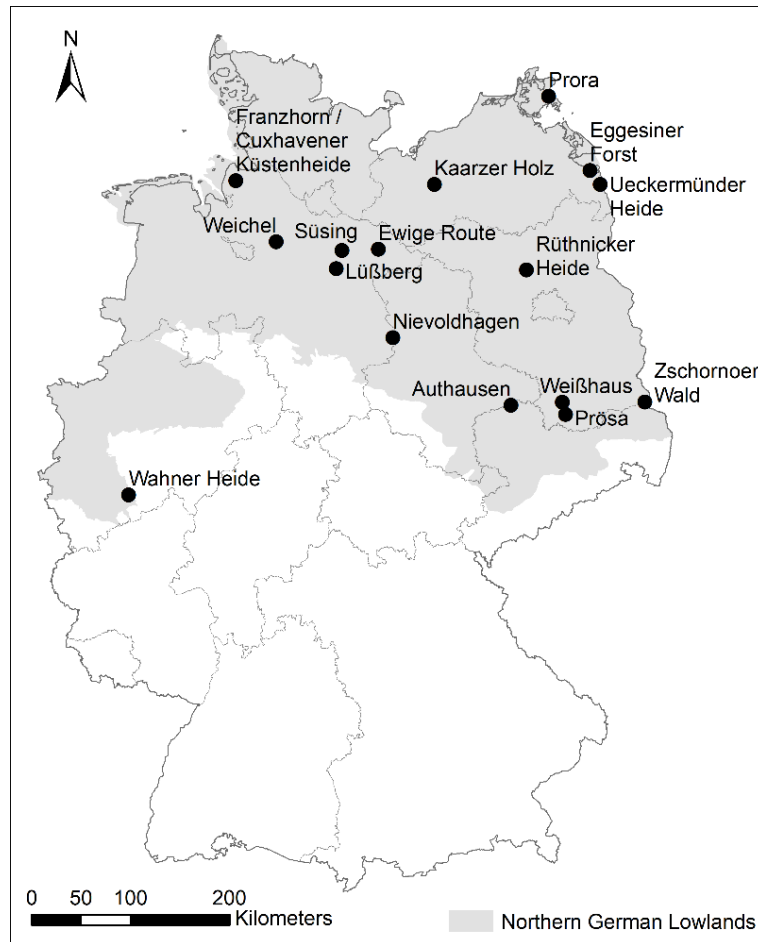
Figure 1.1 Map of Germany with the 16 study sites in the northern German lowlands.

1.3.2 Natural and current vegetation

The landscape of Central Europe and Germany used to be almost completely covered with temperate broadleaf forests, dominated in large areas by European beech (*Fagus sylvatica* L., BfN 2010, Leuschner & Ellenberg 2017, Poschlod 2017). Since the beginning of settlement in Neolithic times, humans have shaped the landscapes of Central Europe. Forests had to give way for settlements and arable fields, and with increasing population sizes, forest cover progressively declined until a minimum was reached during the Middle ages and in the early modern era at around 1800 A.D. (Bork 2001, Poschlod 2017). The forests were used as pastures, provided fuelwood, wood for construction or energy for early

industries (Kaplan et al. 2009, Poschlod 2017). Continuously high timber demand resulted in severe timber shortage, and in response, large areas were afforested. Since overexploitation of forests and the replacing landscapes had left degraded soils and locally even led to the formation of inland dunes, these soils could often be afforested only with Scots pine (*Pinus sylvestris* L.), as this species has low water and nutrient demands (Milnik 2007, Leuschner & Immenroth 1994, Leuschner & Ellenberg 2017). Consequently, planted pine forests are dominating the current forests of the northern German lowlands, while the once dominating beech forests are reduced to less than 7 % (TI 2015, chapter 4).

Rethinking pine forest management

It has become more and more apparent that pure, typically managed pine forests are labile forest ecosystems when compared to broadleaf or mixed forest stands. For example, they are more frequently affected by mass outbreaks of pest species and more prone to windthrow (Majunke et al. 2005, Knoke et al. 2006, Möller et al. 2007). Furthermore, pine forests have a comparably dry litter layer, which makes them vulnerable to wildfires, especially in the northeast of Germany, where annual precipitation is low (Schlick & Möller 2007, Schunk et al. 2017). These calamities could all become more frequent in the future due to climate change (see section 1.1.2). Furthermore, pines can have an acidifying effect on the forest soil and enhance podsolization, and can thus impair a sustainable forest growth (Riek et al. 2007, Leuschner et al. 2013).

As a consequence of these drawbacks, forest policy in Germany and neighboring countries has changed towards the aim of reducing pure pine forests in favor of mixed and broadleaf stands, and thus their share of the forest area is progressively declining (Lust et al. 2000, NLF 2016, Purkus et al. 2019). However, the presumable lower water availability in the near future, and the high wood demand still provoke the call for a promotion of pine, as this species can grow on dry soils, has high economic value and is used to a high share for products with a long lifespan (Anders et al. 2005, NLF 2016, Purkus et al. 2019).

The WiNat project – Recreating wilderness on natural heritage sites

This study was embedded in a collaborative biodiversity research and implementation project entitled 'Wildnis Naturerbe' ('WiNat', https://www.wildnis-naturerbe.de). Natural heritage sites in Germany are permanently reserved for nature conservation, and they are an important contribution to the national strategy for biodiversity (BMU 2007). A majority of these protected areas are owned and managed by the *DBU Natural Heritage*, and a large proportion are forests or forest rich landscapes located in the northern German lowlands (DBU 2021). In these forests, management has ceased or will cease with the goal of obtaining natural forests with natural development, which will finally result in secondary wilderness. However, many of the forests are planted pine forests, with hitherto regular management and thus far from a natural state. The WiNat project created a monitoring concept for the development of forests to a more natural state (Schneider et al. 2021a), that integrates biodiversity, structure and functions of the forests. A renaturation experiment

complemented the monitoring system. In a large forested area with a high number of stands of similar soil and structural conditions, different measures, namely timber extraction, creation of deadwood and planting of deciduous trees, were tested for their efficacy to accelerate the development to a more natural state (Schneider et al. 2021b).

1.4 Study objectives and design

Primary objective of this thesis was an estimation of the carbon pools and sequestration potential of the currently dominating versus the naturally dominating forest type (Scots pine forests vs. mostly European beech forests) of the northern German lowlands, in order to evaluate their prospective contribution to climate change mitigation. Since no true primary forests are left in the lowland area of Germany or Central Europe, forests where management has ceased served in the presented study as surrogates for the natural forests before human impact. Therefore, a further aim of this thesis was to assess a potential effect of management cessation on carbon pools and sequestration in forest.

To address these questions, three distinct forest categories were defined, differing in the vegetation type, the stand age and the current management (Table 1.1). In forests with natural development (ND), management ceased and the last thinning operations happened 6 to 41 years before data collection (18 years on average). These forests were primarily European beech forests, but included as well two sessile oak (*Quercus petraea* (Matt.) Liebl.) and one Scots pine forest in the more continental east. The young pine forests (YP) represent the dominant current vegetation. Due to large-scale afforestation after the world-war-II epoch, the age class of these forests (55 – 81 years, mean: 65) is currently frequent. The old pine forests (OP) were at the end of their rotation period and represent a transitional stage to (mixed) broadleaf forests.

Table 1.1. Selection criteria of the three distinct forest categories investigated in this study.

Forest category	Forests with natural development (ND)	Old pine forests (OP)	Young pine forests (YP)
Vegetation type	Potential natural forest type	Scots pine-dominated forests, with broadleaf trees in the understory	Pure, even aged, Scots pine forests
Stand age	> 100 years	> 90 years	~ 65 years
Management	Released from management	Regularly thinned	Regularly thinned

The presented study was conducted at 16 study sites, distributed throughout the northern German lowlands, covering its climate continentality gradient from west to east (Fig. 1.1). At each study site, three forests, i.e. one forest per category, on similar geological substrate were selected for data collection, which was conducted at (6-)10 randomly distributed

0.1-ha circular plots in the stands. All forests were located on acidic sandy soils with low to medium fertility and without groundwater influence.

The study is divided into two separate parts, presented in chapters 2 and 3. Chapter 2 focuses on the carbon stocks and sequestration potential in the aboveground tree biomass, which comprises the largest biomass carbon pool in forests (Wördehoff et al. 2011) and that can be modulated directly by management decisions. This was complemented by an investigation on the fine root systems of European beech (category ND) and Scots pine (category YP) forests (chapter 3). Fine roots highly contribute to soil organic carbon formation in the soil, and their biomass and morphology along environmental gradients may give information about adaptation strategies of the trees. Specifically, I tested the following hypotheses:

(i) Carbon stocks in the aboveground biomass are higher in hardwood-dominated forests with natural development than in managed pine forests and in the pine-beech transitional stage (chapter 2).

(ii) Fine root biomass is higher in beech forests with natural development than in managed pine forests (chapter 3)

(iii) Aboveground net primary productivity is higher in hardwood-dominated forests with natural development than in managed pine forests (chapter 2)

(iv) Fine root productivity is higher in beech forests with natural development than in managed pine forests (chapter 3)

In both chapters, I analyzed the influence of stand characteristics such as tree species identity, basal area, stand age or time elapsed since the last thinning operation, and of the climatic gradient of the study region, on the biomass carbon pool and productivity. Characteristics of the fine root systems were also related to the acidity and the carbon and nutrient status of the forest soils.

A secondary aim of this thesis was to estimate the extent of historic forest conversion in the northern German lowlands, in order to assess its consequences on a landscape-scale. I compared the current with the potential natural distribution of beech and pine forests using data from the third national forest inventory (BWI[3], TI 2015) and the map of the potential natural vegetation of Germany (BfN 2010). The gained knowledge on carbon pools and sequestration of chapters 2 and 3 was integrated into a more holistic assessment of forest conversion. Data on the forest water cycle, microclimate and soil carbon storage and acidity were compiled and compared between pine and beech forests of northern Germany, in order to evaluate their prospects in times of climate change (chapter 4).

References

Anders, S., Beck, W., Hornschuch, F., Müller, J., Steiner, A., 2005. Zur Zukunftsfähigkeit des Kiefern-Buchen-Mischbestandes – Ökologische Voraussetzungen, forstliche Steuerungsmöglichkeiten, waldwachstumskundliche und umweltrelevante Wirkungen. In: Ministerium für Ländliche Entwicklung, Umwelt und Verbraucherschutz des Landes Brandenburg, Landesforstanstalt Eberswalde (eds.). Ökologischer Waldumbau im nordostdeutschen Tiefland. Eberswalder Forstliche Schriftenreihe, Vol. XXIII: 12-32.

Ashton, M.S., Tyrrell, M.L., Spalding, D., Gentry, B. (eds.), 2012. Managing forest carbon in a changing climate. Springer, Dordrecht, Netherlands.

Babst, F., Poulter, B., Trouet, V., Tan, K., Neuwirth, B., Wilson, R., et al., 2013. Site-and species-specific responses of forest growth to climate across the European continent. Global Ecol. Biogeogr. 22, 706-717.

Bartsch, N., von Lüpke, B., Röhrig, E., 2020. Waldbau auf ökologischer Grundlage. Ulmer, Stuttgart, Germany.

Bauhus, J., Puettmann, K.J., Kühne, C., 2013. Close-to-nature forest management in Europe: Does It Support Complexity and Adaptability of Forest Ecosystems In: Messier, C., Puettmann, K.J., Coates, K.D. (eds.). Managing Forests as Complex Adaptive Systems: building resilience to the challenge of global change: 187-213.

BfN (Bundesamt für Naturschutz), 2010. Karte der potentiellen natürlichen Vegetation Deutschlands. Maßstab 1:500.000. Bonn-Bad Godesberg, Germany.

Blanco, J.A., Zavala, M.A., Imbert, J.B., Castillo, F.J., 2005. Sustainability of forest management practices: Evaluation through a simulation model of nutrient cycling. For. Ecol. Manage. 213, 209-228.

BMU (Bundesministerium für Umwelt, Naturschutz und Reaktorsicherheit), 2007. Nationale Strategie zur biologischen Vielfalt. Berlin, Germany, 178 p.

Boisvert-Marsh, L., Périé, C., de Blois, S., 2014. Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. Ecosphere 5, 1-33.

Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320, 1444–1449.

Bork, H.-R., 2001. Landnutzung in Deutschland. Petermanns Geogr. Mitt. 145, 36–37.

Bösch, M., Elsasser, P., Rock, J., Weimar, H., Dieter, M., 2019. Extent and costs of forest-based climate change mitigation in Germany: accounting for substitution. Carbon Manag. 10, 127-134.

Böse M., Ehlers J., Lehmkuhl F., 2018. Deutschlands Norden: vom Erdaltertum zur Gegenwart. Springer Berlin, Germany. 201p.

Bowditch, E., Santopuoli, G., Binder, F., Del Río, M., La Porta, N., Kluvankova, T., et al., 2020. What is Climate-Smart Forestry? A definition from a multinational collaborative process focused on mountain regions of Europe. Ecosyst. Serv. 43, 101113.

Brang, P., Spathelf, P., Larsen, J.B., Bauhus, J., Bončìna, A., Chauvin, C., et al., 2014. Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. Forestry 87, 492-503.

Brockerhoff, E.G., Barbaro, L., Castagneyrol, B., Forrester, D.I., Gardiner, B., González-Olabarria, J.R., et al., 2017. Forest biodiversity, ecosystem functioning and the provision of ecosystem services. Biodivers. Conserv. 26, 3005-3035.

Büntgen, U., Urban, O., Krusic, P.J., Rybníček, M., Kolář, T., Kyncl, T., et al., 2021. Recent European drought extremes beyond Common Era background variability. Nat. Geosci. 14, 190-196.

Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science, 333, 1024-1026.

Clemmensen, K.E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., et al., 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science 339, 1615–1618.

Çolak, A.H., Rotherham, I.D., Çalikoglu, M., 2003. Combining 'naturalness concepts' with close-to-nature silviculture. Forstw. Cbl. 122, 421-431.

Creed, I.F., van Noordwijk, M. (eds.), 2018. Forest and Water on a Changing Planet: Vulnerability, Adaptation and Governance Opportunities. A Global Assessment Report, IUFRO World Series Volume 38. IUFRO, Vienna, Austria. 192 p.

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature, 440, 165-173.

DBU (Deutsche Bundesstiftung Umwelt) (ed.), 2021. DBU Naturerbe. Osnabrück, Germany. 40 p.

De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B.R., Zellweger, F., Aalto, J., et al., 2021. Forest microclimates and climate change: Importance, drivers and future research agenda. Glob. Chang. Biol. 27, 2279-2297.

De Frenne, P., Zellweger, F., Rodríguez-Sanchez, F., Scheffers, B.R., Hylander, K., Luoto, M., et al., 2019. Global buffering of temperatures under forest canopies. Nat. Ecol. Evol. 3, 744-749.

DWD CDC (Deutscher Wetterdienst Climate Data Center), 2019. Grids of climate data over Germany. https://opendata.dwd.de/climate_environment/CDC/grids_germany/. (Access: 07.2019).

Eckhardt, K., Ulbrich, U., 2003. Potential impacts of climate change on groundwater recharge and streamflow in a central European low mountain range. J. Hydrol. 284, 244-252.

Ellison, D., Futter, M.N., Bishop, K, 2012. On the forest cover–water yield debate: from demand-to supply-side thinking. Glob. Chang. Biol. 18, 806-820.

FAO (Food and Agriculture Organization), 2020. Global Forest Resources Assessment 2020: Main report. Rome, Italy. https://doi.org/10.4060/ca9825en

FOREST EUROPE, 2020: State of Europe's Forests 2020. 394 p.

Fuhrer, J., Beniston, M., Fischlin, A., Frei, C., Goyette, S., Jasper, K., Pfister, C., 2006. Climate risks and their impact on agriculture and forests in Switzerland. Clim. Chang. 79, 79-102.

Fukuyama, T., Onda, Y., Gomi, T., Yamamoto, K., Kondo, N., Miyata, S., et al., 2010. Quantifying the impact of forest management practice on the runoff of the surface-derived suspended sediment using fallout radionuclides. Hydrol. Process. 24, 596-607.

Glatthorn, J., Feldmann, E., Pichler, V., Hauck, M., Leuschner, C., 2018. Biomass stock and productivity of primeval and production beech forests: greater canopy structural diversity promotes productivity. Ecosystems 21, 704–722.

Gustafson, E.J., Miranda, B.R., De Bruijn, A.M.G., Sturtevant, B.R., Kubiske, M.E., 2017. Do rising temperatures always increase forest productivity? Interacting effects of temperature, precipitation, cloudiness and soil texture on tree species growth and competition. Environ. Model. Softw. 97, 171-183.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., et al., 2012. Retention forestry to maintain multifunctional forests: a world perspective. BioScience 62, 633-645.

Gutsch, M., Lasch-Born, P., Suckow, F., Reyer, C.P., 2016. Evaluating the productivity of four main tree species in Germany under climate change with static reduced models. Ann. For. Sci. 73, 401-410.

Haines-Young, R., Potschin, M.B., 2018: Common International Classification of Ecosystem Services (CICES) V5.1 and Guidance on the Application of the Revised Structure. Available from www.cices.eu.

IPCC (Intergovernmental Panel on Climate Change), 2021: Summary for Policymakers. In: Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S. L., Péan, C., Berger, S., et al. (eds.). Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press. In Press.

Jackson, R.B., Mooney, H.A., Schulze, E.-D., 1997. A global budget for fine root biomass, surface area, and nutrient contents. Proc. Natl. Acad. Sci. USA 94, 7362-7366.

Jones, M.W., Smith, A., Betts, R., Canadell, J.G., Prentice, I.C., Le Quéré, C., 2020. Climate change increases risk of wildfires. ScienceBrief Review.

Kalyn, A.L., Van Rees, K.C.J., 2006. Contribution of fine roots to ecosystem biomass and net primary production in black spruce, aspen, and jack pine forests in Saskatchewan. Agric. For. Meteorol. 140, 236–243.

Kaplan, J.O., Krumhardt, K.M., Zimmermann, N., 2009. The prehistoric and preindustrial deforestation of Europe. Quat. Sci. Rev. 28, 3016-3034.

Kaufmann, S., Hauck, M., Leuschner, C., 2017. Comparing the plant diversity of paired beech primeval and production forests: Management reduces cryptogam, but not vascular plant species richness. For. Ecol. Manage. 400, 58-67.

Knohl, A., Schulze, E.-D., Kolle, O., Buchmann, N., 2003. Large carbon uptake by an unmanaged 250-year-old deciduous forest in Central Germany. Agric. For. Meteorol. 118, 151-167.

Knoke, T., Ammer, C., Stimm, B., Mosandl, R., 2008. Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. Eur. J. Forest. Res. 127, 89-101.

Lal, R., 2005. Forest soils and carbon sequestration. For. Ecol. Manage. 220, 242-258.

Lenoir, J., Hattab, T., Pierre, G., 2017. Climatic microrefugia under anthropogenic climate change: implications for species redistribution. Ecography 40, 253-266.

Leuschner, C., Ellenberg, H., 2017. Ecology of Central European Forests: Vegetation Ecology of Central Europe, Vol. I. Springer, Cham, Switzerland.

Leuschner, C., Immenroth, J., 1994. Landschaftsveränderungen in der Lüneburger Heide 1770–1985. Dokumentation und Bilanzierung auf der Grundlage historischer Karten. Arch. Nat.schutz Landsch.forsch. 33, 35–139.

Leuschner, C., Wulf, M., Bäuchler, P., Hertel, D., 2013. Soil C and nutrient stores under Scots pine afforestations compared to ancient beech forests in the German Pleistocene: The role of tree species and forest history. For. Ecol. Manage. 310, 405–415.

Lindner, M., Fitzgerald, J.B., Zimmermann, N.E., Reyer, C., Delzon, S., van der Maaten, E., et al., 2014. Climate change and European forests: what do we know, what are the uncertainties, and what are the implications for forest management?. J. Environ. Manage. 146, 69-83.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., et al., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For. Ecol. Manage. 259, 698-709.

Lindroth, A., Lagergren, F., Grelle, A., Klemedtsson, L., Langvall, O., Weslien, P., Tuulik, J., 2009. Storms can cause Europe-wide reduction in forest carbon sink. Glob. Chang. Biol. 15, 346-355.

Luo, P., Zhou, M., Deng, H., Lyu, J., Cao, W., Takara, K., et al., 2018. Impact of forest maintenance on water shortages: Hydrologic modeling and effects of climate change. Sci. Total Environ. 615, 1355-1363.

Lust, N., Geudens, G., Olsthoorn, A.F.M., 2000. Scots pine in Belgium and the Netherlands. Investig. Agrar.: Sist. Recur. For. 9, 213–231.

Luyssaert, S., Ciais, P., Piao, S.L., Schulze, E.-D., Jung, M., Zaehle, S., et al., 2010. The European carbon balance. Part 3: forests. Glob. Chang. Biol. 16, 1429-1450.

Luyssaert, S., Schulze, E.-D., Börner, A., Knohl, A., Hessenmöller, D., Law, B.E., et al., 2008. Old-growth forests as global carbon sinks. Nature 455, 213-215.

Marchi, M., Paletto, A., Cantiani, P., Bianchetto, E., De Meo, I., 2018. Comparing thinning system effects on ecosystem services provision in artificial black pine (*Pinus nigra* J.F. Arnold) forests. Forests 9, 188.

McCormack, M.L., Dickie, I.A., Eissenstat, D.M., Fahey, T.J., Fernandez, C.W., Guo, D., et al., 2015. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. New Phytol. 207, 505–518.

Majunke, C., Dreger, F., Schulz, U., Rös, M., Torkler, F. 2005. Zur Bedeutung des Waldumbaus für die Erhöhung von Biodiversität und der Selbstregulation – Potenziale in kieferndominierten Waldbeständen. In: Ministerium für Ländliche Entwicklung, Umwelt und Verbraucherschutz des Landes Brandenburg,

Landesforstanstalt Eberswalde (eds.). Ökologischer Waldumbau im nordostdeutschen Tiefland. Eberswalder Forstliche Schriftenreihe, Vol. XXIII: 121-138.

Meier, I.C., Brunner, I., Godbold, D.L., Helmisaari, H.-S., Ostonen, I., Soudzilovskaia, N.A., Prescott, C.E., 2019. Roots and rhizospheres in forest ecosystems: Recent advances and future challenges. For. Ecol. Manage. 431, 1–5.

Milnik, A., 2007. Zur Geschichte der Kiefernwirtschaft in Nordostdeutschland. In: Ministerium für Ländliche Entwicklung, Umwelt und Verbraucherschutz des Landes Brandenburg, Landesforstanstalt Eberswalde (eds.). Die Kiefer in nordostdeutschen Tiefland – Ökologie und Bewirtschaftung. Eberswalder Forstliche Schriftenreihe, Vol. XXXII: 14-21.

Möller, K., Walter, C., Engelmann, A., Hielscher, K., 2007. Die Gefährdung der Gemeinen Kiefer durch Insekten. In: Ministerium für Ländliche Entwicklung, Umwelt und Verbraucherschutz des Landes Brandenburg, Landesforstanstalt Eberswalde (eds.). Die Kiefer in nordostdeutschen Tiefland – Ökologie und Bewirtschaftung. Eberswalder Forstliche Schriftenreihe, Vol. XXXII: 245–257.

Mooney, H., Larigauderie, A., Cesario, M., Elmquist, T., Hoegh-Guldberg, O., Lavorel, S., et al., 2009. Biodiversity, climate change, and ecosystem services. Curr. Opin. Environ. Sustainability 1, 46-54.

NLF (Niedersächsische Landesforsten) (ed.), 2016. 25 Jahre ökologische Waldentwicklung in den Niedersächsischen Landesforsten. Eine Bilanz. Aus dem Walde – Schriftenreihe Waldentwicklung in Niedersachsen, 60. Braunschweig, Germany.

Nabuurs, G.-J., Delacote, P., Ellison, D., Hanewinkel, M., Lindner, M., Nesbit, M., et al., 2015. A new role for forests and the forest sector in the EU post-2020 climate targets. From Science to Policy 2. European Forest Institute.

Oren, R., Ellsworth, D.S., Johnsen, K.H., Phillips, N., Ewers, B.E., Maier, C., et al., 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. Nature 411, 469-472.

Poschlod, P., 2017: Geschichte der Kulturlandschaft: Entstehungsursachen und Steuerungsfaktoren der Entwicklung der Kulturlandschaft, Lebensraum- und Artenvielfalt in Mitteleuropa. Ulmer, Stuttgart, Germany.

Potapov, P., Hansen, M.C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., et al., 2017. The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. Sci. Adv. 3, e1600821.

Pregitzer, K.S., Euskirchen, E.S., 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. Glob. Chang. Biol. 10, 2052–2077.

Purkus A., Lüdtke J., Becher G., Jochem D., Polley H., Rüter S., et al., 2019. Charta für Holz 2.0 – Kennzahlenbericht 2019 Forst & Holz. Fachagentur Nachwachsende Rohstoffe e. V. (FNR), Gülzow-Prüzen, Germany. 45 p.

Riek, W., Strohbach, B., Kallweit, R., 2007. Bodenzustand und Stoffhaushalt von Kiefernbeständen in Brandenburg. In: Ministerium für Ländliche Entwicklung, Umwelt und Verbraucherschutz des Landes Brandenburg, Landesforstanstalt Eberswalde (eds.). Die Kiefer im nordostdeutschen Tiefland – Ökologie und Bewirtschaftung. Eberswalder Forstliche Schriftenreihe, Vol. XXXII: 54-63.

Roberts, J.M. 2009. The role of forests in the hydrological cycle. In: Owens, J.N., Lund, H.G. (eds.). Forests and Forest Plants, pp. 42 – 76.

Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., et al., 2018. Where are Europe's last primary forests?. Divers. Distrib. 24, 1426-1439.

Schär, C., Vidale, P.L., Lüthi, D., Frei, C., Häberli, C., Liniger, M.A., Appenzeller, C., 2004. The role of increasing temperature variability in European summer heatwaves. Nature 427, 332–336.

Schlick, R., Möller, K., 2007. Waldbrandrisiko und Waldbrandschutz in Brandenburg. In: Ministerium für Ländliche Entwicklung, Umwelt und Verbraucherschutz des Landes Brandenburg, Landesforstanstalt Eberswalde (eds.). Die Kiefer im nordostdeutschen Tiefland – Ökologie und Bewirtschaftung. Eberswalder Forstliche Schriftenreihe, Vol. XXXII: 306–310.

Schmithüsen, F., 2007. Multifunctional forestry practices as a land use strategy to meet increasing private and public demands in modern societies. J. For. Sci. 53, 290–298.

Schneider, H., Culmsee, H., Aljes, M., Förster, A., Meyer, P., Leuschner, C., 2021a. Aufnahmemethoden für das Naturnähemonitoring in Wäldern im Projekt „Wildnis Naturerbe" (WiNat). Stand: 12.01.2021. 82p.

Schneider, H., Culmsee, H., Aljes, M., Diers, M., Förster, A., Meyer, P., Leuschner, C., 2021b. Methodenbeschreibung zur Waldrenaturierung von Kiefernreinbeständen im Projekt „Wildnis Naturerbe". Stand: 12.01.2021. 78p.

Schunk, C., Wastl, C., Leuchner, M., Menzel, A., 2017. Fine fuel moisture for site-and species-specific fire danger assessment in comparison to fire danger indices. Agric. For. Meteorol. 234, 31-47.

Seedre, M., Kopáček, J., Janda, P., Bače, R., Svoboda, M., 2015. Carbon pools in a montane old-growth Norway spruce ecosystem in Bohemian Forest: Effects of stand age and elevation. For. Ecol. Manage. 346, 106–113.

TI (Thünen-Institut), 2014. Dritte Bundeswaldinventur – Ergebnisdatenbank. Waldfläche [ha] nach Land und Nutzungseinschränkung, Filter: Jahr=2012. https://bwi.info. Accessed: 05.08.2021, Query: 77Z1JI_L222of_2012, Archived: 2014-5-5 16:32:14.980.

TI (Thünen-Institut), 2015. Dritte Bundeswaldinventur - Basisdaten (Stand 20.03.2015). https://bwi.info/Download/de/BWI-Basisdaten/ACCESS2003/bwi20150320_alle_ daten2012.zip.

Vautard, R., van Oldenborgh, G.J., Otto, F.E.L., Yiou, P., de Vries, H., van Meijgaard, E., et al., 2019. Human influence on European winter wind storms such as those of January 2018. Earth Syst. Dynam. 10, 271-286.

Verkerk, P.J., Costanza, R., Hetemäki, L., Kubiszewski, I., Leskinen, P., Nabuurs, G.J., et al., 2020. Climate-Smart Forestry: the missing link. For. Policy Econ. 115, 102164.

Verkerk, P.J., Mavsar, R., Giergiczny, M., Lindner, M., Edwards, D., Schelhaas, M.J., 2014. Assessing impacts of intensified biomass production and biodiversity protection on ecosystem services provided by European forests. Ecosyst. Serv. 9, 155-165.

Vogt, K.A., Vogt, D.J., Palmiotto, P.A., Boon, P., O'Hara, J., Asbjornsen, H., 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 187, 159–219.

von Arx, G., Graf Pannatier, E., Thimonier, A., Rebetez, M., 2013. Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. J. Ecol. 101, 1201-1213.

Walker, A.P., De Kauwe, M.G., Bastos, A., Belmecheri, S., Georgiou, K., Keeling, R.F., et al., 2020. Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO2. New Phytol. 299, 2413-2445.

Watson, J.E.M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., et al., 2018. The exceptional value of intact forest ecosystems. Nat. Ecol. Evol. 2, 599-610.

Watson, J.E.M., Shanahan, D.F., Di Marco, M., Allan, J., Laurance, W.F., Sanderson, E.W., et al., 2016. Catastrophic declines in wilderness areas undermine global environment targets. Curr. Biol. 26, 2929-2934.

WBAE (Wissenschaftlicher Beirat Agrarpolitik, Ernährung und gesundheitlicher Verbraucherschutz) und WBW (Wissenschaftlicher Beirat Waldpolitik) beim BMEL (eds.) 2016: Klimaschutz in der Land- und Forstwirtschaft sowie den nachgelagerten Bereichen Ernährung und Holzverwendung. Gutachten. Berlin, Germany.

Weemstra, M., Mommer, L., Visser, E.J., van Ruijven, J., Kuyper, T.W., Mohren, G.M.J., Sterck, F.J., 2016. Towards a multidimensional root trait framework: a tree root review. New Phytol. 211, 1159–1169.

Westgarth-Smith, A.R., Leroy, S.A.G., Collins, P.E.F., Harrington, R., 2007. Temporal variations in English populations of a forest insect pest, the green spruce aphid (Elatobium abietinum), associated with the North Atlantic Oscillation and global warming. Quat. Int. 173, 153-160.

Wördehoff R, Spellmann H, Evers J, Nagel J, 2011. Kohlenstoffstudie Forst und Holz Niedersachsen. Nordwestdeutsche Forstliche Versuchsanstalt (ed.) Beiträge aus der Nordwestdeutschen Forstlichen Versuchsanstalt. Vol. 6. Universitätsverlag Göttingen, Göttingen, Germany.

Chapter 2

Thinned northern German Scots pine forests have a low carbon storage and uptake potential in comparison to naturally developing beech forests

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Abstract

In Europe, production forests with conifers widely replace native broadleaf trees. In the Pleistocene lowlands of northern Germany, >1.7 million hectares of pine forests (*Pinus* spp., mostly *P. sylvestris*) have replaced natural broadleaf forests. We compared aboveground biomass carbon (C) pools and net primary productivity (ANPP) of broadleaf forests with natural development (ND; mostly *Fagus sylvatica* or *Quercus petraea* forests; 146 years old on average) to nearby young pine forests (YP; 65 years old on average) and old pine forests (OP; >90 years) in northern Germany. Study aims where (i) to estimate the aboveground biomass C loss resulting from forest transformation, (ii) to compare the ANPP of broadleaf and pine forests, and (iii) to identify the main factors causing differences in biomass C storage and ANPP between forest types. YP forests stored only half of the biomass C of the ND forests (means: 72 vs. 147 Mg C ha^{-1}); OP stands exceeded YP stands only by ~20% (87 vs. 72 Mg C ha^{-1}). The main factor driving the biomass C pool differences was tree species identity, while stand age was not influential. Mean ANPP was 1.1 Mg C ha^{-1} year^{-1} higher in ND forests than in YP stands due to higher litter production, while wood production was similar. We conclude that large-scale forest conversion to Scots pine forests has decreased the aboveground biomass carbon storage by half and the C sequestration potential with aboveground productivity by ~25%; this effect must be assessed together with changes in soil organic carbon stocks.

Keywords: Aboveground productivity, Biomass carbon storage, Climate change mitigation, *Fagus sylvatica*, Forest conversion, *Pinus sylvestris*

2.1 Introduction

Forests are an important part of the carbon (C) cycle. They store about 45% of terrestrial C in above- and belowground biomass and the soil, and contribute about half of terrestrial net primary production, even though they cover < 30% of the earth's land surface area (Bonan 2008). Europe's forests annually sequester about 100 Tg C more than they release and thus actually represent an important carbon sink (Bellassen and Luyssaert 2014). In the face of global warming, forest management is increasingly confronted with the need to increase the carbon storage and sequestration of forests through silvicultural measures, where possible.

Forestry and wood industry can contribute to the goal of sequestering atmospheric carbon dioxide through four pathways, (i) by increasing the long-term C storage in biomass and soil, (ii) by increasing the amount of wood stored in long-lived products, (iii) by substituting energy-intensive construction materials such as steel or concrete, and (iv) by substituting fossil fuels that are burnt to generate energy or heat. The forests of Germany, which cover 32% of the country (~11 million ha, BMEL 2017), contribute to climate change mitigation by annually fixing c. 58 million t CO_2 (~15.8 Tg C), which is equivalent to 7.4% of the nation's net CO_2 emissions in 2017 (Umweltbundesamt 2019). In addition, the annual material substitution effect is c. 30 million t CO_2-equivalent (~8.2 Tg C) and the annual fixation in the wood product pool is c. 3 million t CO_2-equivalent (~0.8 Tg C, WBAE and WBW 2016). Many silvicultural decisions directly influence the biomass C store of forests by the choice of tree species, the intensity of the thinning regime, and the length of the rotation cycle (Carroll et al. 2012). McKinley et al. (2011) identify two alternative management strategies to increase the carbon pool of existing forests, (1) by decreasing forest harvesting intensity through longer rotation cycles or a decreased amount of timber extraction, and (2) by increasing forest productivity through fertilization, irrigation, planting of fast-growing trees and the control of weeds, diseases and pest insects. Planting more productive, faster growing species and/or reducing the length of the rotation cycle will increase timber yield, which can benefit mitigation pathways (ii) to (iv), but often at the cost of (i), as average biomass stocks may decrease. Consequently, it is intensively debated whether high-throughput (high yield) silvicultural systems with short rotation length or high storage (high biomass) systems with longer rotation should be given priority in order to meet climate change mitigation goals (e.g. Bellassen and Luyssaert 2014).

Tree species identity is one of the key factors determining the C storage in biomass and soil, besides many other factors such as climate, elevation, soil chemistry and fertility, clay content, soil moisture, and stand structure, age and forest history (Johnson and Curtis 2001, Pregitzer and Euskirchen 2004, Jandl et al. 2007, Wördehoff et al. 2011, Seedre et al. 2015, Grüneberg et al. 2019). The choice of tree species is therefore an important management decision that can affect the forest C balance for decades and even centuries. While many case studies have investigated the C sequestration and storage capacity of single tree species

(e.g. Law et al. 2003, Xiao et al. 2003, Bruckman et al. 2011, Seedre et al. 2015), only few studies exist about landscape-scale consequences of widely conducted species substitutions (Vallet et al. 2009).

In Europe, where forests are only rarely left to their natural development (Parviainen 2005), the forest management regime generally controls the appearance of a forest and thus also its carbon balance. The question of how forest management decisions affect the carbon balance and how silviculture can help mitigating climate warming has been addressed in greater depth in forest science only recently (Bellassen and Luyssaert 2014). The actual forest cover of Central Europe consists largely of tree species that do not represent the natural forest vegetation, which once was dominated by European beech (*Fagus sylvatica* L.) in many regions (Leuschner and Ellenberg 2017). Before humans opened the forests, about two-third of Germany's forest area was covered by *F. sylvatica* forests (Bohn and Neuhäusl 2003). Since Neolithic times, forest cover has been progressively reduced until a minimum extension was reached in the Middle Ages and the early modern era. From the 19th century onwards, systems of planned forestry have been implemented in Germany and other Central European countries, and many deforested areas were planted preferentially with conifers, notably Scots pine (*Pinus sylvestris* L.) in the lowlands and Norway spruce (*Picea abies* Karst.) at higher elevations. Conifer forests were established on former arable land, heathland, grassland and wasteland, but they also replaced part of the remaining natural broadleaf forest cover, as conifers, in particular pine, are less demanding for nutrients and water and grow faster at young age than the native broadleaf trees (Leuschner and Ellenberg 2017). Moreover, many of the degraded, once forest-bearing soils could in the first generation of forest re-establishment only be planted with pine, which helped to stabilize the soils and to provide fuelwood (e.g. Milnik 2007, NLF 2011).

Especially in the Pleistocene lowlands of the North of Poland, Germany, and the Netherlands, where sandy, less fertile soils prevail, large parts of the woodlands are nowadays dominated by monospecific, even-aged Scots pine forests. In the northern German lowlands between the rivers Ems in the west and Oder in the east, 52.1% of the current forest area is covered by pine forests, extending over > 1.7 million ha (analysis based on TI 2015). Under current climatic and edaphic conditions, forests of Scots pine would naturally occur on only 2.1% of the region's area once covered by forests, while beech-dominated forest would occur on 58.1% (BfN 2010, analysis conducted with ESRI ArcMap 10.1). Today, beech forests have been reduced to 6.5% of the current forest area (analysis based on TI 2015). Only few regions on earth have experienced such a fundamental change in forest cover from broadleaf to conifer forests (FAO 2016). A knowledge gap exists with respect to the consequences for forest biogeochemistry and the carbon balance of this large-scale forest transformation. Yet, replacing native hardwood trees by conifers on several million hectares in Germany, Poland and the Netherlands must have had far-reaching consequences for important ecosystem functions, notably ecosystem carbon cycling, groundwater recharge, soil biological activity and nutrient supply, forest disturbance regimes, and the regulation of

regional climates. While the consequences of such a transformation for soil carbon storage have been studied in a number of case studies (e.g. Heinsdorf 2002, Schulp et al. 2008, Leuschner et al. 2013, see also the *meta*-analysis by Guo and Gifford 2002), related effects on biomass C storage and annual C sequestration have not been investigated in more detail.

Forest restoration can be an effective way to rehabilitate ecosystem services (Aerts and Honnay 2011). The increasing awareness of the concurrent loss of biodiversity and ecosystem services has raised political interest in ecosystem restoration (Aronson and Alexander 2013), and in March 2019, the United Nations (UN) declared the UN Decade on Ecosystem Restoration 2021 – 2030 (https://www. decadeonrestoration.org). During the last decades, forest policy in Germany has gradually changed toward concepts that value ecosystem services other than timber production as well, notably the provision of drinking water, the protection of forest soils, carbon storage, and the conservation of habitats for forest-specific biota (BMEL 2017). In various regions, forestry has declared the goal to replace part of the monospecific conifer forests by more natural mixed and broadleaf forests in order to increase stand resistance against pests, storm damage, fire and future climatic hazards, and to increase biodiversity (Anders et al. 2005, MLUR Brandenburg 2004, NLF 2011, MLU Sachsen-Anhalt 2014). These shifts in opposite direction will also affect the forest carbon balance. In many woodlands, altered management concepts have resulted in stands that are currently passing through a transitional stage with broadleaf trees thriving under a shelter of older pines (e.g. NLF 2011), while pine itself does not regenerate on the dark forest floor. Nevertheless, pine forests still dominate the woodlands of the northern German, Dutch and Polish lowlands to a large extent (Leuschner and Ellenberg 2017).

In a network of 48 forest plots from all over northern Germany along a gradient from sub-oceanic to sub-continental climate, this study compares the carbon pools in the aboveground biomass (live trees, deadwood and saplings) and annual C sequestration of naturally developing broadleaf forests, with the currently dominating Scots pine forests and the transitional stage to the natural forest vegetation with broadleaf trees under pine shelter. Study aim was to supply data for carbon accounting of forestry in the northern German lowlands and to assess the consequences for the aboveground biomass carbon stocks and C sequestration of large-scale forest transformation from broadleaf to conifer forest, as it has occurred in the past and may partially be reversed in the future. We hypothesize that (i) aboveground biomass carbon stocks and (ii) aboveground net primary productivity are higher in hardwood-dominated forests with natural development than in the managed pine forests and the pine-beech transitional stage. Furthermore, we analyze which characteristics of the compared forest types (tree species identity, tree age, forest management, and abiotic factors) are influencing the biomass carbon stocks and sequestration most.

2.2 Methods

2.2.1 Study region

The study was conducted at 16 study sites in the northern German Pleistocene lowlands (North German Plain), extending from the North Sea and Baltic Sea coasts in the north to the border of the central German low mountain ranges in the south and covering a continentality and precipitation gradient from the Dutch border in the west to the Polish border in the east (Fig. 2.1). The North German Plain was mainly formed by glacial processes during the Pleistocene, in which moraine landscapes with mostly flat or undulating reliefs were shaped (Böse et al. 2018). The study sites are located on moderately dry to fresh sandy soils with low to medium fertility, which mainly originate from moraine deposits of the last (Weichselian) or penultimate (Saalian) glacials. The climate of the North German Plain is cool-temperate; the gradient from a sub-oceanic climate in the west to a sub-continental climate in the east manifests in slightly higher summer temperatures but lower winter temperatures and lower precipitation at the Polish border. Mean annual temperature at the study sites ranges from 8.6 to 10.3 °C and mean annual precipitation from 555 to 908 mm year^{-1} (means of 1981 – 2010, DWD CDC 2019). A list of the study sites with stand characteristics and climatic conditions is given in supplemental Table A2.1.
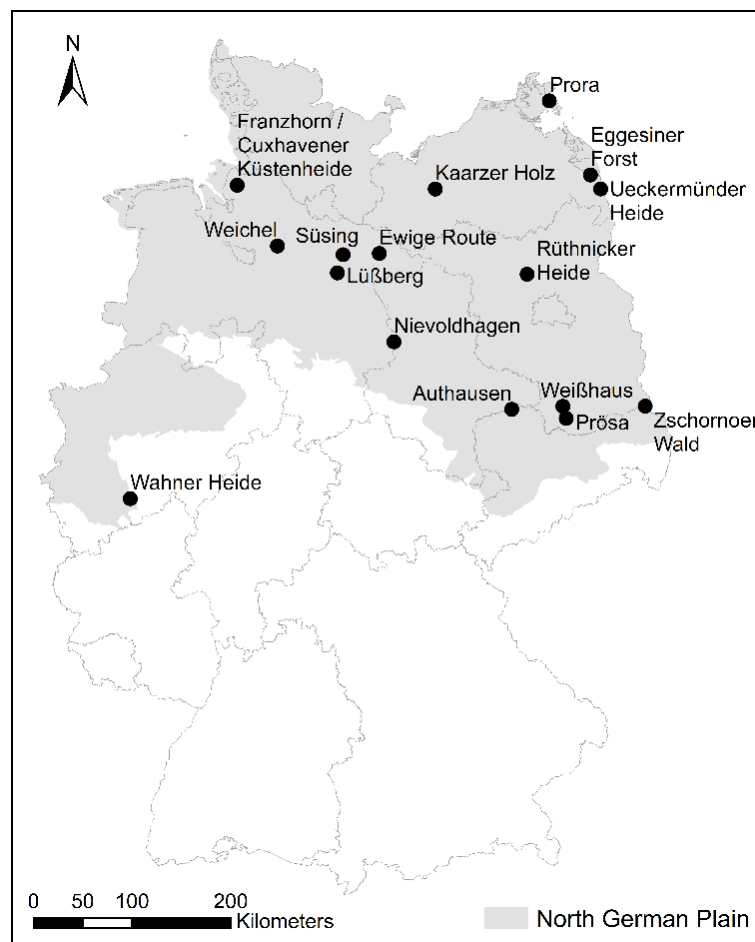
Figure 2.1. Map of the North German Plain with the 16 study sites.

2.2.2 Study design

At the 16 sites, we compared planted Scots pine forests with naturally developing forests, in the large majority broadleaf forests, which represent the vegetation that was present before forest transformation. Since true primary forests do no longer exist in Central Europe, we investigated at 13 of the sites formerly managed beech forests (*Fagus sylvatica* L.), at two sites formerly managed sessile oak forests (*Quercus petraea* Matt. Liebl.) and at one site in the east a formerly managed pine forest (*Pinus sylvestris* L.) in a protected area. In these forests, the last thinning operations happened 6 to 41 years ago and the forests are currently developing without further forestry impact (forests with natural development, ND). Stand age exceeded 100 years in all stands (104 – 230 years old, mean: 146). At all 16 sites, we chose nearby planted Scots pine forests of two different age classes (young: YP, old: OP) for comparison. At site 02, *Pinus nigra* J. F. Arnold forests instead of *P. sylvestris* were investigated. We decided to include this site at a coastal location, to extend the geographic and climatic gradient. The three forest stands at a site (ND, OP and YP) were located on similar geological substrate to ensure comparable growing conditions. Young pine forests (YP) are pure pine stands of about 65 years (55 – 81 years old, mean: 65), of even age and managed by regular thinning. A large part of the pine forests in northern Germany are of this age, as they were planted after clear-cut in the late 1940s in the post-WWII epoch (Milnik 2007). Old pine forests (OP) are pine-dominated forests with broadleaf trees in the understory that approach the end of the rotation cycle, with a stand age of at least 90 years (90 – 155 years old, mean: 112). These stands are also managed; they represent a transitional stage to more natural, mixed or broadleaf forests. In total, 48 stands with a minimum size of 6 ha were investigated, i.e. each three (ND, OP, YP) at similar edaphic conditions at the 16 study sites. In each stand, 10 randomly distributed circular plots with a size of 0.1 ha (r = 17.84 m) and a minimum distance of 66 m to the next plot were established in the field. This resulted in a total of 480 circular plots.

2.2.3 Stand inventory

In the 0.1 ha plots, all trees with a diameter at breast height (DBH) > 7 cm were recorded with respect to species identity, DBH, vitality (living, dying, dead) and assigned to three categories (intact crown, partial crown breakage, snag). The height of canopy trees was measured for at least three living, intact trees per plot of each occurring species and also for all dead and fragmented trees (partial crown breakage). The height of the remaining trees was estimated with species-specific stand height curves using Petterson's function (Schmidt 1967). Dead lying trunks with a diameter at the thicker end > 20 cm were also inventoried (categories: crown, stem, root plate, or combination of these). For all dead trees, the decay stage was determined according to Albrecht (1991). Saplings (living trees with a DBH < 7 cm) were recorded with respect to species identity and height class in the northeastern quadrant (trees taller than 1.5 m) or in a transect of 25 m^2 (trees smaller than 1.5 m). The root

collar diameter was measured of up to 4 saplings per tree species and height class. In total, 19,218 living and 8,892 dead trees were measured in the 480 plots.

2.2.4 Carbon pool estimation

Aboveground biomass in the plots was calculated separately for three different compartments. The biomass of live and dying intact trees (1) was calculated using species-specific allometric regressions (see Table A2.2). These equations allow calculating the biomass of individual trees (wood and leaves or needles, fruits not included) from DBH and, in some cases, height. The volume of dead trees and tree fragments (2) was calculated with the approach of Meyer (1999), using SAS-routines developed by Meyer et al. (2009). According to the degree of wood decay, correction factors were applied (Meyer et al. 2009). Biomass was then calculated by multiplying wood volume with species-specific values of wood density, taken from the global wood density database (Chave et al. 2009, Zanne et al. 2009). The biomass of the saplings (3) was calculated using species-specific allometric regressions developed for young temperate tree species by Annighöfer et al. (2016).

To calculate biomass carbon, recent studies encourage the use of tree species-specific values of carbon concentrations, since the commonly used C concentration of 50% (e.g. Penman et al. 2003, Wirth et al. 2004, Wördehoff et al. 2011) can lead to over- or underestimation of carbon stocks (e.g. Bert and Danjon 2006, Zhang et al. 2009). However, intraspecific variation exceeds interspecific variation (Wirth et al. 2004) and C concentrations in the literature for European beech and Scots pine both vary around 50% in the different tree tissues and study regions (e.g. Laiho and Laine 1997, Janssens et al. 1999, Rademacher et al. 2009, Husmann et al. 2018). Hence, we decided to adopt a carbon concentration of 50% for all biomass fractions.

2.2.5 Aboveground net primary productivity

Aboveground net primary productivity was measured on six randomly chosen circular plots in the forests with natural development (ND) and young pine forests (YP). Dendrometer tapes were attached at breast height to 15 representative trees (according to tree species and DBH, minimum DBH = 7 cm) per plot. In plots with < 15 trees, all individuals were measured. The diameters of the selected trees were recorded annually in autumn after the growing season in the years 2015 to 2017 (study sites 01 and 16: 2016 – 2017). This resulted in about 2,500 annual DBH-measurements. The diameter increase of trees that were not measured was estimated from species-specific relationships between DBH and DBH increase calculated for each year. Wood production was obtained as the difference in woody biomass between subsequent years as calculated with allometric regressions (Table A2.2). Litter production was measured in 2015 (no data for YP stands of study sites 02 and 11) and 2016 (no data for YP stands of study sites 02, 11 and 12) using one circular litter trap per plot with a diameter of 0.6 m (beech and oak forests) or 0.2 m (pine forests). The traps were emptied in autumn after litter fall and checked again in spring. In the pine stands, traps were

additionally emptied in summer. The litter material was sorted for fruits and leaves or needles of the main and admixed tree species, oven-dried at 70°C for 48 h and weighed. Since cone production in the pine forests was not adequately recorded by the litter traps, it was additionally measured in 2016 by removing all cones from the forest floor on one marked square of 1 m^2 area per plot and collecting all cones fallen into this square after 1 year. This data was also applied to the 2015 data. The sum of wood production and litter production adds up to give aboveground net primary productivity (ANPP).

2.2.6 Statistical analyses

All statistical analyses were conducted with R 3.4.0 software (R Core Team 2017). Since each three forest stands of a site are clustered, our samples are partly dependent. For all statistical analyses, we used mean values of the forest stands. Due to inhomogeneous variances between groups, we tested for differences in stand characteristics and carbon stocks between the three forest types and for differences in wood production between years with Friedman rank sum tests (Hollander and Wolfe 1973). Post-hoc tests with Bonferroni correction of p-values were applied (Eisinga et al. 2017, Pohlert 2018). To detect differences in wood production, litter production and ANPP between forest types, and differences in litter production and ANPP between years, Wilcoxon signed rank tests or paired t-tests were applied, depending on the normality or non-normality of data distribution. When analyzing only the ND forests and the YP forest, effects of the stand characteristics were difficult to disentangle from the effect of the main tree species. Therefore, influences of the following variables on ANPP were analyzed separately for the two forest types: stand age, time since last timber extraction, the main tree species' share of basal area, mean growing season (April - October) precipitation and temperature. Correlations were tested with Spearman rank correlation analysis due to non-normal data distribution of ANPP and most other variables. A significance level of $\alpha = 0.05$ was adopted for all analyses.

To identify the underlying causes of differences in the total aboveground biomass C pool between forest types, a linear mixed-effects model was used (Pinheiro et al. 2017). The following variables and their interactions were included as fixed effects: stand age, time since last timber extraction, main tree species (*Pinus sylvatica* L. and *P. nigra* J. F. Arnold summarized as Pine), the main tree species' share of basal area, mean annual precipitation and mean annual temperature. Study site was included as random intercept to account for the study design. Since most explanatory variables are stand-level parameters, stand means of C-pools were used in the model (n = 48). For comparison of effect sizes, all explanatory variables were scaled and centered. Due to heteroscedasticity of residuals, we included specified variance structures (Pinheiro et al. 2017). The starting model included all explanatory variables and the maximum number of interactions and was fitted with maximum likelihood. The model with the best variance structure was selected based on small-sample AIC (AICc, Mazerolle 2017). Then, all variables with p > 0.05 were dropped consecutively. The model with the lowest AICc ($\Delta > 2$) and the lowest number of included

variables was chosen as the final model. It was refitted with restricted maximum likelihood. For model validation, (standardized) residuals of the final model were plotted and generalized variance inflation factors were calculated.

2.3 Results

2.3.1 Stand structural characteristics

Stand characteristics of the three forest ecosystem types ND forests, YP forests and OP forests are given in Table 2.1. Due to the study design, the time since last timber extraction was higher in ND forests than in OP forests and YP forests, stand age was lower in YP forests than in ND forests and OP forests, and the main tree species' share of the basal area was lower in OP forests than in YP forests. While quadratic mean diameter was higher and stem density lower in ND forests than in OP forests and YP forests, stand basal area did not differ between the three forest types.

Table 2.1. Some stand characteristics in the three forest types forests with natural development (ND), old pine forests (OP), and young pine forests (YP) (means ± SE). χ^2 and p-values of Friedman rank sum tests, df = 2 in all cases. Different letters indicate significant differences between forest types.

	ND	OP	YP	χ^2	p-value
Time since last timber extraction (year)	18 ± 11 [a]	6 ± 7 [b]	5 ± 5 [b]	17.5	< 0.001
Stand age (year)	146 ± 31 [a]	112 ± 20 [a]	65 ± 6 [b]	26.0	< 0.001
Main tree species' share of basal area (%)	88.3 ± 7.9 [ab]	65.7 ± 22.8 [a]	91.0 ± 12.6 [b]	15.1	< 0.001
Quadratic mean diameter (cm)	41.8 ± 9.4 [a]	31.0 ± 4.4 [b]	26.4 ± 3.3 [b]	22.9	< 0.001
Stem density (n ha^{-1})	251.9 ± 94.3 [a]	405.8 ± 128.0 [b]	541.4 ± 133.0 [b]	20.4	< 0.001
Stand basal area (m² ha^{-1})	29.1 ± 6.4 [a]	27.5 ± 6.2 [a]	28.1 ± 4.8 [a]	0.4	0.829

2.3.2 Carbon stocks in the aboveground biomass

Carbon stocks in the aboveground biomass (live trees, deadwood, and saplings) were higher in forests with natural development than in old and young pine forests ($\chi^2 = 21.5$, df = 2, p < 0.001), with about double the amount of carbon stored in the ND stands (147.2 ± 48.8 Mg C ha^{-1}) than in the YP stands (72.0 ± 17.0 Mg C ha^{-1}). Live trees constituted by far the largest fraction of stored biomass C in all forest types; this pool was greater in forests with natural development than in old and young pine stands ($\chi^2 = 21.5$, df = 2, p < 0.001). C pools in deadwood mass were smaller in young pine forests than in the two other forest types ($\chi^2 = 15.9$, df = 2, p < 0.001); this pool was smaller than 5 Mg C ha^{-1}

in all three groups. In the biomass of saplings, < 1 Mg C ha^{-1} was stored in all three forest types, with no differences between groups ($\chi^2 = 0.88$, df = 2, p = 0.646). Variation in C pools among sites was highest in the forests with natural development and lowest in the young pine forests (except for the C pool in the saplings, Table 2.2). In the group of forests with natural development, beech forests had larger carbon pools in the live tree biomass and in the saplings than oak and pine forests, whereas the deadwood C pool was largest in the oak forests. Not only the pine forests (YP and OP) had much smaller total biomass C pools than the ND forests, but the studied naturally developing pine forest (ND group) as well (Table 2.2).

Table 2.2. Carbon pools in the different compartments and total aboveground biomass C pool in the three forest types, in case of ND forests additionally given for the plots with the three main tree species. The value for ND forests is the weighted mean of the three species. Different letters indicate significant differences between forest types.

Forest type	Live tree biomass (Mg C ha^{-1})	Deadwood mass (Mg C ha^{-1})	Biomass of saplings (Mg C ha^{-1})	Total aboveground biomass (Mg C ha^{-1})
ND	141.64 ± 48.97 [a]	4.56 ± 3.17 [a]	0.97 ± 2.24 [a]	147.17 ± 48.77 [a]
Fagus sylvatica	154.28 ± 43.03	4.08 ± 2.02	1.10 ± 2.48	159.45 ± 42.51
Quercus petraea	107.82 ± 7.27	9.35 ± 6.51	0.45 ± 0.63	117.62 ± 13.15
Pinus sylvestris	45.02	1.24	0.36	46.63
OP	83.16 ± 23.7 [b]	3.33 ± 1.92 [a]	0.31 ± 0.29 [a]	86.8 ± 24.58 [b]
YP	69.99 ± 16.77 [b]	1.64 ± 0.87 [b]	0.41 ± 0.47 [a]	72.04 ± 17.02 [b]

The final mixed-effects model to explain total aboveground biomass C pools from possible biotic and abiotic factors contained the covariates main tree species, time since last timber extraction and the main tree species' share of basal area (Table 2.3). The main tree species pine, in comparison to beech, had the strongest, negative effect on the carbon pool in the aboveground biomass, whereas the negative effect of oak was not significant (Fig. 2.2a). Time since last timber extraction had a positive effect on the carbon stocks (Fig. 2.2b), and the main tree species' share of basal area had a negative effect. In contrast, the covariates stand age, mean annual temperature and mean annual precipitation had no significant influence and were thus not included in the final model (Fig. 2.2c-e). Plots of the (standardized) residuals of the model and generalized inflation factors are given in supplemental Fig. A2.1 and Table A2.3, respectively.

Table 2.3. Estimated values of the scaled and centered covariates of the final model to explain aboveground biomass C pools; given are the standard error, degrees of freedom, and t- and p-values.

	Value	Standard error	df	t-value	p-value
Intercept	142.05523	8.213522	28	17.295288	< 0.001
Main tree species: Pine	−58.43927	10.281453	28	−5.68395	< 0.001
Main tree species: Oak	−16.58132	17.164018	28	−0.966051	0.342
Time since last timber extraction	12.97134	6.220711	28	2.085185	0.046
Main tree species' share of basal area	−14.71903	2.297965	28	−6.405244	< 0.001
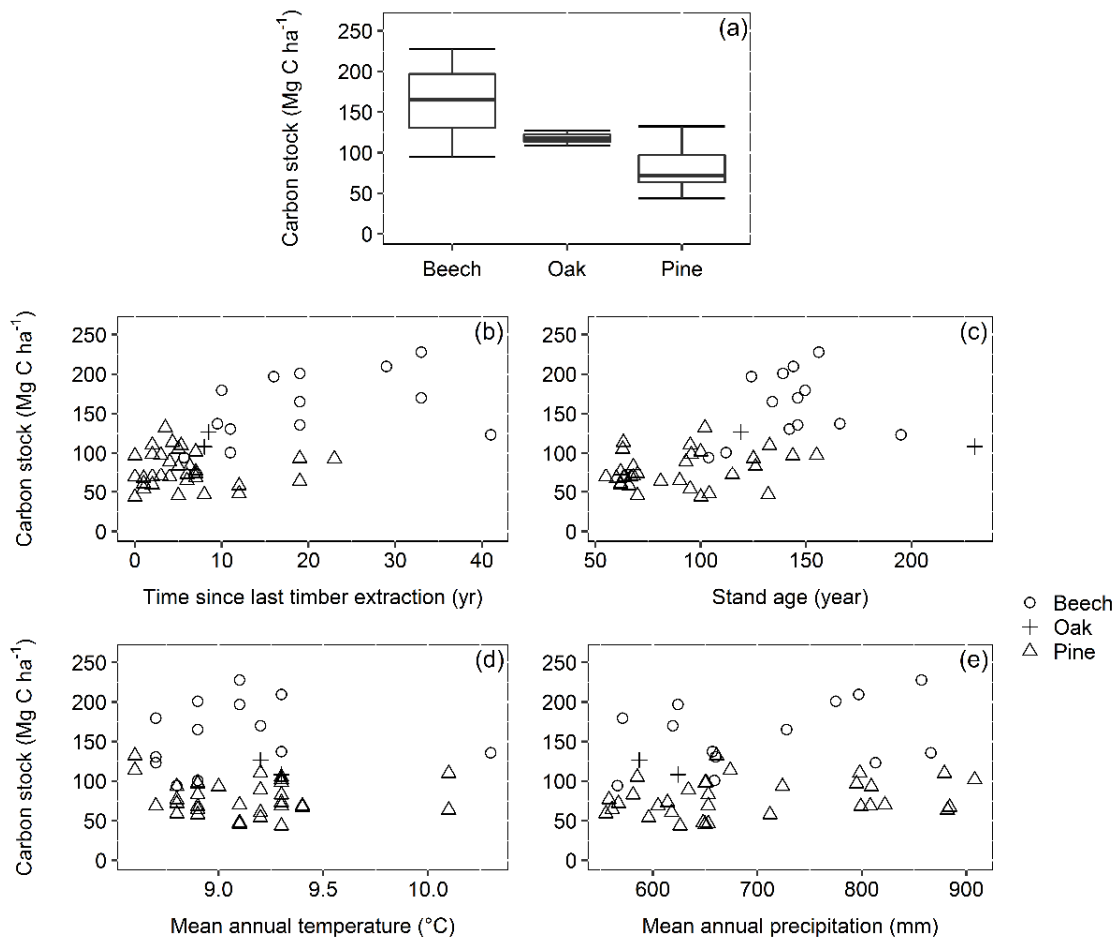
Figure 2.2. Carbon stocks in the aboveground biomass in dependence on the variables main tree species (a), time since last timber extraction (b), stand age (c), mean annual temperature (d) and mean annual precipitation (e).

2.3.3 Aboveground net primary productivity

In the years 2015 and 2016, litter production was higher in forests with natural development than in young pine forests (Fig. 2.3). The mean difference between the two groups was larger in 2016 (1.36 Mg C ha^{-1} year^{-1}) than in 2015 (0.55 Mg C ha^{-1} year^{-1}), due

to a higher litter production in ND forests in 2016 than in the year before (V = 2, p < 0.001). In 2015, a trend to a higher wood production in ND forests than in YP forests existed, which was absent in the following two years (Fig. 2.3). Wood production in ND forests differed between years (χ^2 = 9, df = 2, p = 0.011), with a higher production value in 2015 than in 2016. In the YP forests, wood production increased from 2015 to 2017, but the differences between years were not significant (χ^2 = 5.5, df = 2, p = 0.063). Aboveground net primary productivity in ND forests was higher in 2016 than 2015 (V = 15, p = 0.017), but did not differ between years in YP forests (V = 29, p = 0.764). In 2015 and 2016, ANPP was higher in ND forests than in YP forests (2015: V = 75, p = 0.002; 2016: t = 4.96, p < 0.001), with a larger difference in 2016 (1.35 Mg C ha^{-1} year^{-1}) than in 2015 (0.99 Mg C ha^{-1} year^{-1}). ANPP averaged over the recorded years was also higher in ND forests than in YP forests (4.33 vs. 3.27 Mg C ha^{-1} year^{-1}, Fig. 2.4a), with a mean difference of 1.07 Mg C ha^{-1} year^{-1}. In the group of forests with natural development, beech stands had higher ANPP than the two oak stands; the lowest ANPP was measured in the pine forest with natural development (Fig. 2.4b).

In both, the ND and YP forests, ANPP did not correlate with any of the stand- or site-related variables (Fig. 2.5), except for a negative correlation in YP forests between ANPP and the main tree species' share of basal area (r_s = -0.69, p = 0.006).
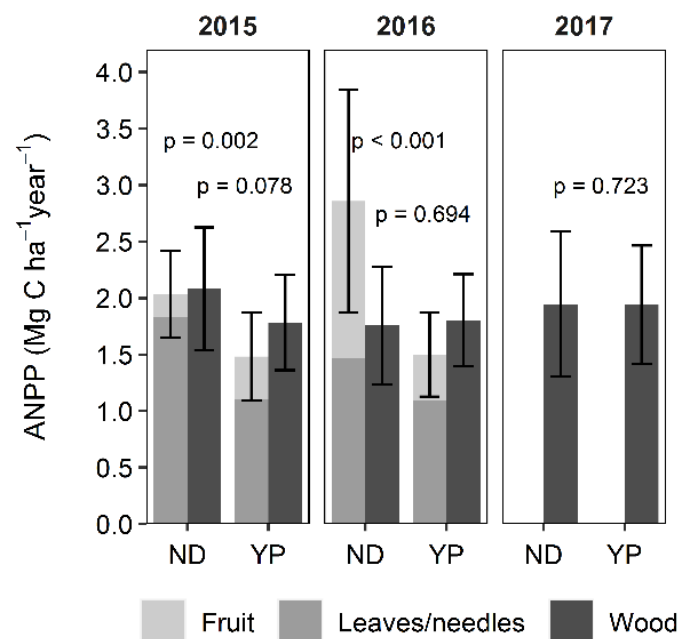
Figure 2.3. Means and standard errors of litter and wood production in the years 2015 – 2017 in forests with natural development (ND) and young pine forests (YP). The p-values of paired t-tests and Wilcoxon signed rank tests are given for differences between forest types in litter production (upper values) and wood production (lower values). No litter data were available for 2017.
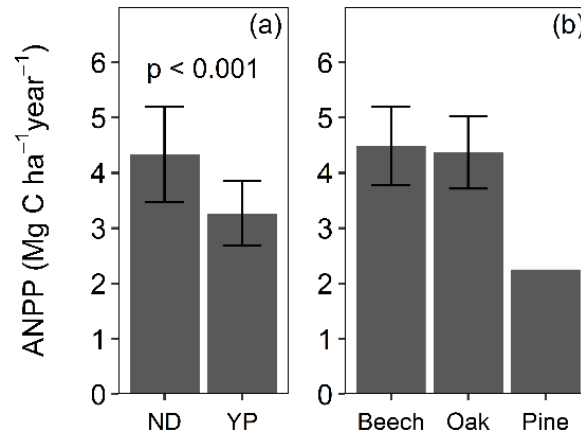
Figure 2.4. Means and standard errors of aboveground net primary productivity by forest type (a) and by main tree species in forests with natural development (b). The p-value of a Wilcoxon signed rank test for the difference in ANPP between the forest types is given.

2.4 Discussion

2.4.1 Consequences of historic forest conversion for aboveground biomass carbon storage

For managed European beech forests with stand ages > 100 years, a wide range of aboveground biomass carbon pool sizes has been reported ($105 - 330$ Mg C ha^{-1} in live trees, Rademacher et al. 2009), reflecting differences in climate, soil moisture and soil fertility, but also in thinning regimes and related stem density. With a mean of 154 Mg C ha^{-1} in live tree biomass, the 13 unmanaged beech forests (ND) of our study are in the lower range of this span. The YP and OP forests show similar biomass carbon pool sizes like other Scots pine forests of comparable age in Central and Western Europe (~75 Mg C ha^{-1} in a 73-year-old Belgian stand, Xiao et al. 2003; ~ 80 Mg C ha^{-1} in $60 - 80$-year-old pine forests from different regions of Germany, Burschel et al. 1993), but values also vary widely with soil fertility (Heinsdorf 2007).
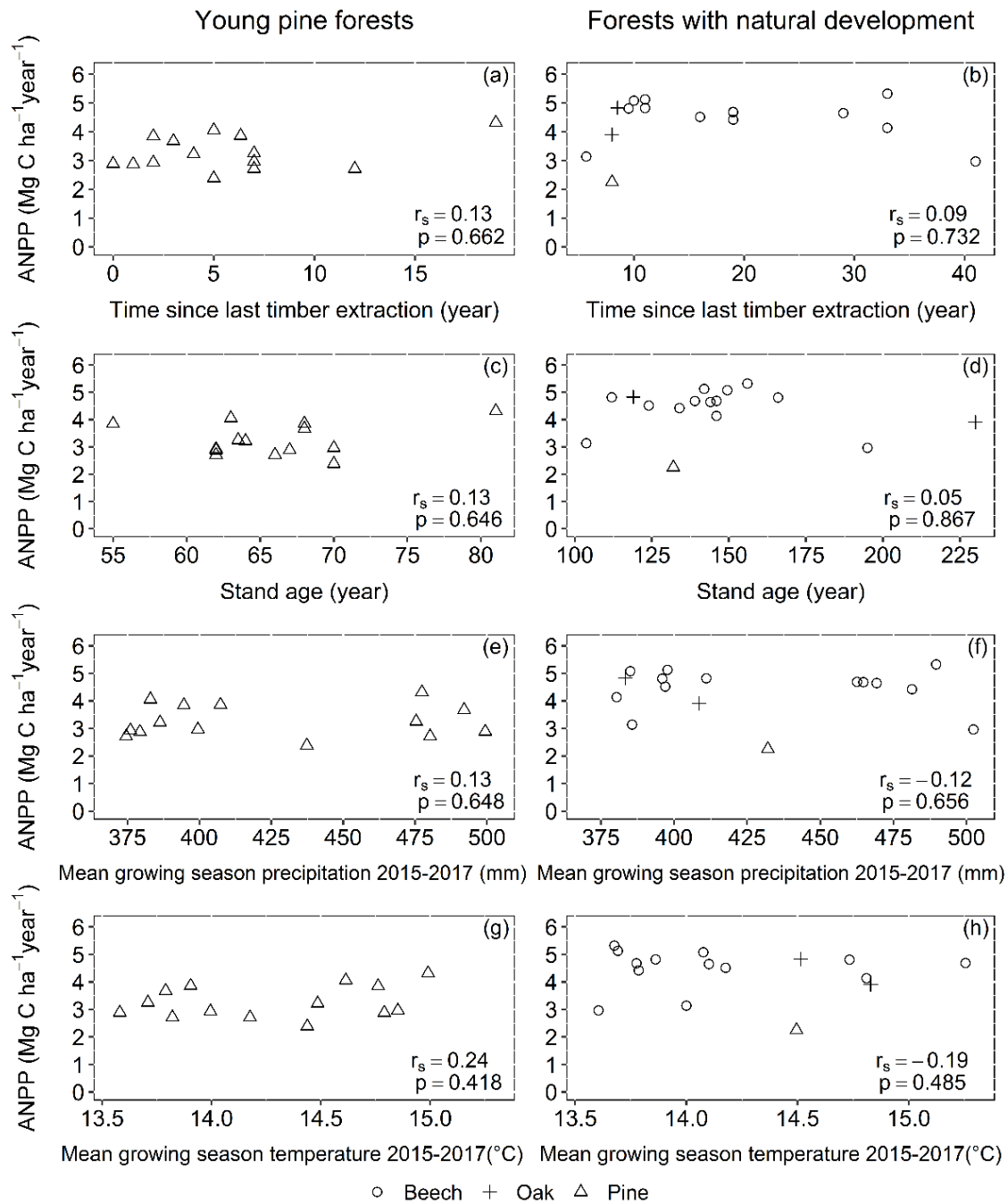
Figure 2.5. Spearman rank correlation analysis for relations between aboveground net primary productivity and time since last timber extraction (a,b), stand age (c,d), mean growing season precipitation 2015 – 2017 (e,f) and mean growing season temperature 2015 – 2017 (g,h) in young pine forests and forests with natural development. Correlation coefficients (r_s) and p-values are given. Note the different time scales for time since last timber extraction and stand age in the two forest types.

With a mean of 72 Mg C ha^{-1}, the aboveground biomass (live trees, deadwood and saplings) of the young pine forests was about 45% of that of the beech ND forests and half of the biomass of all ND forests (including oak and pine). Contrary to expectations, the large biomass difference cannot be explained by the greater mean age of the ND forests (means of ND and YP: 146 vs. 65 years). Our mixed model clearly reveals the dominant role of tree species for biomass C storage in the studied forests, while stand age, which usually has a

large effect (e.g. Pregitzer and Euskirchen 2004), was not influential in our 48 stands. The large influence of the species' characteristic productivity is enhanced by species-specific silvicultural practices applied to beech and pine stands. Inventory data from stands in the north German lowlands show that the biomass accumulation rate (trunk, branches, coarse roots) in Scots pine forests starts to level off at a stand age of about 60 – 80 years, while it continues to increase until 120 – 140 years in beech stands (Burschel et al. 1993). As a consequence, the old pine forests in transition to hardwood forest (OP) with nearly 50 years higher stand age had an only 20% larger biomass C pool than the YP stands. That the beech ND stands of our study have accumulated considerably more aboveground biomass carbon than the pine forests (OP) at similar age, is not a consequence of basal area differences between the two forest types, but only caused by the higher carbon gain of beech, which leads to superior trunk and branch volume production rates of beech. In addition, *F. sylvatica* has an about 39% higher wood density than *P. sylvestris* (0.59 vs. 0.42 g cm^{-3}, Zanne et al. 2009), which results in a higher carbon accumulation rate, when volume growth is similar.

The absence of a stand age effect on the biomass carbon pool is surprising, as our stands cover an age interval of ~100 years for both beech (103 – 195 years old) and pine stands (55 – 155 years old). One reason is forest management, i.e. the regular extraction of stems in the course of stand thinning, which has reduced the slope of the biomass accumulation curve. In particular in the old pine forests (OP), a considerable fraction of the standing wood volume must already have been extracted in past decades. In the beech or oak forests with natural development, thinning has been conducted in the more distant past as well, which also must have reduced age-related differences in biomass C pools.

2.4.2 Carbon sequestration potential of naturally developing broadleaf forests vs. thinned pine forests

Managed beech forests at maturity (80 – 120 years old) have an aboveground productivity (ANPP) in the range of 2.85 – 6.25 Mg C ha^{-1} year^{-1} (Rademacher et al. 2009, Leuschner and Ellenberg 2017); Leuschner and Ellenberg (2017) give a mean value for Central European managed beech forests of about 5.3 Mg C ha^{-1} year^{-1}. These studies refer to beech stands mostly at submontane to montane elevation, where productivity should be somewhat lower than in the warmer lowlands. Yet, many of the studied sites are more fertile than our studied stands on Pleistocene sands. This agrees well with the slightly lower mean ANPP of 4.5 Mg C ha^{-1} year^{-1} measured in the 13 beech ND forests in this study. With an ANPP of about 3.3 Mg C ha^{-1} year^{-1} in the YP forests, productivities are smaller than in many other Scots pine stands in Central and Western Europe. For example, Art and Marks (1971), DeAngelis et al. (1981) and Cannell (1982) give ANPP values between 3.95 and 11.0 Mg C ha^{-1} year^{-1} for various pine stands of 35 – 55 years, and Hagemeier (2002) values of 7.2 and 9.0 Mg C ha^{-1} year^{-1} for two 48- and 50-year-old pine forests, which are higher than our values. Yet, Anders et al. (2005) measured only 3.2 Mg C ha^{-1} year^{-1} in an 84-year-old pine stand in north-eastern Germany. Besides low soil fertility, one main driver of the

relatively low productivity of our pine forests is the considerably smaller stem density and basal area than in many other pine stands.

In confirmation of our second hypothesis, aboveground net primary productivity was about 25% lower in the young pine forests than in the forests with natural development (means of 3.27 vs. 4.33 Mg C ha^{-1} year^{-1}), whereas basal area was very similar (28.1 vs. 29.1 m^2 ha^{-1}). The difference is mainly a consequence of the typically much lower leaf area index of pine (about 1.8 – 3 in pine vs. 5 – 8.5 in beech; Leuschner and Ellenberg 2017), which must result in a lower canopy carbon gain. The smaller leaf area is reflected in the lower litter production of the pine stands. While wood production was roughly similar between ND and YP stands (1.8 – 1.9 Mg C ha^{-1} year^{-1}) despite different ages, litter production was higher in the former. The difference existed in the years 2015 and 2016, but was especially large in the year 2016, when fruit production increased at all beech stands except for site 14, indicating a beech masting event. This masting event could also explain the simultaneous decrease in wood production in beech (Müller-Haubold et al. 2015, Hacket-Pain et al. 2018).

An unexpected result is the lack of climatic factors with a significant influence on ANPP in our stand sample. Climate during the study period varied largely between years. In 2015, growing season temperature and precipitation were similar to the multi-annual mean (average values in the studied stands in 2015: 13.75 °C/ 393 mm; 1981 – 2010: 13.82 °C/ 416 mm, DWD CDC 2019). Thus, the measured ANPP values in 2015 should be typical for the forests under past climatic conditions. In contrast, the growing season of 2016 was very warm and dry (14.65 °C and 351 mm). Under these conditions, which likely will become more frequent in the future (IPCC 2014, Schär et al. 2004), ANPP increased in the beech forests due to the high fruit production value, thus increasing the ANPP difference between beech and pine compared to the year before. In contrast, wood production was similar in ND and YP stands in 2016. In 2017, both growing season temperature and precipitation were high compared to the multi-annual mean (14.22 °C and 547 mm), which had no significant influence on wood production, when compared to the typical year of 2015. The restoration of non-structural carbohydrate reserves that have been used for fruit production in the preceding beech mast is probably one reason for the relatively low wood production in ND forests in 2017 (Hoch et al. 2003). Furthermore, wide variation in mean growing season precipitation 2015 – 2017 (~375 – 550 mm year^{-1}) across the climate continentality gradient from the North Sea coast to the Polish border apparently had no significant effect on the aboveground productivity of beech (and oak) and pine. A similar pattern has been observed in a precipitation transect study of beech forests in the north-west German lowlands, where wood and leaf production decreased but fruit production and belowground productivity increased, and total ANPP remained unchanged from moist to dry sites (Hertel et al. 2013, Müller-Haubold et al. 2013). This may suggest that reduced precipitation acts mainly on tree-internal allocation of carbohydrates, while canopy carbon gain and total NPP seem to be affected relatively little by the precipitation regime. If the production of a large fruit crop in

beech turns out to be the main driver of the ANPP difference between beech and pine, then it is possible that this difference will increase in future due to the recently observed growing frequency of beech masting in parts of Europe (Schmidt 2006, Övergaard et al. 2007). Productivity measurements over a longer time period would help to verify the ANPP differences between beech and pine under varying climatic conditions.

In the young pine forests, as in the ND forests, variation in stand age and time since management abandonment did not significantly influence ANPP. The relative uniformity of ANPP with time could partly be caused by the regular stand thinning activities, which may adjust stand leaf area and thus photosynthetic carbon gain to a relatively constant level.

Understory vegetation was not considered in our data and is often neglected in studies investigating the net primary productivity of forests. While the relative contribution of understory plants to aboveground biomass is typically < 1% in Northern Hemispheric forests, its relative contribution to net primary productivity is estimated at c. 4% (Gilliam 2007).

2.4.3 Comparing our forests with natural development with true primary forests

In Central Europe, true primeval forests without human influence since many centuries (except for atmospheric deposition) are virtually absent in the lowlands and restricted to very small patches in the Alps and Carpathians (Parviainen 2005, Sabatini et al. 2018). Due to the lack of a good primeval forest reference, we compare the biomass and productivity data of the ND forests to true beech primeval forests in the Slovakian Carpathians, from where comparable data are available. Clearly, these forests are at montane instead of lowland elevation, which limits comparability, but they may indicate the magnitude of natural C pools and fluxes.

The possible end point of aboveground biomass carbon accumulation in a development toward a natural forest, which is indicated by the biomass C pools in live trees of the three Slovakian beech primeval forests (~193 Mg C ha^{-1}, Glatthorn et al. 2018), is only 25% larger than the mean of our formerly managed beech forests. Our beech forests showed a tendency of increasing total aboveground biomass C pools since management abandonment by roughly 16 Mg C ha^{-1} year^{-1} during the first 40 years. Yet, certain ND stands currently have even greater aboveground C pools in live trees (up to 225 Mg C ha^{-1}) than the primeval forest average. High biomass C values in managed beech forests can result from the stand's cohort structure, when the bulk of stems are contributed by mature trees with relatively high stem volume. This is reflected in the quadratic mean diameters of the 13 beech ND forests, which are relatively high for mature *Fagus sylvatica* forests (34.3 – 38.9 cm, Burrascano et al. 2013), while the stand basal areas are relatively low in comparison to other German mature beech production forests (32.7 m^2 ha^{-1}, von Oheimb et al. 2005; 24.4 – 44.9 m^2 ha^{-1}, mean: 31.9 m^2 ha^{-1}, Müller-Haubold et al. 2013). The difference between the north German unmanaged beech forests and the Carpathian primeval forests was much greater for the

deadwood C pool, which was about 9 times larger in the primeval forests (35 Mg C ha^{-1}, Glatthorn et al. 2018) than in the ND beech forests 6 – 41 years after management abandonment (about 4 Mg C ha^{-1}). Our aboveground net primary production value (4.5 Mg C ha^{-1} year^{-1}) also compares well with the ANPP measured in the Slovakian primeval beech forests (5.0 Mg C ha^{-1} year^{-1}, Glatthorn et al., 2018). Thus, beech primeval and ND forests mainly differ in the population structure of the living stand, the deadwood pool and the total aboveground C pool (159 Mg C ha^{-1} in ND beech forests vs. 228 Mg C ha^{-1} in Slovakian beech primeval forests), but much less in terms of aboveground biomass in live trees.

Mature oak forests without forestry impact are rare in the temperate forest biome of Europe and therefore are much less studied than beech primeval forests (Petritan et al. 2012). Oak-dominated forests seem to have a lower wood volume, but typically a larger deadwood volume, than beech forests (Burschel et al. 1993, Petritan et al. 2012), which agrees with the findings of our study. No good reference for the biomass of natural Scots pine forests does exist for Central Europe. In two protected old-growth Scots pine-dominated forest stands in Poland, basal area ranged between 28.9 m^2 ha^{-1} and 36.4 m^2 ha^{-1} and increased over time (Brzeziecki et al. 2020). The basal area in our pine forest with natural development was only 21.8 m^2 ha^{-1} and did not exceed the basal area in the young and old pine stand at the same site. The very small biomass C pool therefore seems to be a result of past management and of poor growing conditions at the study site on dry Pleistocene sandy substrates. This is also reflected in low quadratic mean diameters of all three stands at this site.

To conclude, management cessation, as it is foreseen for 5% of the forest area in Germany (BMU 2007), will increase biomass C pools, especially in the deadwood pool. However, low intensity management can also help to accumulate more biomass carbon in German forests. This is indicated by the significant effect of time since last timber extraction on the aboveground biomass C pool, even though the last timber extraction occurred on average only 18 years ago in our ND forests.

2.4.4 Conclusions

This landscape-scale assessment shows that the clearing of the native beech and oak forests centuries ago and their eventual replacement by Scots pine forests was associated with a biomass carbon loss in the magnitude of 70 Mg C ha^{-1}, when averaged data from the YP and OP stands are used for calculation. A rough extrapolation to the > 1.7 million ha of current pine forests in the northern German lowlands yields a reduction in aboveground biomass C in a magnitude of ~120 Tg C, which likely had been accumulated in the primeval forests of the past in excess of the recent biomass storage. This is more than the recent annual carbon sequestration of all European forests.

Clearly, this is a rough estimation with many uncertainties. The age classes of the pine forests studied here are representative of about half of the pine forest area in the northern German lowlands (~54% > 60 years old, analysis based on TI 2015). For younger forest stands, the biomass carbon difference to the former natural broadleaf forests in the region

should be even larger. The comparison with the three Slovakian primeval forests, where different development stages are included, and the relatively short period since management abandonment of our forests with natural development, also suggest that this might be an under- rather than an overestimation. Our conclusions are valid for sandy soils, which dominate large parts of the northern German lowlands and are the sites, were most pine stands have been established. If the carbon pools and C sequestration of the pine forests would be compared to beech forests that are still managed, the difference between the two stand types would likely be smaller, as thinning operations reduce the aboveground biomass carbon pool. Furthermore, about 49% of the beech forests in the northern German lowlands are younger than 100 years (analysis based on TI 2015) and biomass carbon differences between beech and pine forests at young ages will be smaller than the values found in our study, as the period available for biomass accumulation is shorter. In any case, our rough extrapolation to the landscape scale demonstrates the immense impact of past forest conversion practices on the carbon storage in temperate forests.

The superior biomass carbon accumulation of European beech is clearly reflected in our study by the 1.1 Mg C ha^{-1} year^{-1} higher ANPP of the hardwood compared to the conifer stands. Even though European beech is often characterized as a drought-sensitive species (Geßler et al. 2007), the ANPP of the ND stands increased in the warm and dry growing season of 2016. In the beech stands, the decrease in wood production was more than compensated by the high fruit production, indicating no drought-induced decrease of carbon gain.

For assessing the climate change mitigation potential of beech and pine forests, carbon pools in the belowground biomass, the soil, and in durable wood products need to be taken into account as well. Root/ shoot ratios seem to be somewhat smaller in European beech (Bolte et al. 2004) than in Scots pine (Xiao et al. 2003), suggesting slightly smaller differences in belowground biomass than found aboveground. Planting beech in Scots pine forests has been found to decrease soil C stocks slightly (Prietzel 2004), and SOC inventories in our forest stands found an on average 45% greater soil carbon pool under pine than beech (130.0 vs. 88.8 Mg C ha^{-1} in 0 – 100 cm and organic layer; Diers et al., unpubl.). This balances the lower biomass carbon pool partly. In addition, coniferous species are used to a higher proportion for longlived wood products than broadleaf tree species (WBAE and WBW 2016). Yet, when assessing this difference, it must be kept in mind that the long-term storage of carbon in long-lived wood products still accounts for only a few percent of the biomass C stored in the world's forests (c. 4 – 20 Pg C vs. 280 – 363 Pg C, Pan et al. 2011, Larson et al. 2012, Chen et al. 2019).

Further research on the carbon balance of beech and pine forests under a changing climate is required to evaluate whether the restoration of beech forests (or other hardwood forests) on current pine forest area represents a viable option with respect to the goal of mitigating climate warming, especially in the moister western part of the north German lowlands, where forests are less threatened by summer droughts and future climate warming. It is perhaps

more relevant, that converting part of the existing Scots pine forest area into beech (or oak) forests would be favorable for other ecosystem services as well, notably biodiversity conservation, and fire and pest damage control. Equally relevant is groundwater recharge, which is significantly higher under beech than pine stands in the Pleistocene lowlands (Leuschner 2001, Leuschner 2002, Müller 2001, Anders et al. 2005), and may become a key ecosystem service of forests in regions with a future decrease in summer rainfall. Thus, the carbon storage potential in biomass (and soil) must be carefully weighed against other consequences of largescale forest conversion.

CRediT authorship contribution statement

Agnes Förster: Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Heike Culmsee:** Conceptualization, Writing - review & editing, Project administration. **Christoph Leuschner:** Conceptualization, Methodology, Resources, Writing - review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Appendix

Table A2.1. List of the study sites sorted from west to east with stand characteristics and climatic variables (means of 1981-2010) used in the mixed-effects model. Climate data source: DWD CDC (Deutscher Wetterdienst Climate Data Center) 2019. Grids of the multi-annual means over Germany 1981-2010. https://opendata.dwd.de/climate_environment/CDC/grids_germany/multi_annual/. (Access: 07.2019).

Number	Name	Forest type	Main tree species	Stand age (year)	Time without management (year)	Main tree species' share of basal area (%)	Mean annual temperature (°C)	Mean annual precipitation (mm)
1	Wahner Heide	ND	Beech	146	19	66	10.3	866
		OP	Pine	133	5	39	10.1	879
		YP	Pine	81	19	71	10.1	882
2	Franzhorn / Cuxhavener Küstenheiden	ND	Beech	156	33	90	9.1	857
		OP	Pine	100	7	47	9.3	908
		YP	Pine	60	1	98	9.4	884
3	Weichel	ND	Beech	144	29	92	9.3	797
		OP	Pine	95	2	43	9.2	798
		YP	Pine	68	3	82	9.1	822
4	Lüßberg	ND	Beech	195	41	96	8.7	813
		OP	Pine	125	23	89	9	809
		YP	Pine	67	0	100	8.7	808
5	Süsing	ND	Beech	139	19	90	8.9	775
		OP	Pine	144	0	55	8.9	795
		YP	Pine	64	7	91	8.9	799
6	Ewige Route	ND	Beech	134	19	92	8.9	728
		OP	Pine	125	19	75	8.8	724
		YP	Pine	66	12	100	8.9	712

Number	Name	Forest type	Main tree species	Stand age (year)	Time without management (year)	Main tree species' share of basal area (%)	Mean annual temperature (°C)	Mean annual precipitation (mm)
7	Nievoldhagen	ND	Beech	124	16	83	9.1	624
		OP	Pine	93	4	47	9.2	634
		YP	Pine	64	4	83	9.4	605
8	Kaarzer Holz	ND	Beech	112	11	97	8.9	659
		OP	Pine	155	3	36	8.9	650
		YP	Pine	68	6	95	8.9	653
9	Authausener Wald	ND	Beech	166	10	82	9.3	657
		OP	Pine	96	2	50	9.3	651
		YP	Pine	55	2	93	9.3	653
10	Rüthnicker Heide	ND	Oak	119	9	87	9.2	587
		OP	Pine	126	5	64	9.3	581
		YP	Pine	63	5	97	9.3	585
11	Prora	ND	Beech	142	11	84	8.7	660
		OP	Pine	102	4	48	8.6	661
		YP	Pine	63	4	55	8.6	674
12	Weißhaus	ND	Beech	146	33	86	9.2	619
		OP	Pine	95	1	98	9.2	596
		YP	Pine	62	1	98	9.2	618

Number	Name	Forest type	Main tree species	Stand age (year)	Time without management (year)	Main tree species' share of basal area (%)	Mean annual temperature (°C)	Mean annual precipitation (mm)
13	Prösa	ND	Oak	230	8	92	9.3	624
		OP	Pine	100	0	92	9.3	626
		YP	Pine	70	7	100	9.3	614
14	Eggesiner Forst	ND	Beech	104	6	84	8.8	566
		OP	Pine	115	6	86	8.8	567
		YP	Pine	62	2	97	8.8	555
15	Ueckermünder Heide	ND	Beech	150	10	90	8.7	571
		OP	Pine	90	6	84	8.9	561
		YP	Pine	62	7	99	8.8	558
16	Zschornoer Wald	ND	Pine	132	8	100	9.1	653
		OP	Pine	104	12	100	9.1	648
		YP	Pine	70	5	98	9.1	650

Table A2.2. References of allometric regression equations used for calculation of aboveground tree biomass (including woody biomass and leaves or needles) and woody biomass. Equations were developed for species printed in bold. DBH ranges of the trees used for equation development and at our study sites are given. Equations were selected based on quality of data base (large number of harvested trees with large DBH range) and comparability of the study region. If no species-specific equations were available, equations for species with similar wood density were used (Zanne A. E., Lopez-Gonzalez G., Coomes D. A., Ilic J., Jansen S., Lewis S. L., …, Chave J. 2009. Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository. https://doi.org/10.5061/dryad.234). List is sorted by abundance of tree species on the study plots.

Tree species	Wood density (g cm^{-3})	References	DBH range (cm) for equations	DBH range and median (cm) at study sites
Pinus sylvestris L.	0.422			
Pinus nigra J.F. Arnold	0.417	Cienciala E, Černý M, Tatarinov F, Apltauer J, Exnerová Z. 2006. Biomass functions applicable to Scots pine. Trees 20: 483-495.	5 – 42	7 – 79 (28)
Pinus strobus L.	0.340			
Larix decidua Mill.	0.474			
Larix spec.				
Fagus sylvatica L.	0.585	Wutzler T, Wirth C, Schumacher J. 2008. Generic biomass functions for Common beech (*Fagus sylvatica*) in Central Europe: predictions and components of uncertainty. Canadian Journal of Forest Research 38: 1661-1675.	1 – 79	7 – 118 (24)
Betula pendula Roth	0.525	Hagemeier M. 2002: Funktionale Kronenarchitektur mitteleuropäischer Baumarten am Beispiel von Hängebirke, Waldkiefer, Traubeneiche, Hainbuche, Winterlinde und Rotbuche. Cramer, Berlin, Stuttgart, Germany.	no information available	7 – 54 (12)
Acer platanoides L.	0.517			
Acer pseudoplatanus L.	0.509			
Corylus avellana L.	0.517			
Quercus spec.	0.560	Aboveground Biomass: Muukkonen P. 2007. Generalized allometric volume and biomass equations for some tree species in Europe. European Journal of Forest Research 126: 157-166. Woody biomass: Cienciala E, Apltauer J, Exnerová Z, Tatarinov F. 2008. Biomass functions applicable to oak trees grown in Central-European forestry. Journal of Forest Science 54: 109-120.	10 – 50 / 6 – 59	7 – 88 (25)
Quercus petraea (Matt.) Liebl.	0.560			
Quercus robur L.	0.560			
Quercus rubra L.	0.560			
Fraxinus excelsior L.	0.560			
Picea abies (L.) H. Karst.	0.370	Muukkonen P. 2007. Generalized allometric volume and biomass equations for some tree species in Europe. European Journal of Forest Research 126: 157-166.	10 – 40	7 – 75 (15)
Picea sitchensis (Bong.) Carrière	0.362			
Abies alba Mill.	0.353			

Tree species	Wood density (g cm⁻³)	References	DBH range (cm) for equations	DBH range and median (cm) at study sites
Carpinus betulus L.	0.693	Hochbichler E. 2008: Fallstudien zur Struktur, Produktion und Bewirtschaftung von Mittelwäldern im Osten Österreichs (Weinviertel). Österr. Gesellschaft für Waldökosystemforschung und experimentelle Baumforschung an der Universität für Bodenkultur, editor. Forstliche Schriftenreihe. Vol. 20. Universität für Bodenkultur, Wien, Austria.	1 – 18	7 – 61 (14)
Crataegus spec.	0.660			
Ilex aquifolium L.	0.650			
Prunus avium L.	0.474			
Prunus serotina Ehrh.	0.470			
Prunus padus L.	0.465			
Alnus glutinosa (L.) J. Gaertn.	0.439			
Castanea sativa Mill.	0.463			
Frangula alnus Mill.	0.499	Hochbichler E. 2008: Fallstudien zur Struktur, Produktion und Bewirtschaftung von Mittelwäldern im Osten Österreichs (Weinviertel). Österr. Gesellschaft für Waldökosystemforschung und experimentelle Baumforschung an der Universität für Bodenkultur, editor. Forstliche Schriftenreihe. Vol. 20. Universität für Bodenkultur, Wien, Austria.	1 – 10	7 – 54 (10)
Populus spec.	0.362			
Salix spec.				
Salix caprea L.	0.396			
Tilia spec.				
Tilia cordata Mill.	0.422			
Sorbus aucuparia L.	0.629	Korsmo H. 1995: Weight equations for determining biomass fractions of young hardwoods from natural regenerated stands. Scandinavian journal of forest research 10: 333–346.	1 – 10	7 – 17 (8)

Table A2.3. Generalized inflation factor (GVIF) of the included variables of the final mixed effects model for C pools in total aboveground biomass.

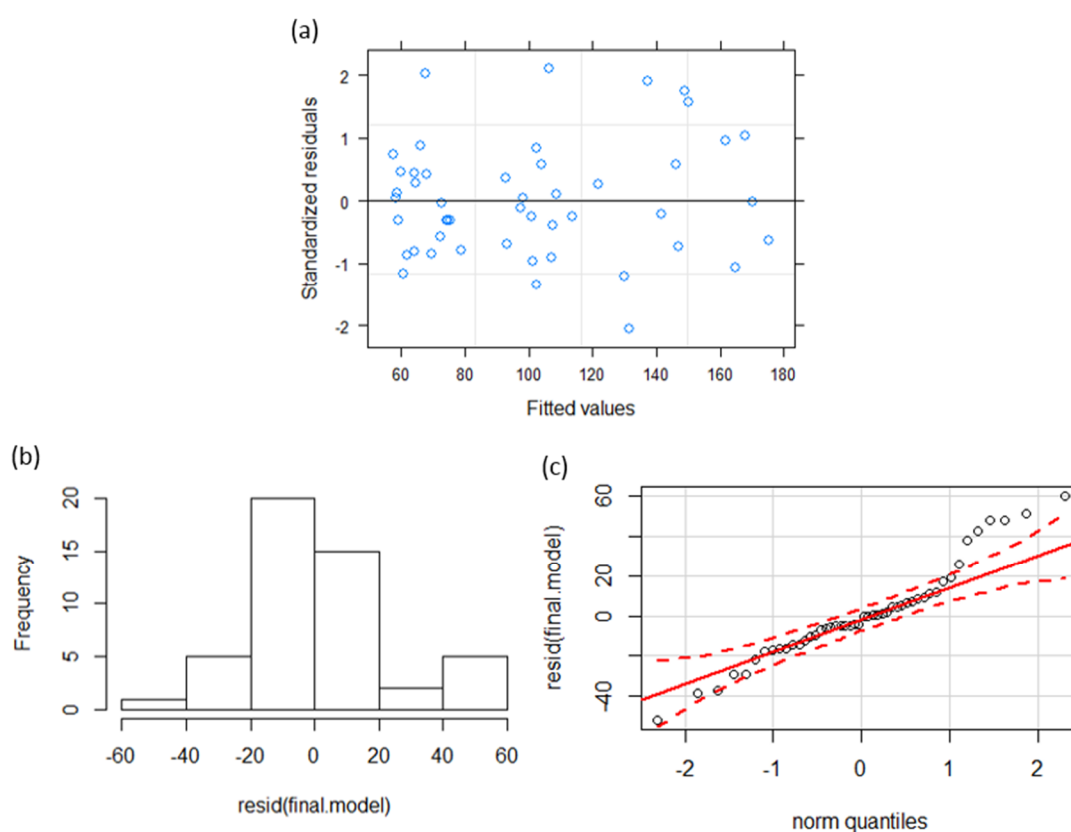|	GVIF	df	GVIF^(1/(2*df))
Main tree species	1.593073	2	1.123463
Time since last timber extraction	1.559686	1	1.248874
Main tree species' share of basal area	1.074578	1	1.036618

Figure A2.1. Model diagnostics of the final mixed effects model for C pools in aboveground biomass: Standardized model residuals plotted against the fitted values (a), and histogram (b) and qqPlot (c) of the model residuals.

References

Aerts, R., Honnay, O., 2011. Forest restoration, biodiversity and ecosystem functioning. BMC Ecol. 11, 29.

Albrecht, L., 1991. Die Bedeutung des toten Holzes im Wald. Forstwiss. Cent.bl. 110, 106–113.

Anders S, Beck W, Hornschuch F., Müller J, Steiner A. 2005. Zur Zukunftsfähigkeit des Kiefern-Buchen-Mischbestandes – ökologische Voraussetzungen, forstliche Steuerungsmöglichkeiten, waldwachstumskundliche und umweltrelevante Wirkungen. Ministerium für Ländliche Entwicklung, Umwelt und Verbraucherschutz des Landes Brandenburg, editor. Ökologischer Waldumbau im nordostdeutschen Tiefland. Eberswalder Forstliche Schriftenreihe, Vol. XXIII: 12-32.

Annighöfer, P., Ameztegui, A., Ammer, C., Balandier, P., Bartsch, N., Bolte, A., Mund, M., 2016. Species-specific and generic biomass equations for seedlings and saplings of European tree species. Eur. J. For. Res. 135, 313–329.

Aronson, J., Alexander, S., 2013. Ecosystem restoration is now a global priority: time to roll up our sleeves. Restor. Ecol. 21, 293–296.

Art HW, Marks PL. 1971. A summary table of biomass and net annual primary production in forest ecosystems of the world. XVth IUFRO Congress, Working Group on Forest Biomass Studies, Section 25, Growth and Yield, University of Florida, Gainsville, Florida, USA. International Union of Forest Research Organizations. p3-32.

Bellassen, V., Luyssaert, S., 2014. Carbon sequestration: Managing forests in uncertain times. Nature 506, 153–155.

Bert, D., Danjon, F., 2006. Carbon concentration variations in the roots, stem and crown of mature *Pinus pinaster* (Ait.). For. Ecol. Manage. 222, 279–295.

BfN (Bundesamt für Naturschutz). 2010. Karte der potentiellen natürlichen Vegetation Deutschlands. Maßstab 1:500.000. Bonn-Bad Godesberg, Germany.

BMEL (Bundesministerium für Ernährungund Landwirtschaft). 2017. Waldbericht der Bundesregierung 2017. BMEL, Bonn, Germany.

BMU (Bundesministerium für Umwelt, Naturschutz und Reaktorsicherheit). 2007. Nationale Strategie zur biologischen Vielfalt. Berlin, Germany.

Bohn U, Neuhäusl R. 2003. Karte der natürlichen Vegetation Europas/Map of the natural vegetation of Europe. Maßstab/Scale 1 : 2 500 000. Landwirtschaftsverlag, Münster, DE.

Bolte, A., Rahmann, T., Kuhr, M., Pogoda, P., Murach, D., Kv, Gadow, 2004. Relationships between tree dimension and coarse root biomass in mixed stands of European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* [L.] Karst.). Plant Soil 264, 1–11.

Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320, 1444–1449.

Böse M, Ehlers J, Lehmkuhl F. 2018. Deutschlands Norden: vom Erdaltertum zur Gegenwart. Springer. 201p.

Bruckman, V.J., Yan, S., Hochbichler, E., Glatzel, G., 2011. Carbon pools and temporal dynamics along a rotation period in *Quercus* dominated high forest and coppice with standards stands. For. Ecol. Manage. 262, 1853–1862.

Brzeziecki, B., Zajączkowski, J., Olszewski, A., Bolibok, L., Andrzejczyk, T., Bielak, K., Żybura, H., 2020. Structure and dynamics of unven-aged Scots pine-dominated old growth stands in Kaliszki and Sieraków strict reserves in Kampinos National Park. Sylwan 164, 392–403.

Burrascano, S., Keeton, W.S., Sabatini, F.M., Blasi, C., 2013. Commonality and variability in the structural attributes of moist temperate old-growth forests: a global review. For. Ecol. Manage. 291, 458–479.

Burschel, P., Kürsten, E., Larson, B.C., 1993. Die Rolle von Wald- und Forstwirtschaft im Kohlenstoffhaushalt – Eine Betrachtung für die Bundesrepublik Deutschland. Forstl. Forsch.ber. Münch. 126, 1–135.

Cannell, M.G.R., 1982. World forest biomass and production data. Academic Press, London, pp. 391.

Carroll, M., Milakovsky, B., Finkral, A., Evans, A., Ashton, M.S., 2012. Managing carbon sequestration and storage in temperate and boreal forests. In: Ashton, M.S., Tyrell, M.L., Spalding, D., Gentry, B. (Eds.), Managing Forest Carbon in a Changing Climate. Springer, Dordrecht, Netherlands, pp. 205–226.

Chave, J., Coomes, D.A., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12, 351–366.

Chen, A., Peng, S., Fei, S., 2019. Mapping global forest biomass and its changes over the first decade of the 21st century. Sci. China Earth Sci. 62, 585–594.

DeAngelis, D.L., Gardner, R.H., Shugart, H.H., 1981. Productivity of forest ecosystems studied during the IBP: The woodland data set. In: Reichle, D.E. (Ed.), Dynamic Properties of Forest Ecosystems. Cambridge Univ. Press, Cambridge, pp. 567–672.

Diers M, Weigel R, Culmsee H, Leuschner C. unpublished. Soil carbon and nutrient stocks under Scots pine plantations in comparison to European beech forests along a climate gradient: a paired-plot study.

DWD CDC (Deutscher Wetterdienst Climate Data Center) 2019. Grids of the multi-annual means over Germany 1981-2010. https://opendata.dwd.de/climate_environment/ CDC/grids_germany/multi_annual/. (Access: 07.2019).

Eisinga, R., Heskes, T., Pelzer, B., Te Grotenhuis, M., 2017. Exact p-values for pairwise comparison of Friedman rank sums, with application to comparing classifiers. BMC Bioinform. 18, 68.

FAO (editor). 2016. Global Forest Resources Assessment 2015. FAO, Rome.

Geßler, A., Keitel, C., Kreuzwieser, J., Matyssek, R., Seiler, W., Rennenberg, H., 2007. Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. Trees 21, 1–11.

Gilliam, F.S., 2007. The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems. BioScience 57, 845–858.

Glatthorn, J., Feldmann, E., Pichler, V., Hauck, M., Leuschner, C., 2018. Biomass stock and productivity of primeval and production beech forests: greater canopy structural diversity promotes productivity. Ecosystems 21, 704–722.

Grüneberg, E., Schöning, I., Riek, W., Ziche, D., Evers, J., 2019. Carbon Stocks and Carbon Stock Changes in German Forest Soils. In: Status and Dynamics of Forests in Germany. Springer, Cham, Switzerland, pp. 167–198.

Guo, L.B., Gifford, R.M., 2002. Soil carbon stocks and land use change: a meta analysis. Glob. Chang. Biol. 8, 345–360.

Hacket-Pain, A.J., Ascoli, D., Vacchiano, G., Biondi, F., Cavin, L., Conedera, M., Zang, C.S., 2018. Climatically controlled reproduction drives interannual growth variability in a temperate tree species. Ecol. Lett. 21, 1833–1844.

Hagemeier M. 2002. Funktionale Kronenarchitektur mitteleuropäischer Baumarten am Beispiel von Hängebirke, Waldkiefer, Traubeneiche, Hainbuche, Winterlinde und Rotbuche. J. Cramer, Berlin, Stuttgart, Germany.

Heinsdorf, D., 2002. Einfluss der Bewirtschaftung auf den Kohlenstoffhaushalt von Forstökosystemen im nordostdeutschen Tiefland. Beitr. Forstwirt. u. Landsch.ökol. 36, 168–174.

Heinsdorf D. 2007. Dendromassenvorräte und Nährelementspeicherung in Kiefernbeständen. Ministerium für Ländliche Entwicklung, Umwelt und Verbraucherschutz des Landes Brandenburg, editor. Die Kiefer in nordostdeutschen Tiefland – Ökologie und Bewirtschaftung. Eberswalder Forstliche Schriftenreihe, Vol. XXXII: 357-362.

Hertel, D., Strecker, T., Müller-Haubold, H., Leuschner, C., 2013. Fine root biomass and dynamics in beech forests across a precipitation gradient–is optimal resource partitioning theory applicable to water-limited mature trees? J. Ecol. 101, 1183–1200.

Hoch, G., Richter, A., Körner, Ch., 2003. Non-structural carbon compounds in temperate forest trees. Plant Cell Environ. 26, 1067–1081.

Hollander, M., Wolfe, D.A., 1973. Nonparametric Statistical Methods. John Wiley & Sons, New York, USA.

Husmann, K., Rumpf, S., Nagel, J., 2018. Biomass functions and nutrient contents of European beech, oak, sycamore maple and ash and their meaning for the biomass supply chain. J. Clean. Prod. 172, 4044–4056.

IPCC 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland, 151 pp.

Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Byrne, K.A., 2007. How strongly can forest management influence soil carbon sequestration? Geoderma 137, 253–268.

Janssens, I.A., Sampson, D.A., Cermak, J., Meiresonne, L., Riguzzi, F., Overloop, S., Ceulemans, R., 1999. Above-and belowground phytomass and carbon storage in a Belgian Scots pine stand. Ann. For. Sci. 56, 81–90.

Johnson, D.W., Curtis, P.S., 2001. Effects of forest management on soil C and N storage: meta-analysis. For. Ecol. Manage. 140, 227–238.

Laiho, R., Laine, J., 1997. Tree stand biomass and carbon content in an age sequence of drained pine mires in southern Finland. For. Ecol. Manage. 93, 161–169.

Larson, C., Chatellier, J., Lifset, R., Graedel, T., 2012. Role of Forest Products in the Global Carbon Cycle: From the Forest to Final Disposal. In: Ashton, M.S., Tyrell, M.L., Spalding, D., Gentry, B. (Eds.), Managing Forest Carbon in a Changing Climate. Springer, Dordrecht, Netherlands, pp. 257–282.

Law, B.E., Sun, O.J., Campbell, J., Van Tuyl, S., Thornton, P.E., 2003. Changes in carbon storage and fluxes in a chronosequence of ponderosa pine. Glob. Chang. Biol. 9, 510–524.

Leuschner, C., 2001. Changes in forest ecosystem function with succession in the Lüneburger Heide. Tenhunen JD, Lenz R, Hantschel R, editors. Ecosystem Approaches to Landscape Management in Central Europe. Ecol. Stud. 147, 517–568.

Leuschner C. 2002. Forest succession and water resources: soil hydrology and ecosystem water turnover in early, mid and late stages of a 300-yr-long chronosequence on sandy soil. Dohrenbusch A, Bartsch N, editors. Forest Development, Succession, Environmental Stress and Forest Management. Springer, Berlin. p1-68.

Leuschner, C., Ellenberg, H., 2017. Ecology of Central European Forests: Vegetation Ecology of Central Europe. Springer, Cham, Switzerland.

Leuschner, C., Wulf, M., Bäuchler, P., Hertel, D., 2013. Soil C and nutrient stores under Scots pine afforestations compared to ancient beech forests in the German Pleistocene: The role of tree species and forest history. For. Ecol. Manage. 310, 405–415.

Mazerolle MJ. 2017. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.1-1. https://cran.r-project.org/ package=AICcmodavg.

McKinley, D.C., Ryan, M.G., Birdsey, R.A., Giardina, C.P., Harmon, M.E., Heath, L.S., Skog, K.E., 2011. A synthesis of current knowledge on forests and carbon storage in the United States. Ecol. Appl. 21, 1902–1924.

Meyer, P., 1999. Totholzuntersuchungen in nordwestdeutschen Naturwäldern: Methodik und erste Ergebnisse. Forstwiss. Cent.bl. 118, 167–180.

Meyer P, Menke N, Nagel J, Hansen J, Kawaletz H, Paar U, Evers J. 2009. Entwicklung eines Managementmoduls für Totholz im Forstbetrieb. Abschlussbericht des von der Deutschen Bundesstiftung Umwelt (DBU) geförderten Projektes. Nordwestdeutsche Forstliche Versuchsanstalt, Göttingen, Germany.

Milnik A. 2007. Zur Geschichte der Kiefernwirtschaft in Nordostdeutschland. Ministerium für Ländliche Entwicklung, Umwelt und Verbraucherschutz des Landes Brandenburg, editor. Die Kiefer in nordostdeutschen Tiefland – Ökologie und Bewirtschaftung. Eberswalder Forstliche Schriftenreihe, Vol. XXXII: 14-21.

MLU Sachsen-Anhalt (Ministerium für Landwirtschaft und Umwelt des Landes SachsenAnhalt), editor. 2014. Leitlinie Wald 2014: Zur Erhaltung und weiteren nachhaltigen Entwicklung des Waldes im Land Sachsen-Anhalt. Ministerium für Landwirtschaft und Umwelt Sachsen-Anhalt.

MLUR Brandenburg (Ministerium für Landwirtschaft, Umweltschutz und Raumordnung des Landes Brandenburg), editor. 2004. Waldbau-Richtlinie 2004. "Grüner Ordner" der Landesforstverwaltung Brandenburg. Sonderdruck. Ministerium für Landwirtschaft, Umweltschutz und Raumordnung.

Müller, J., 2001. Ermittlung von Kennwerten des Wasserhaushaltes in Kiefern- und Buchenbeständen des nordostdeutschen Tieflandes. Beitr. Forstwirtsch. Landsch.ökol. 35, 14–18.

Müller-Haubold, H., Hertel, D., Seidel, D., Knutzen, F., Leuschner, C., 2013. Climate responses of aboveground productivity and allocation in *Fagus sylvatica*: a transect study in mature forests. Ecosystems 16, 1498–1516.

Müller-Haubold, H., Hertel, D., Leuschner, C., 2015. Climatic drivers of mast fruiting in European beech and resulting C and N allocation shifts. Ecosystems 18, 1083–1100.

NLF (Niedersächsische Landesforsten) (ed.) 2011. Das LÖWE-Programm. 20 Jahre Langfristige Ökologische Waldentwicklung. Niedersächsische Landesforsten, Braunschweig, Germany.

Övergaard, R., Gemmel, P., Karlsson, M., 2007. Effects of weather conditions on mast year frequency in beech (*Fagus sylvatica* L.) in Sweden. Forestry 80, 555–565.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. Science 333, 988–993.

Parviainen, J., 2005. Virgin and natural forests in the temperate zone of Europe. For. Snow Landsc. Res. 79, 9–18.

Penman J, Gytarsky M, Hiraishi T, Krug T, Kruger D, Pipatti R, et al., editors. 2003. Good Practice Guidance for Land Use, Land Use Change and Forestry. Intergovernmental Panel on Climate Change, Kamiyamaguchi, Japan.

Petritan, A.M., Biris, I.A., Merce, O., Turcu, D.O., Petritan, I.C., 2012. Structure and diversity of a natural temperate sessile oak (*Quercus petraea* L.)–European Beech (*Fagus sylvatica* L.) forest. For. Ecol. Manage. 280, 140–149.

Pinheiro J, Bates D, Debroy S, Sarkar D, R Core Team. 2017. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-131. https://CRAN.R-project.org/ package=nlme.

Pohlert T. 2018. PMCMRplus: Calculate Pairwise Multiple Comparisons of Mean Rank Sums Extended. R package version 1.2.0. https://CRAN.R-project.org/ package=PMCMRplus.

Pregitzer, K.S., Euskirchen, E.S., 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. Glob. Chang. Biol. 10, 2052–2077.

Prietzel, J., 2004. Humusveränderungen nach Einbringung von Buche und Eiche in Kiefernreinbestände. J. Plant Nutr. Soil Sci. 167, 428–438.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rademacher, P., Khanna, P.K., Eichhorn, J., Guericke, M., 2009. Tree growth, biomass, and elements in tree components of three beech sites. In: Brumme, R., Khanna, P.K. (Eds.), Functioning and management of European beech ecosystems. Springer, Berlin, Germany, pp. 105–136.

Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., Kuemmerle, T., 2018. Where are Europe's last primary forests? Divers. Distrib. 24, 1426–1439.

Schär, C., Vidale, P.L., Lüthi, D., Frei, C., Häberli, C., Liniger, M.A., Appenzeller, C., 2004. The role of increasing temperature variability in European summer heatwaves. Nature 427, 332–336.

Schmidt, W., 2006. Zeitliche Veränderung der Fruktifikation bei der Rotbuche (*Fagus sylvatica* L.) in einem Kalkbuchenwald (1981–2004). Allg. Forst- Jagdztg. 177, 9–19.

Schmidt, A.V., 1967. Der rechnerische Ausgleich von Bestandeshöhenkurven. Forstwiss. Cent.bl. 86, 370–382.

Schulp, C.J.E., Nabuurs, G.-J., Verburg, P.H., de Waal, R.W., 2008. Effect of tree species on carbon stocks in forest floor and mineral soil and implications for soil carbon inventories. For. Ecol. Manage. 256, 482–490.

Seedre, M., Kopáček, J., Janda, P., Bače, R., Svoboda, M., 2015. Carbon pools in a montane old-growth Norway spruce ecosystem in Bohemian Forest: Effects of stand age and elevation. For. Ecol. Manage. 346, 106–113.

TI (Thünen-Institut) 2015. Dritte Bundeswaldinventur - Basisdaten (Stand 20.03.2015). https://bwi.info/Download/de/BWI-Basisdaten/ACCESS2003/bwi20150320_alle_ daten2012.zip.

Umweltbundesamt (ed.) 2019. Berichterstattung unter der Klimarahmenkonvention der Vereinten Nationen und dem Kyoto-Protokoll 2019. Nationaler Inventarbericht zum Deutschen Treibhausgasinventar 1990 – 2017. Dessau-Roßlau, Germany.

Vallet, P., Meredieu, C., Seynave, I., Bélouard, T., Dhôte, J.-F., 2009. Species substitution for carbon storage: Sessile oak versus Corsican pine in France as a case study. For. Ecol. Manage. 257, 1314–1323.

von Oheimb, G., Westphal, C., Tempel, H., Härdtle, W., 2005. Structural pattern of a nearnatural beech forest (*Fagus sylvatica*) (Serrahn, North-east Germany). For. Ecol. Manage. 212, 253–263.

Wirth C, Schwalbe G, Tomczyk S, Schulze E-D, Schumacher J, Vetter M, Böttcher H, Weber G, Weller G. 2004. Dynamik der Kohlenstoffvorräte und-flüsse in den Wäldern Thüringens. Thüringer Landesanstalt für Wald, Jagd und Fischerei, editors. Mitteilungen 23/2004, Gotha, 308p.

Wissenschaftlicher Beirat Agrarpolitik, Ernährung und gesundheitlicher Verbraucherschutz (WBAE) und Wissenschaftlicher Beirat Waldpolitik (WBW) beim BMEL (eds.) 2016: Klimaschutz in der Land- und Forstwirtschaft sowie den nachgelagerten Bereichen Ernährung und Holzverwendung. Gutachten. Berlin, Germany.

Wördehoff R, Spellmann H, Evers J, Nagel J. 2011. Kohlenstoffstudie Forst und Holz Niedersachsen. Nordwestdeutsche Forstliche Versuchsanstalt, editor. Beiträge aus der Nordwestdeutschen Forstlichen Versuchsanstalt. Vol. 6. Universitätsverlag Göttingen, Göttingen.

Xiao, C.-W., Yuste, J.C., Janssens, I.A., Roskams, P., Nachtergale, L., Carrara, A., Ceulemans, R., 2003. Above-and belowground biomass and net primary production in a 73-year-old Scots pine forest. Tree Physiol. 23, 505–516.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Chave, J., 2009. Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository. https://doi.org/10.5061/dryad.234.

Zhang, Q., Wang, C., Wang, X., Quan, X., 2009. Carbon concentration variability of 10 Chinese temperate tree species. For. Ecol. Manage. 258, 722–727.

Chapter 3

Belowground consequences of converting broadleaf to conifer forest: Comparing the fine root systems of European beech and Scots pine

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Abstract

Planted forests of Scots pine (*P. sylvestris* L.) and other *Pinus* species extend over >1.7 million hectares in the Pleistocene lowlands of northern Germany, replacing former broadleaf forests (primarily European beech, *Fagus sylvatica* L.). This transformation belongs to the world's largest broadleaf-conifer forest conversions; yet, the belowground consequences of this species shift are poorly studied. Based on root coring, an ingrowth core study and root morphological analyses, we compared (i) the bio- and necromass, productivity and morphology of fine roots in pairs of beech and pine stands and (ii) analyzed the species' fine root system response to variation in soil properties and climatic conditions across a climate continentality gradient. Fine root biomass was on average 6.5 times higher (237 vs. 37 g m^{-2}) and fine root productivity 1.9 times greater (147 vs. 77 g m^{-2} yr^{-1}, difference not significant) in beech than pine stands. Beech responded with considerable plasticity in fine root system size and fine root morphology to variation in soil acidity and soil fertility and to the contrasting growing conditions in organic layer and mineral soil, but was not responsive to the climatic gradient. In contrast, pine modified fine root biomass and root morphology in response to precipitation and temperature, but did not respond to soil chemistry and fertility. Pine had a somewhat higher mean fine root diameter and also higher specific fine root surface area than beech, while its fine root tip abundance and mean fine root lifespan were lower than in beech (4 vs. 13 months). We conclude that the conversion of broadleaf (beech) to coniferous (pine) forest is accompanied by marked root system changes, notably the reduction of standing fine root biomass and productivity and an

apparently contrasting belowground responsiveness to climatic and edaphic changes, with possible consequences for the trees' susceptibility to climate-warming and drought.

3.1 Introduction

Since the establishment of the earliest permanent settlements in Neolithic times, humans have shaped the landscapes of Central Europe, which once were nearly completely covered with temperate broadleaf forests (Leuschner & Ellenberg 2017, Poschlod 2017). With the expansion of arable fields and increasing timber extraction, forest cover has progressively decreased in most Central European regions, reaching forest cover minima during the Middle Ages and in the early modern era at around 1800 A.D. (Bork 2001). Forest loss was particularly large in the Pleistocene lowlands of the Netherlands, northern Germany and northern Poland, while more forest remained in the mountainous landscapes more in the south of Central Europe. Century-long forest destruction on the mostly nutrient-poor soils of the lowlands led to the expansion of heathlands on large areas and locally also to the formation of inland dunes (Leuschner & Immenroth 1994). With further increase in human population size and the beginning of industrialization, timber shortage increased, and heathlands, sand dunes as well as abandoned arable land was increasingly afforested to meet the timber demand and halt land devastation. As soils were mostly infertile and often had lost part of their soil organic carbon (SOC) stock, fast-growing conifers, mostly Scots pine (*Pinus sylvestris* L.) and subsequently also Norway spruce (*Picea abies* Karst.), were preferably planted (Kremser 1990, Milnik 2007). In the Pleistocene lowlands of northern Germany and Poland and in the Netherlands, large monospecific Scots pine forests have been established, in most cases on soils that were once covered by forests of native European beech (*Fagus sylvatica* L.) or other broadleaf trees. The century-long history of human impact is still visible in many forest soils in form of enhanced podzolization and reduced SOC pools (Riek et al. 2007, Leuschner et al. 2013), in contrast to soils that have kept their forest cover continuously.

Even though forestry in Germany and neighboring countries has seen initiatives to increase the proportion of natural broadleaf trees in the production forests in recent time (e.g. Lust et al. 2000, MLUR Brandenburg 2004, NLF 2011), pine forests (*Pinus* spp., mostly *P. sylvestris*) still cover 53% (>1.7 million ha) of the current forest area in the northern German lowlands, while the share of European beech is only 7% (analysis based on TI 2015, slightly different area reference than depicted in Fig. 3.1). This contrasts with a natural share of pine of only 2% of the potential forest area, while beech would potentially cover 51% (BfN 2010, analysis conducted with ESRI ArcMap 10.1). This demonstrates the dimension of change that has happened in the woodlands of the northern German lowlands during the last

250 years, transforming a former temperate broadleaf forest landscape to woodlands widely dominated by planted conifers. Few regions in the world have experienced such a fundamental change in forest structure and composition, which comes close to a man-made biome shift from temperate broadleaf to temperate (or boreal) coniferous. This must have had consequences for the forest-dwelling biota, biogeochemical cycles and forest-related ecosystem services, especially for the local and regional climate, the soil moisture regime, evapotranspiration and groundwater recharge, above- and belowground carbon (C) cycling, and soil chemistry and biology and nutrient supply (Leuschner & Rode 1999, Majunke et al. 2005, Anders et al. 2005, Förster et al. 2021, Diers et al., submitted). Here, we investigate the consequences of a shift from broadleaf to conifer forest for fine root system structure and dynamics, comparing broadleaf (beech) stands with conifer (pine) stands on the same soil.

Tree fine roots (≤2 mm in diameter) represent only a few percent of the trees' biomass (Vogt et al. 1996, Kalyn & Van Rees 2006), but their consumption of assimilates is disproportionately high. McCormack et al. (2015) estimated that fine root productivity (FRP) accounts for 22% of global terrestrial net primary production. Fine roots may also contribute largely to the transfer of plant carbon to the SOC pool (Tefs & Gleixner 2012, Clemmensen et al. 2013). Root exudates can stimulate microbial activity in the rhizosphere and thereby may have a profound influence on soil nutrient availability (Bardgett et al. 2014). Despite considerable progress in our understanding in recent time (Meier et al. 2019), we still know much less about the functioning of root systems and its variation among species than about aboveground tree organs (Leuschner & Hertel 2003, McCormack et al. 2015, Weemstra et al. 2016, Fuchs et al. 2020).

Comparing tree species with respect to fine root system size and dynamics has to consider that fine root biomass (FRB) and fine root dynamics vary with soil properties, notably soil pH and soil fertility, and climate, but may also depend on stand structural characteristics such as basal area and tree age (e.g. Leuschner & Hertel 2003, Helmisaari et al. 2007, Hertel et al. 2013, Weemstra et al. 2017, Brunner et al. 2019). As the belowground response to environmental change appears to be species-specific, generalization across species is difficult (e.g. Leuschner & Hertel 2003, Finér et al. 2011a, b, Fuchs et al. 2020). Studying the changes in fine root system size and dynamics of different tree species along climatic and edaphic gradients could help to compare different species with respect to above/belowground allocation strategies and in terms of root system sensitivity to drought and soil chemical stress.

With the adoption of a more functional perspective of the fine root system, research has increasingly focused on root trait variation and its relation to plant and ecosystem functioning (Freschet et al. 2021). Among the more easily measured fine root morphological traits, specific root length (SRL, root length per root dry weight), specific root area (SRA, root surface area per root dry weight) and, less often, root tip frequency (RTF, root tip number per root dry weight) have been used as proxies to characterize the putative efficiency of fine root resource uptake, as they relate the C cost of root production to a benefit

(Eissenstat & Yanai 1997, Lõhmus et al. 2006, Ostonen et al. 2007, Weemstra et al. 2017, Hertel et al. 2013). Other widely measured fine root morphological traits are root tissue density (RTD, root dry weight per root volume) and average fine root diameter, which both influence SRL and SRA and are related to fine root longevity (McCormack et al. 2012, Eissenstat et al. 2000). Two strategies to cope with low resource availability in the soil have been distinguished, an 'intensive strategy' and an 'extensive strategy' (Lõhmus et al. 2006, Ostonen et al. 2007). In the first strategy, plants increase the efficiency of soil resource exploitation through root morphological modifications, while the extensive strategy consists of an absolute increase in total fine root biomass, surface area and length.

In a paired-plot study at eight study sites in the Pleistocene lowlands of northern Germany, we compared the fine root systems of naturally developing beech forests and managed pine forests on similar soil across a gradient from a more oceanic to a more continental climate. Study aim was to elucidate the belowground consequences of the large-scale forest conversion in the study area, i.e. to understand changes in the fine root systems resulting from the conversion of broadleaf to conifer forest on infertile sandy parent material. We hypothesized that fine root biomass (i) and fine root productivity (ii) are higher in the naturally occurring beech forests than in planted pine forests replacing them. We further analyzed differences in fine root morphological traits between European beech and Scots pine, and compared the response of the species' fine root systems to variation in soil properties and climatic conditions in order to reveal adaptive belowground strategies of European beech and Scots pine to stressful environmental conditions.

3.2 Methods

3.2.1 Study area

The study was conducted at eight study sites, distributed over large parts of the North German Pleistocene lowlands between the Dutch and the Polish borders (Fig. 3.1). The study sites are located on acidic sandy soils with low to medium silt content and thus low to moderate fertility, which mainly originate from moraine deposits of the penultimate (Saalian) or last (Weichselian) glacial. Soil types are spodo-dystric Cambisols and Podzols. None of the study sites is influenced by groundwater. The cool- temperate climate in the study area shows a continentality gradient from west to east with decreasing mean annual precipitation (MAP, range: 822–555 mm year^{-1}), and slightly increasing summer, but decreasing winter, temperatures. Mean annual temperature (MAT) ranges from 8.7 to 9.4 °C (means of 1981–2010, DWD CDC, 2019).
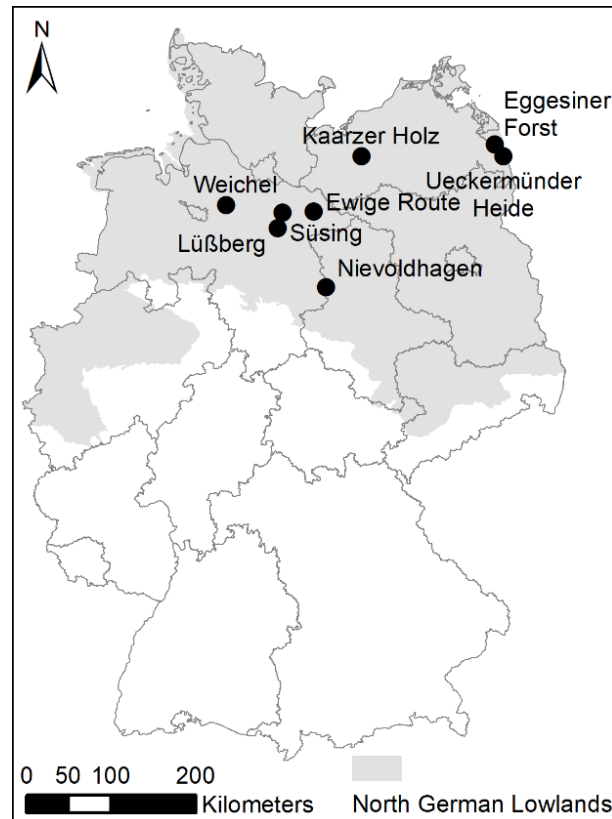
Figure 3.1. Map of Germany with the eight study sites in the North German Lowlands.

3.2.2 Study design

At each of the eight study sites, we compared a naturally developing European beech (*Fagus sylvatica* L.) forest, with a management history in the past, with a nearby planted Scots pine (*Pinus sylvestris* L.) stand on similar geological substrate. The beech forests had a minimum stand age of 100 years (138 years on average), and the last thinning operations happened between 6 and 41 years ago (19 years on average). These forests represent the natural vegetation of the study area before forest conversion. The planted pine forests, which represent the dominant current vegetation, were regularly thinned and between 62 and 68 years old (65 years on average). This age class is widespread in the study region, since many clear-cuts were afforested after World War II. All 16 forest stands had a minimum size of 6 ha. In each stand, six circular 0.1 ha-plots (r = 17.84 m) were established at random positions and at a minimum distance of 66 m to each other.

3.2.3 Fine root mass and morphology

We conducted two root inventories at the beginning of the growing season in the 96 plots, one in February/ March 2015, and a second one in March/ April 2017. During each inventory, we took in every circular plot one fine root sample at random location with a minimum distance of 1 m to the next tree, resulting in 192 fine root samples in total. The organic layer and upper 20 cm of the mineral soil profile were extracted with a soil corer of 3.5 cm in

diameter. The samples were transferred to plastic bags and stored at 4°C until being processed. To extract the roots from the soil, samples were soaked with tap water and sieved at a mesh size of 0.2 mm. All tree fine root segments with >1 mm length and diameter ≤2 mm were considered for analysis. Large rootlets (>10 mm length) were picked out by hand with tweezers. Fine roots were sorted into living and dead fractions through the inspection of the degree of cohesion of stele and periderm, root elasticity and color under a stereomicroscope (e.g. Hertel & Leuschner 2002). Furthermore, we separated tree fine roots by species (beech, pine and some admixed species) based on root cortex color and surface structure, ramification patterns, and root elasticity (Table A3.1).

While most of the living fine roots in a soil sample can be detected by this method, a large part of the dead fine root fraction (fine root necromass, FRN), mostly composed of very small root fragments, would be missed. Therefore, 20 randomly selected samples per forest type of the root inventory of 2015 were additionally analyzed with an approach developed by van Praag et al. (1988) and adapted by Hertel (1999). These samples were sieved with a mesh size of 0.063 mm. Larger fine root segments were extracted as described above. The remaining sample was evenly spread on a sheet of filter paper (730 cm^2), which was divided into 36 squares of even size. On six randomly chosen squares, all remaining root fragments were picked out by hand with tweezers under a stereomicroscope, dried and weighed. The proportion of the FRN fraction determined by the rough method in comparison to that retrieved with the precise method was analyzed with linear regression analysis. The resulting equations (Table A3.2) were used to estimate total FRN for the remaining samples without precise determination.

Live fine roots of beech and pine were scanned with a flat-bed scanner and fine root diameter, length, surface area, volume and root tip abundance were determined with WinRhizo software (Regent In´struments Inc., Quebec, Canada). All root fractions were dried at 70 °C for 48 h and subsequently weighed. We calculated SRL, SRA and RTF as the fine root length, surface area or root tip number of a sample divided by its dry weight. RTD was obtained by dividing fine root dry weight by root volume. Root area index (RAI) was calculated as cumulative fine root surface area divided by the ground area (9.62 cm^2) of a sample. To enable better comparison with other studies, we extrapolated our FRB data to 60 cm soil depth using FRB-depth functions for beech and pine, that were established for sandy Pleistocene soils in northern Germany (after data in Scherfose 1990, Meier et al. 2018). An overview of all investigated root-related variables is given in Table 3.1.

Table 3.1. List of all investigated root-related variables. Given are the abbreviations, units and definitions.

Variable	Abbreviation	Unit	Definition
Fine root biomass	FRB	$g\,m^{-2}$	Dry weight of live fine roots of the main tree species (*Fagus sylvatica* or *Pinus sylvestris*)
Fine root necromass	FRN	$g\,m^{-2}$	Dry weight of dead fine roots of the main tree species (*Fagus sylvatica* or *Pinus sylvestris*)
Fine root productivity	FRP	$g\,m^{-2}\,yr^{-1}$	Dry weight of fine roots of the main tree species (*Fagus sylvatica* or *Pinus sylvestris*) measured in ingrowth-cores
Root area index	RAI	$m^2\,m^{-2}$	Cumulative root surface area per ground area
Root tip abundance	–	$n\,m^{-2}$	Absolute root tip number per ground area
Root tip frequency	RTF	$n\,g^{-1}$	Root tip number per root dry weight
Root tissue density	RTD	$g\,cm^{-3}$	Root dry weight per root volume
Specific root area	SRA	$cm^2\,g^{-1}$	Root surface area per root dry weight
Specific root length	SRL	$cm\,g^{-1}$	Root length per root dry weight

3.2.4 Fine root productivity

We measured the annual production of fine roots by an adapted ingrowth core approach (Persson 1980, Majdi 1996), in which the re-growth of fine roots into root-free soil after an initial root cut-off is measured. Soil cores of the upper 20 cm of the soil, including the organic layer, were extracted with a soil corer with a diameter of 3.5 cm. We sieved the extracted soil and picked out remaining roots by hand with tweezers. Additional root-free soil was obtained from a second soil core taken from a location inside the plot. Three plastic sticks were pushed into the walls of the hole to ensure exact relocation of the core. The hole was then refilled with the root-free material by inserting the soil layer by layer and attempting to reproduce the texture of the extracted soil. We did not use a mesh bag in order to reduce the penetration resistance for ingrowing roots as much as possible.

We installed two ingrowth cores in each plot, both at 10 m distance from the center of the plot, but in opposite directions. In total, 192 ingrowth cores were installed in May and June 2015. Sampling of three test cores in April 2016 demonstrated that fine root growth into the cores had started at this time. We harvested all intact ingrowth cores at the end of March and April 2017, i.e. after about 22 months, and assumed a 12-month period with root growth. The samples from the study site 'Süsing' were excluded from the analysis due to low number of intact (non-disturbed) cores. From the remaining study sites, 112 intact ingrowth cores were retrieved, i.e. on average 7 (range: 5–11) samples per forest stand from on average 5 (range: 4–6) different plots. The samples were analyzed with the same protocol as the FRB samples, but live and dead root fractions were not separated and root morphology was not

studied. The fine root mass detected in the ingrowth cores was interpreted as the fine root production of one year. As a rough estimate of fine root turnover, we divided the plot-level FRP (0–20 cm incl. organic layer) by the FRB (0–20 cm plus organic layer) of the root inventory in spring 2017 (Aber et al. 1985).

3.2.5 Climatic data, stand inventory and soil analyses

Climatic data were derived from the German Weather Service (DWD CDC, 2019). For all plots, we extracted 30-year means (1981–2010) of annual, summer (JJA) and winter (DJF) precipitation and temperature. In addition, we retrieved precipitation and mean temperature data of the calendar year, and of the summer and winter before recollecting of the ingrowth cores.

For all trees in the circular plots with a diameter at breast height (DBH) > 7 cm, species identity, DBH and vitality (living, dying, dead) were recorded. Species identity and height class of young trees (DBH < 7 cm) were recorded in a subplot. Aboveground live tree biomass was calculated with allometric regressions. Wood production was obtained by annual DBH measurements with dendrometer tapes and calculation of woody biomass increment between years. Litter production was determined with 6 litter traps per forest stand. Aboveground net primary productivity (ANPP) was calculated as the sum of wood and litter production. A detailed description of biomass calculation methods and ANPP measurements is given in Förster et al. (2021).

In each plot, three samples of the mineral soil (0–10 cm) were taken and combined to a composite sample for chemical analysis. pH(H_2O), soil organic carbon (SOC), nitrogen (N), and phosphor (P) concentrations, the effective cation exchange capacity (CECe), the $BaCl_2$-exchangeable base cation concentration (Ca^{2+}, Mg^{2+}, K^+), and base saturation were determined. Details of soil sampling design and soil chemical analyses are given in Diers et al. (submitted). Climatic data, stand structural and top soil characteristics of the forest stands are given in Table A3.3.

3.2.6 Statistical analyses

All statistical analyses were conducted with R 3.4.0 software (R core team 2017). Fine root mass and morphological traits were averaged over the two sampling years (2015, 2017). We conducted a principal component analysis (PCA) with the function 'prcomp' and used scaled and centered data of all plots, including FRB, FRN and FRP, and a selection of climatic, structural and topsoil characteristics. For FRP, we used mean values of the plots. Missing values of FRP were replaced by the mean of the respective forest stand (in case of study site 'Süsing': overall mean of the respective tree species).

For all other statistical tests, we used mean values of the forest stands. Due to the sample size of eight stands per species (seven stands in case of FRP), we used non-parametric Wilcoxon signed rank tests for paired samples to test for differences between tree species and soil layers. We tested for correlations between FRB, FRP and root morphological traits,

and local climatic, stand structural and soil characteristics using Spearman rank correlation. A significance level of p = 0.05 was used throughout. p values > 0.05 and < 0.1 are interpreted as tendencies.

3.3 Results

3.3.1 Fine root mass and fine root productivity in beech and pine stands

Fine root biomass in the organic layer and the 0–20 cm mineral soil layer ranged between 121.5 and 355.9 g m^{-2} in naturally developing beech forests and between 16.2 and 58.1 g m^{-2} in managed pine forests. The profile means were on average about 6.5 times higher in beech than in pine stands (236.9 ± 33.2 g m^{-2} vs. 36.5 ±5.2 g m^{-2}, Fig. 3.2a). When extrapolated to 60 cm depth (including the organic layer), this factor increases to 8.2 (399.5 g m^{-2} for beech vs. 48.5 g m^{-2} for pine). Admixed tree species contributed with only small amounts to FRB (11.7 ± 3.6 vs. 19.8 ± 10.2 in beech and pine forests, respectively; difference not significant).

Fine root necromass in the organic layer and the 0–20 cm mineral soil layer ranged between 208.3 and 645.7 g m^{-2} in the beech and between 87.8 and 451.9 g m^{-2} in the pine stands, yielding on average about 2.4 times larger profile totals under beech than pine (420.3 ± 55.1 g m^{-2} vs. 174.7 ±43.9 g m^{-2}, Fig. 3.2b). FRB and FRN were higher in the mineral soil (0–20 cm) than in the organic layer in both beech and pine forests. Fine root biomass/necromass ratio was twice as high in the beech than in the pine forests (total profile), and in the beech forests higher in the organic layer than in the mineral soil, which was not the case in the pine forests (Table 3.2).

Fine root productivity to 20 cm soil depth (incl. the organic layer) ranged between 65.7 and 239.8 g m^{-2} yr^{-1} in the beech forests and between 26.6 and 194.7 g m^{-2} yr^{-1} in the pine forests, with the average being 1.9 times higher in the beech than the pine stands (147.2 ± 22.0 g m^{-2} yr^{-1} vs. 76.6 ± 24.6 g m^{-2} yr^{-1}); the difference was significant only in 10–20 cm depth. In both forest types, FRP was not different between the two horizons studied, i.e. the 0–10 cm and the 10–20 cm layer (Fig. 3.3a). Fine root turnover, i.e. FRP per standing FRB, was about 3 times higher in the pine than in the beech forests (2.79 ± 0.80 yr^{-1} vs. 0.94 ± 0.16 yr^{-1}, Fig. 3.3b). This corresponds to a mean fine root lifespan of 4 month for pine and of 13 month for beech.
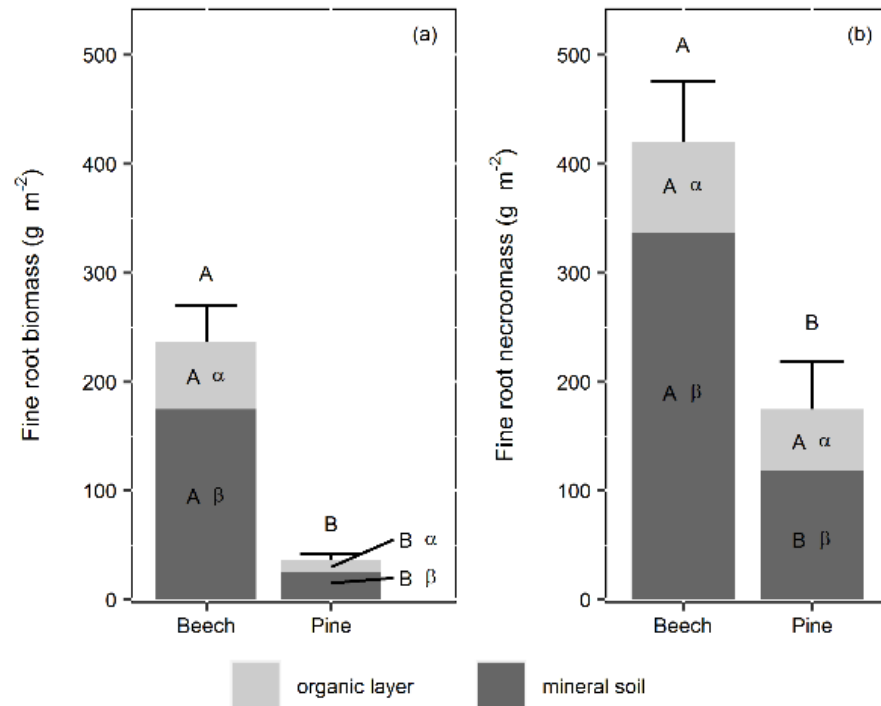
Figure 3.2. Means and standard errors of fine root biomass (a) and fine root necromass (b) in beech and pine stands in the organic layer and the mineral soil (0–20 cm). Different capital letters indicate significant differences between tree species in the organic layer, the mineral soil and the total profile; different Greek letters indicate significant differences between organic layer and mineral soil ($p < 0.05$).
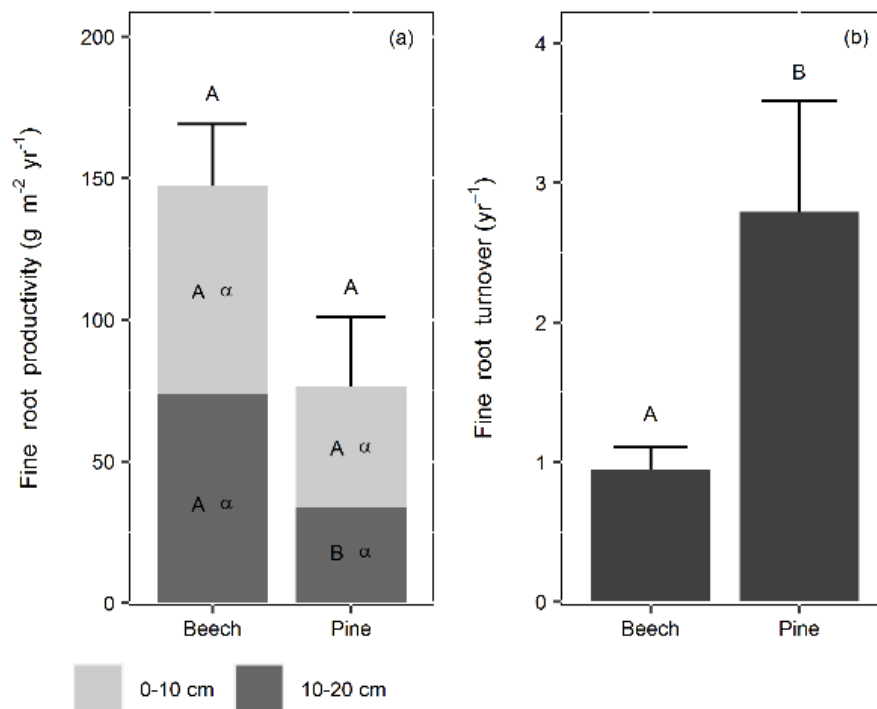
Figure 3.3. Means and standard errors of fine root productivity in 0–10 cm (including the organic layer) and 10–20 cm soil depth (a) and fine root turnover (b) in beech and pine stands. Different capital letters indicate significant differences between tree species in 0–10 cm soil depth, 10–20 cm soil depth and profile total; different Greek letters indicate significant differences between soil depths ($p < 0.05$).

3.3.2 Fine root morphological differences between beech and pine

Beech fine roots in the organic layer were thinner and had a lower RTD, but a higher SRA, SRL and RTF compared to beech fine roots in the mineral soil. Beech reached similar cumulative root surface areas (RAI) and root tip abundances in the organic layer and the mineral soil to 20 cm depth. Pine fine roots in the organic layer were also thinner than in the mineral soil, but had a lower RAI and a lower root tip abundance than in the mineral soil. Other morphological traits did not differ between organic layer and mineral soil. Compared to pine, fine roots of beech had smaller average diameters and a higher RTD (difference in RTD not significant in the organic layer), whereas SRL and RTF did not differ between the tree species (Fig. 3.4). Fine roots of pine had a higher SRA in the mineral soil than fine roots of beech. Across the whole profile, beech maintained a fivefold higher RAI and an almost ninefold higher root tip abundance than pine (Table 3.2).

3.3.3 The fine root systems of beech and pine in relation to environmental variation

The profile totals of FRB in the eight beech forests did not correlate with any climatic or stand structural characteristics (except for non- significant negative correlations with basal area and aboveground tree biomass), but it was negatively related to pH(H_2O) and base saturation, and positively to the SOC concentration and soil C/N ratio (Table 3.3). From the sites with lowest pH and base saturation and highest soil C/N to the sites with highest pH and base saturation and lowest C/N (pH range: 4.5–3.7, base saturation range: 5.5–33.8%, C/N ratio range: 14.5–26.1 g g^{-1}), beech FRB almost tripled (122 vs. 356 g m^{-2}).

The profile totals of pine FRB correlated negatively with mean annual and summer precipitation and positively with summer temperature. From the sites with the highest to the lowest summer precipitation (range: 180–239 mm), FRB increased by 184% (20 vs. 58 g m^{-2}). From the two sites with the lowest to the site with the highest summer temperature (range: 16.7–17.6 °C), biomass almost doubled (27 vs. 52 g m^{-2}). Pine FRB further correlated negatively with stand age and ANPP, but did not correlate with any of the soil chemical variables (Table 3.3).

FRP of beech correlated positively with soil C/N ratio and tended to correlate negatively with pH(H_2O). FRP of pine correlated negatively with base saturation and the concentration of exchangeable base cations in the mineral soil (Table 3.3).

Table 3.2. Means and standard errors of fine root biomass/necromass ratio, specific root area, root area index and root tip abundance in beech and pine stands in the organic layer, the mineral soil (0–20 cm) and the profile total. Different capital letters indicate significant differences between tree species; different Greek letters indicate significant differences between layers (p < 0.05).

	Layer	Beech	Pine
Fine root biomass/necromass ratio (g g^{-1})	org	1.55 ± 0.32 $^{A\,\alpha}$	0.33 ± 0.07 $^{B\,\alpha}$
	min	0.59 ± 0.08 $^{A\,\beta}$	0.30 ± 0.06 $^{B\,\alpha}$
	total	0.66 ± 0.07 ^{A}	0.29 ± 0.06 ^{B}
Specific root area (cm^2 g^{-1})	org	390.3 ± 53.2 $^{A\,\alpha}$	441.1 ± 49.7 $^{A\,\alpha}$
	min	194.2 ± 13.5 $^{A\,\beta}$	401.5 ± 123.3 $^{B\,\alpha}$
	total	205.6 ± 10.1 ^{A}	336.8 ± 56.4 ^{A}
Root area index (m^2 m^{-2})	org	1.6 ± 0.4 $^{A\,\alpha}$	0.3 ± 0.04 $^{B\,\alpha}$
	min	3.1 ± 0.5 $^{A\,\alpha}$	0.6 ± 0.1 $^{B\,\beta}$
	total	4.7 ± 0.6 ^{A}	0.9 ± 0.1 ^{B}
Root tip abundance (10^3 n m^{-2})	org	758 ± 181 $^{A\,\alpha}$	97 ± 9 $^{B\,\alpha}$
	min	1365 ± 308 $^{A\,\alpha}$	140 ± 12 $^{B\,\beta}$
	total	2139 ± 320 ^{A}	243 ± 13 ^{B}

Fine root morphological traits of beech depended on none of the climatic and stand structural variables investigated. Only beech RAI tended to correlate negatively with stand basal area and aboveground tree biomass. Average fine root diameter and RAI of beech correlated negatively with pH(H$_2$O) and base saturation and positively with soil C/ N ratio (p < 0.1 for correlation of RAI with base saturation and C/N ratio). The average fine root diameter of beech increased by almost 50% (0.35 vs. 0.52 mm) from the sites with lowest to highest pH(H$_2$O) and base saturation, and highest to lowest C/N ratio, respectively. Soil N$_t$ concentration and CECe correlated negatively with beech SRA, SRL and RTF (p < 0.1 for the relation between N$_t$ and RTF, Table 3.4). From the sites with the lowest to the highest soil N$_t$ concentration (0.88–5.11 mg g^{-1}) and CECe (25.2–126.7 µmol$_c$ g^{-1}), beech SRL increased by 64%, SRA by 34% and RTF by 68%.

The fine root morphological traits of pine did not correlate with any of the soil chemical variables (except for a tendency of a negative correlation between the CECe and RTD). Mean annual and mean summer precipitation correlated negatively with pine RTD (p < 0.1 for mean summer precipitation). Consequently, mean annual and mean summer precipitation were positively related to RTF and tended to do so in case of SRA. From the pine forest sites

with highest to lowest summer precipitation, RTF and SRA decreased by 68% and 67%, respectively. Mean summer temperature tended to correlate positively with RTD and correlated negatively with SRA, SRL and RTF ($p < 0.1$ for SRL), with decreases by 63%, 62% and 58%, respectively, from the sites with lowest to the site with highest summer temperature. ANPP was positively related to SRL and SRA ($p < 0.1$ for SRA) and correlated negatively with RTD (Table 3.5).
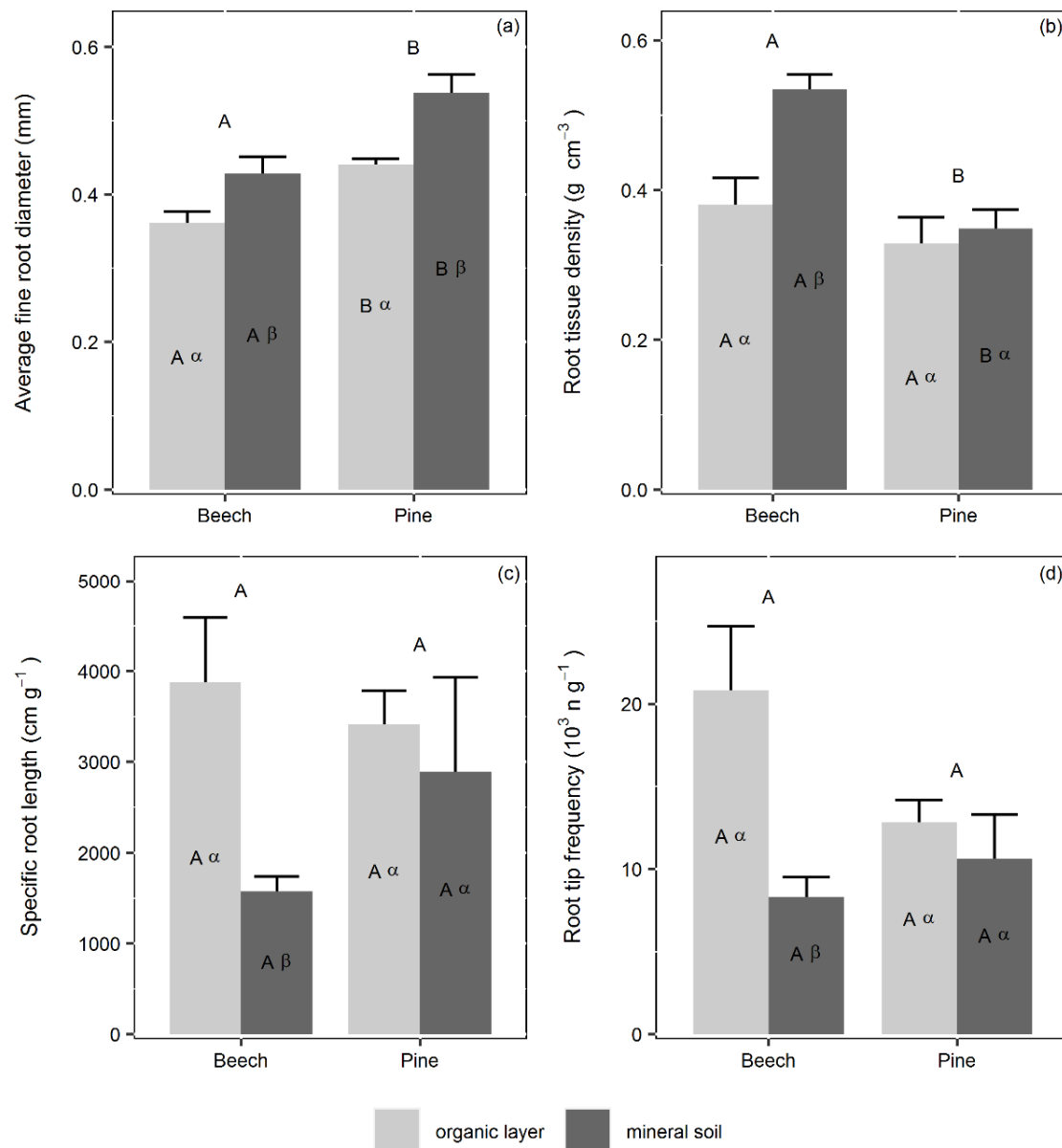
Figure 3.4. Means and standard errors of average fine root diameter (a), root tissue density (b), specific root length (c) and root tip frequency (d) in beech and pine stands in the organic layer and the mineral soil. Different capital letters indicate significant differences between tree species in the organic layer, the mineral soil and total; different Greek letters indicate significant differences between layers ($p < 0.05$).

Table 3.3. Spearman rank correlations of fine root biomass and fine root productivity with stand climatic, structural and topsoil characteristics in beech and pine stands. For correlations with fine root biomass, climatic variables refer to the multi-annual means (1981 – 2010). For correlations with fine root productivity, climatic variables refer to the calendar year, summer and winter before harvesting of the ingrowth cores. Given are correlation coefficients (rho) and p values. Significant correlations ($p < 0.05$) are printed in bold, tendencies ($0.05 < p < 0.1$) are printed in italics.

| | Fine root biomass (n = 8) | | | | Fine root productivity (n = 7) | | | |
| | Beech | | Pine | | Beech | | Pine | |
	rho	p value	rho	p value	rho	p value	rho	p value
Climate								
Annual precipitation	0.19	0.651	**-0.71**	**0.047**	-0.04	0.939	-0.64	0.119
Summer precipitation	0.10	0.823	**-0.76**	**0.028**	0.09	0.848	-0.61	0.148
Winter precipitation	0.19	0.651	*-0.64*	*0.086*	0.14	0.760	-0.39	0.383
Annual temperature	-0.61	0.108	-0.20	0.641	-0.04	0.937	0.20	0.667
Summer temperature	-0.60	0.120	**0.73**	**0.041**	-0.46	0.294	0.32	0.478
Winter temperature	-0.24	0.570	-0.43	0.286	0.11	0.819	-0.38	0.403
Stand structure								
Stand age	0.05	0.911	**-0.78**	**0.022**	-0.46	0.294	-0.62	0.139
Time since last thinning operation	0.13	0.756	-0.11	0.799	-0.21	0.645	0.29	0.535
Mean DBH	-0.29	0.493	-0.02	0.955	-0.64	0.119	-0.43	0.337
Stem density	-0.17	0.693	-0.14	0.736	0.00	1.000	0.36	0.432
Basal area	*-0.69*	*0.058*	-0.24	0.570	-0.57	0.180	0.18	0.702
Proportion of beech/pine	0.31	0.456	0.19	0.651	0.00	1.000	-0.14	0.760
Aboveground live tree biomass	*-0.67*	*0.071*	-0.48	0.233	-0.61	0.148	-0.07	0.879
ANPP (Mean 2015-2017)	-0.50	0.207	**-0.74**	**0.037**	-0.14	0.760	-0.57	0.180
ANPP (2016)					-0.46	0.294	-0.64	0.119
Fine root biomass (Mean 2015/2017)					0.61	0.148	0.50	0.253
Topsoil characteristics								
pH(H$_2$O)	**-0.90**	**0.002**	-0.12	0.778	*-0.71*	*0.071*	-0.43	0.337
Base saturation	**-0.83**	**0.010**	-0.07	0.867	-0.50	0.253	**-0.82**	**0.023**
C/N	**0.81**	**0.015**	0.29	0.493	**0.79**	**0.036**	0.46	0.294
SOC	**0.79**	**0.021**	0.12	0.779	0.46	0.294	-0.54	0.215
N$_t$	0.60	0.120	0.00	1.000	0.29	0.535	-0.64	0.119
CECe	0.40	0.320	-0.17	0.693	-0.04	0.939	-0.54	0.215
Exch. base cation concentration	-0.26	0.531	-0.14	0.736	0.04	0.939	**-0.89**	**0.007**

Table 3.4. Spearman rank correlations between fine root morphological traits of beech and stand climatic, structural and topsoil characteristics. Climatic variables refer to the multi-annual means (1981 – 2010). Given are correlation coefficients (rho) and p values. Significant correlations ($p < 0.05$) are printed in bold, tendencies ($0.05 < p < 0.1$) are printed in italics.

	Average fine root diameter		Root area index		Specific root area		Specific root length		Root tip frequency		Root tissue density	
	rho	p value	rho	p value	rho	p value	rho	p value	rho	p value	rho	p value
Climate												
Mean annual precipitation	0.21	0.610	-0.05	0.911	-0.38	0.352	-0.29	0.493	-0.14	0.736	-0.14	0.736
Mean summer precipitation	0.21	0.610	-0.10	0.823	-0.19	0.651	-0.14	0.736	0.05	0.911	-0.24	0.570
Mean winter precipitation	0.21	0.610	-0.05	0.911	-0.38	0.352	-0.29	0.493	-0.14	0.736	-0.14	0.736
Mean annual temperature	-0.56	0.146	-0.49	0.217	-0.02	0.955	0.13	0.756	-0.12	0.778	0.54	0.168
Mean summer temperature	-0.26	0.531	-0.43	0.289	0.00	1.000	-0.05	0.911	-0.33	0.420	0.62	0.102
Mean winter temperature	-0.31	0.456	-0.19	0.651	0.00	1.000	0.14	0.736	0.14	0.736	0.19	0.651
Stand structure												
Stand age	0.40	0.320	-0.21	0.610	-0.19	0.651	-0.26	0.531	-0.14	0.736	-0.40	0.320
Time since last thinning operation	0.16	0.713	-0.10	0.821	-0.38	0.349	-0.29	0.490	-0.23	0.588	-0.12	0.778
Mean DBH	0.05	0.911	-0.43	0.289	0.21	0.610	0.14	0.736	0.10	0.823	-0.50	0.207
Stem density	-0.43	0.289	0.00	1.000	-0.19	0.651	-0.05	0.911	-0.29	0.493	0.62	0.102
Basal area	-0.48	0.233	*-0.69*	*0.058*	-0.10	0.823	0.02	0.955	-0.31	0.456	0.36	0.385
Proportion of main tree species	0.38	0.352	0.24	0.570	-0.12	0.779	-0.19	0.651	0.07	0.867	-0.12	0.779
Aboveground live tree biomass	-0.40	0.320	*-0.67*	*0.071*	-0.05	0.911	0.05	0.911	-0.21	0.610	0.29	0.493
ANPP (Mean 2015 – 2017)	-0.36	0.385	-0.40	0.320	0.55	0.160	0.55	0.160	0.55	0.160	-0.19	0.651
Top soil characteristics												
pH(H_2O)	**-0.76**	**0.028**	**-0.79**	**0.021**	0.48	0.233	0.55	0.160	0.12	0.779	0.07	0.867
Base saturation	**-0.74**	**0.037**	*-0.69*	*0.058*	0.36	0.385	0.45	0.260	0.05	0.911	0.19	0.651
C/N ratio	**0.79**	**0.021**	*0.67*	*0.071*	-0.55	0.160	-0.62	0.102	-0.19	0.651	0.02	0.955
SOC	0.57	0.139	*0.64*	*0.086*	*-0.67*	*0.071*	*-0.64*	*0.086*	-0.36	0.385	0.17	0.693
N_t	0.50	0.207	0.43	0.289	**-0.86**	**0.007**	**-0.81**	**0.015**	*-0.67*	*0.071*	0.43	0.289
CECe	0.26	0.531	0.24	0.570	**-0.81**	**0.015**	**-0.71**	**0.047**	**-0.76**	**0.028**	0.48	0.233
Exch. base cation concentration	-0.14	0.736	-0.38	0.352	-0.57	0.139	-0.43	0.289	*-0.67*	*0.071*	0.52	0.183

Table 3.5. Spearman rank correlations between fine root morphological traits of pine and stand climatic, structural and topsoil characteristics. Climatic variables refer to the multi-annual means (1981 – 2010). Given are correlation coefficients (rho) and p values. Significant correlations ($p < 0.05$) are printed in bold, tendencies ($0.05 < p < 0.1$) are printed in italics.

	Average fine root diameter		Root area index		Specific root area		Specific root length		Root tip frequency		Root tissue density	
	rho	p value	rho	p value	rho	p value	rho	p value	rho	p value	rho	p value
Climate												
Mean annual precipitation	0.21	0.610	-0.50	0.207	*0.69*	*0.058*	0.62	0.102	**0.83**	**0.010**	**-0.71**	**0.047**
Mean summer precipitation	0.14	0.736	*-0.64*	*0.086*	*0.67*	*0.071*	0.62	0.102	**0.83**	**0.010**	*-0.64*	*0.086*
Mean winter precipitation	0.29	0.493	-0.45	0.260	0.60	0.120	0.50	0.207	**0.74**	**0.037**	-0.62	0.102
Mean annual temperature	-0.33	0.423	-0.28	0.498	0.00	1.000	0.10	0.817	-0.01	0.977	-0.14	0.750
Mean summer temperature	-0.12	0.775	0.50	0.210	**-0.73**	**0.041**	*-0.65*	*0.078*	**-0.86**	**0.006**	*0.69*	*0.058*
Mean winter temperature	-0.25	0.548	-0.37	0.365	0.32	0.435	0.36	0.382	0.32	0.435	-0.47	0.243
Stand structure												
Stand age	-0.10	0.820	-0.54	0.165	*0.63*	*0.096*	*0.66*	*0.073*	**0.73**	**0.038**	*-0.69*	*0.060*
Time since last thinning operation	0.00	1.000	-0.49	0.217	-0.44	0.272	-0.35	0.399	-0.20	0.629	0.50	0.204
Mean DBH	0.05	0.911	0.05	0.911	-0.24	0.570	-0.31	0.456	-0.05	0.911	0.21	0.610
Stem density	-0.21	0.610	-0.24	0.570	0.26	0.531	0.38	0.352	0.10	0.823	-0.21	0.610
Basal area	-0.07	0.867	-0.29	0.493	0.38	0.352	0.48	0.233	0.24	0.570	-0.33	0.420
Proportion of main tree species	0.45	0.260	0.10	0.823	-0.38	0.352	-0.43	0.289	-0.14	0.736	0.52	0.183
Aboveground live tree biomass	-0.24	0.570	-0.48	0.233	0.55	0.160	*0.67*	*0.071*	0.43	0.289	-0.50	0.207
ANPP (Mean 2015 – 2017)	-0.62	0.102	-0.60	0.120	*0.64*	*0.086*	**0.74**	**0.037**	0.55	0.160	**-0.74**	**0.037**
Top soil characteristics												
pH(H2O)	0.34	0.417	-0.23	0.588	-0.26	0.528	-0.31	0.453	-0.04	0.933	0.22	0.608
Base saturation	0.40	0.320	0.02	0.955	0.00	1.000	-0.07	0.867	0.07	0.867	-0.14	0.736
C/N ratio	-0.12	0.779	0.36	0.385	0.21	0.610	0.19	0.651	-0.02	0.955	-0.19	0.651
SOC	0.43	0.289	0.40	0.320	0.38	0.352	0.31	0.456	0.21	0.610	-0.45	0.260
N_t	0.38	0.352	0.21	0.610	0.26	0.531	0.24	0.570	0.17	0.693	-0.33	0.420
CECe	0.24	0.570	0.12	0.779	0.60	0.120	0.55	0.160	0.40	0.320	*-0.69*	*0.058*
Exch. base cation concentration	0.38	0.352	0.02	0.955	0.10	0.823	0.05	0.911	0.17	0.693	-0.24	0.570

3.3.4 Grouping of beech and pine forests according to stand structure and soil chemistry

The naturally developing beech forests were characterized by a higher mean DBH and aboveground tree biomass, but lower stem density, and a higher ANPP than the managed pine forests, whereas basal area did not differ between the forest types. The beech forests were also older than the pine stands, and the time elapsed since last thinning operation was on average greater than in the pine stands, which are still managed. Soil chemical properties did not differ significantly between the neighboring beech and pine stands, except for a higher topsoil N/P ratio in the pine forests. Pine forests also tended to have a wider topsoil C/N ratio than the beech forests (Table 3.6).

The first principal component of the PCA separated the two forest types into distinct groups. The first axis correlated positively with stand age, aboveground tree biomass, the time since the last thinning operation and FRB, and correlated negatively with stem density. This axis thus mainly represents stand structural differences, but also a difference in FRB. The second principal component correlated positively with FRN, and correlated negatively with MAT, base saturation, basal area and pH(H_2O) (Fig. 3.5, Table A3.4). On this axis, the eight sites per forest type showed similar variation. The precipitation gradient of the study sites from west to east was not reflected in their alignment along the first two principal components.

3.4 Discussion

3.4.1 Changes in fine root biomass and productivity with the conversion of beech to pine forests

The PCA results clearly demonstrate that broadleaf (beech) and coniferous forests (pine) differ not only in terms of aboveground stand structural properties but also in the size of the fine root system. In confirmation of our first hypothesis, FRB was 6.5 times higher in the naturally developing beech forests than in the planted pine forests on similar soil. With on average 237 g m^{-2} in the organic layer and the top 20 cm of the mineral soil (extrapolated to 60 cm depth: 400 g m^{-2}), FRB in the beech forests is in the lower range of values found in other studies. The *meta*-analysis by Leuschner & Hertel (2003) gives a mean FRB for beech forests of 470 g m^{-2} (range: 118–960 g m^{-2}) at a mean sampling depth of 49 cm. The FRB of pine was with an average of 36.5 g m^{-2} (extrapolated to 60 cm depth: 49 g m^{-2}) much lower than values reported in other studies for Central European Scots pine stands. At a mean sampling depth of 74 cm, Leuschner & Hertel (2003) give a mean FRB of 399 g m^{-2} (range: 237–725 g m^{-2}) for Scots pine. Thus, the surprisingly large difference in FRB is mainly a result of the low FRB values found in our pine stands.

Table 3.6. Stand structural and topsoil (0-10 cm) characteristics of the studied beech and pine forests. Test statistics and p-values of Wilcoxon signed rank tests for differences between forest types are given.

| Main tree species	Mean (range)		Wilcoxon test	
	Beech	Pine	V	p value
Stand structure				
Stand age (yr)	138 (104 - 195)	65 (62 - 68)	36	**0.008**
Time since last thinning operation (yr)	19 (6 - 41)	5 (0 - 12)	36	**0.012**
Mean diameter at breast height (cm)	39.8 (28.8 - 55.7)	25.8 (22.9 - 31.2)	36	**0.008**
Stem density (n ha^{-1})	230 (103 - 348)	475 (295 - 715)	0	**0.008**
Basal area (m^2 ha^{-1})	29.5 (20.8 - 39.6)	26.7 (23.4 - 30.8)	26	0.313
Proportion of beech/pine (% basal area)	92 (87 - 96)	92 (73 - 100)	17	0.945
Aboveground live tree biomass (Mg dry mass ha^{-1})	300 (163 - 422)	135 (114 - 155)	36	0.008
Aboveground net primary production (Mean 2015 – 2017, Mg dry mass ha^{-1} yr^{-1})	8.5 (5.9 - 10.3)	6.2 (5.1 - 7.6)	35	**0.016**
Top soil characteristics				
pH(H$_2$O)	4.1 (3.7 - 4.5)	4.0 (3.7 - 4.4)	28	0.195
Soil organic carbon (mg g^{-1})	41.0 (15.6 - 135.5)	50.3 (28.0 - 76.2)	12	0.461
N$_t$ (mg g^{-1})	1.87 (0.88 - 5.11)	2.10 (1.24 - 3.21)	13	0.547
P$_{resin}$ (µg g^{-1})	4.69 (1.64 - 9.59)	3.82 (1.24 - 10.28)	25	0.383
C/N ratio (g g^{-1})	19.8 (14.5 - 26.1)	24.1 (20.6 - 29.6)	4	0.055
N/P ratio (g g^{-1})	633 (198 - 1375)	1047 (221 - 1886)	0	0.008
Effective cation exchange capacity (µmol$_c$ g^{-1})	58.0 (25.2 - 126.7)	64.4 (45.1 - 102.3)	13	0.547
Exchangeable base cation concentration (µmol$_c$ g^{-1})	9.5 (3.3 - 33.2)	13.9 (3.1 - 36.4)	8	0.195
Base saturation (%)	15.4 (5.5 - 33.8)	17.4 (4.6 - 36.3)	15	0.742
Organic layer depth (cm)	4.8 (2.9 - 6.2)	6.2 (4.8 - 7.9)	6.5	0.107
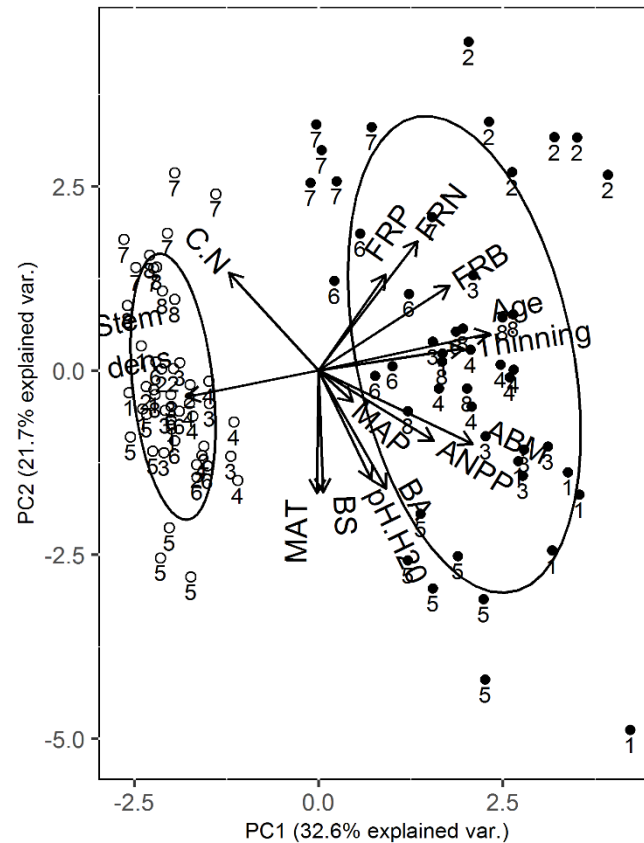
Figure 3.5. Results of the Principal Component Analysis of fine root biomass, necromass and productivity, MAP, and some stand structural and soil chemical properties of the plots in naturally developing beech forests (filled circles) and managed pine forests (open circles). The first and second principal components (PC) are shown. Point labels refer to the study sites from west to east: 1 = Weichel, 2 = Lüßberg, 3 = Süsing, 4 = Ewige Route, 5 = Nievoldhagen, 6 = Kaarzer Holz, 7 = Eggesiner Forst, 8 = Ueckermünder Heide. N = 96 plots. Variable abbreviations: ABM = Aboveground live tree biomass, ANPP = Aboveground net primary productivity, Age = Stand age, BA = Basal area, BS = Base saturation, C.N = C/N ratio, FRB = Fine root biomass, FRN = Fine root necromass, FRP = Fine root productivity, MAP = Mean annual precipitation, MAT = Mean annual temperature, pH.H20 = pH(H2O), Stem dens = Stem density, Thinning = Time since last thinning operation.

One reason for the rather low biomass in both forest types could be underestimation of FRB due to the relatively shallow sampling depth. Yet, we applied FRB-soil depth functions that were established on the basis of quite large field data sets collected in our study region, which makes us confident that the extrapolated values to 60 cm are reliable. These data from the acid soils of the study region suggest that approximately 50% of the FRB profile total has been covered by our sampling in the beech forests (Meier et al. 2018, sampling depth: 3 m) and more than 70% in the pine forests (Scherfose 1990, sampling depth: 1 m). Similarly, Janssens et al. (2002) found 76% of total FRB in the organic layer and the top 15 cm of the mineral soil (sampling depth: 90 cm) in Belgian Scots pine forests. Deeper sampling may have led to slightly different profile totals, but the main picture of FRB variation across the beech and pine stands must be valid.

Another possible cause for relatively low FRB values in our study is seasonal variation. Seasonal FRB patterns are not well understood and they seem to be species-specific (Meinen et al 2009). Beech FRB usually increases after leaf-out until a peak is reached in mid or late summer. Scots pine fine root growth seems to start in Central European pine forests earlier in spring than that of the broadleaf trees, reaching a FRB peak usually also in mid summer. In both species, summer drought may lead to decreases in FRB (MacQueen 1968, Hertel 1999, Konôpka et al. 2005, Mainiero & Kazda 2006, Meinen et al. 2009, Železnik et al. 2016). We sampled in spring at the start of the growing season under conditions of moist soil, in order to avoid the period with soil drying in summer, which varies considerably from year to year and between sites. Due to this sampling design, it is possible that we have missed the annual FRB peak. However, this would be an unlikely explanation for the six- to seven-fold higher FRB in the beech stands, as sampling was conducted simultaneously in pine and beech, and the published work suggests that seasonal fine root dynamics do not differ substantially between the two species.

A more likely explanation of the species difference in FRB is the presence of roots of the understory vegetation, which compete with the trees for space and resources. While in mature beech forests on acidic sandy soils, the understory vegetation is typically sparse, a dense herbaceous and dwarf shrub layer is the rule in pine forests with high canopy transmissivity (Leuschner & Ellenberg 2017). It has been found that the understory of pine forests with abundant dwarf shrubs can account for a high proportion of FRB in the humus layer and the uppermost mineral soil (Makkonen and Helmisaari 2001, Anders et al. 2005, Helmisaari et al. 2007). In contrast, the contribution to FRB seems to be relatively low, when grasses dominate the understory layer (Kalhoff 2000). Some of our managed pine stands indeed are characterized by a high coverage of dwarf shrubs on the forest floor, which makes it probable that intense competition between tree and dwarf shrub roots has contributed to the low pine FRB values at least in certain stands. Thus, including understory FRB in the analysis most likely would have reduced the FRB difference between beech and pine forests. Further, it is possible that a relatively low stem density in our pine stands (mean: 475 ha^{-1}) compared to Scots pine stands investigated in other studies has contributed to the low FRB values in our stands.

FRB may also depend on stand age. In meta-analyses of a large number of field studies, FRB decreased with stand age in beech forests, whereas it increased with stand age in pine forests (Leuschner & Hertel 2003, Finér et al. 2007). In our study, the age hardly varied in the studied pine forests (range: 62–68 years), but was more variable in the beech forests (104–195 years). Nevertheless, we found an age effect on FRB in pine (negative), but no effect in beech. We explain the unexpected age effect in pine with the fact that pine stand age was correlated with MAP in our dataset (rho = 0.71, p = 0.048), which may have simulated a negative age effect, where in reality a negative influence of precipitation on FRB may have been effective. In the beech forests, no age effect on FRB was detectable. This

allows the conclusion that pine and beech FRB values are unlikely to converge, if the beech and pine forests were of more similar age.

We found no effect of time since management cessation on FRB, even though the period varied considerably in the beech (but not in the pine) forests. This result is in line with a study in Slovakian beech forests that found no difference in FRB between primeval and production forests (Klingenberg & Leuschner 2018). This does not rule out that management, together with stand age, are influencing FRB in our sample, and that their effects are masked by a more prominent factor.

FRN is more difficult to compare to literature data, as we employed a more precise analysis than done in most other studies by including even the smallest dead root fragments in the analysis. Small root necromass fragments (<5 mm length) can account for 5.3 times the amount of larger dead fragments (Bauhus & Bartsch 1996). To our knowledge, no studies using the same detailed method are available for pine. From this perspective, our mean necromass total for the pine forests (175 g m^{-2}) appears to be relatively low compared to the mean necromass value of 183 g m^{-2} reported for pine (mean sampling depth: 74 cm) by Leuschner & Hertel (2003) in a meta-analysis. In beech forests, FRN has been investigated with our detailed method earlier, yielding means between 192 g m^{-2} and 2955 g m^{-2} (Bauhus & Bartsch 1996, van Praag et al. 1988, Hertel 1999, Meier & Leuschner 2008). Our mean necromass value of 420 g m^{-2} (sampling depth: 20 cm) for the beech forests is relatively low in comparison to literature data, in agreement with our FRB values.

Even though FRP in the beech forests was almost twice as high as in the pine forests, the difference was only significant in 10–20 cm soil depth but not in the topsoil (0–10 cm). Thus, our second hypothesis could only partly be confirmed. This result was strongly influenced by some very high values in 0–10 cm in the 'Ueckermünder Heide' pine forest (stand mean in 0–10 cm: 125 g m^{-2} yr^{-1}). FRP estimated with the ingrowth core method generally gives rather conservative values in comparison to other methods (Hertel & Leuschner 2002, Finér et al. 2011b). For beech on base-rich soil, Meinen et al. (2009) give a FRP value of 72 g m^{-2} yr^{-1} for the top 20 cm of the soil (ingrowth core study), which is only about half the value found in our study on acid soil. Janssens et al. (2002) observed a FRP of 210 g m^{-2} yr^{-1} in a temperate Scots pine forest in the organic layer and the top 15 cm of the mineral soil, which is more than 2.5 times higher than in our study. While Finér et al. (2011b) found FRP to be closest related to standing FRB among different influencing factors, we could not find a direct correlation between FRB and FRP in either of the two forest types.

FRP differed less between the species than FRB, and fine root turnover thus was much higher in the pine than the beech stands. The shorter average fine root longevity of pine on the acid sandy soils is associated with a lower fine root biomass/necromass ratio in the pine as compared to the beech forests (0.29 vs. 0.66 in the whole profile for pine and beech), even though dead fine roots of pine are decomposed twice as fast (Anders et al. 2005). Fine root turnover in our study was considerably higher than reported in other studies for both, beech (Meinen et al. 2009: 0.26 y^{-1}) and pine (Janssens et al. 2002: 0.74 y^{-1}). It remains an open

question whether the short average lifespan of both species at these acidic and nutrient-poor sites is a consequence of nutrient deficiency, or is caused by other factors such as summer drought. That fine root turnover is higher in conifer than broadleaf stands, as found in our study, contrasts with findings from the boreal zone, where broadleaf forests had higher root turnover rates than coniferous forests (Yuan & Chen 2010).

The about 1.9 fold higher fine root production of the beech than pine stands matches a higher ANPP, which exceeds that of the pine stands by 2.1 Mg ha^{-1} y^{-1} (Förster et al. 2021). Even though pine fine roots are turned over nearly three times faster, the beech fine root system consumes more C (and nutrients) in absolute terms and thus transfers more C to the SOC pool upon root death. While a shorter mean lifespan requires a higher C investment per unit fine root mass, such a strategy could pay off in terms of a higher nutrient and water uptake per root mass, as younger roots generally are more active (Eissenstat & Yanai 1997).

3.4.2 Fine root morphology of beech and pine

Beech fine roots in the organic layer were characterized by lower RTD but higher SRA, SRL and RTF than roots in the mineral soil. This had the consequence that cumulative root surface area (RAI) and total root tip abundance were relatively large in the organic layer despite a much lower FRB in this layer. This was not the case in the pine stands, where fine roots exhibited a similar morphology in both layers, even though average root diameter was smaller in the organic layer. These results point at a lower morphological plasticity of pine fine roots in comparison to beech in response to the vertical resource and soil density gradient in the profile. Alternatively, the findings might indicate that the soil moisture and nutrient conditions in the organic layer of the pine forests are less favorable for root foraging than in the beech organic layer due to higher hydrophobicity and stronger desiccation of the pine needle litter in summer droughts (Leuschner 2002). Whatsoever the reason, beech seems to exploit the organic layer more intensively for the readily available N and P pools and water, than does pine. This is as well suggested by earlier studies in beech forests that also found fine roots with higher SRA, SRL and RTF in the organic layer than in the mineral soil (Kirfel et al. 2019). It is likely that beech develops fine roots with higher specific uptake capacity in the organic layer, where nutrient supply is highest, while average root lifespan is shorter, as suggested by the smaller diameters and lower RTD of these roots (McCormack et al. 2012, Eissenstat et al. 2000).

For pine, that had somewhat thicker fine roots, yet with a lower tissue density than beech, the organic layer is less important for nutrient and water uptake, and the uppermost mineral soil (0–20 cm) is the favored layer for root foraging. This has also been found in boreal pine forests (Makkonen and Helmisaari 1998).

The beech stands maintained an about five times higher cumulative fine root surface area (RAI) in the topsoil than the pine stands. This difference in absorbing surface is only partly matched by a higher leaf area index of beech compared to pine forests (5.0–8.5 vs. 1.5–3.0;

Leuschner & Ellenberg 2017), suggesting that pine fine roots should be more efficient in water uptake. In situ water flux measurements with miniature sap flow gauges in small-diameter roots of beech and pine trees indeed revealed a higher mean specific water uptake rate in pine roots than in beech roots (Burk 2006).

3.4.3 Plasticity in the fine root systems of beech and pine in response to environmental variation

Our FRB data suggest that beech and pine adjusted their standing FRB differently in response to the climatic and edaphic gradients encountered in the study region. The fine root system of beech responded to a decrease in pH and base saturation, and increase in soil C/N ratio, with an increase in FRB and FRP. Similar responses of beech to soil acidity and fertility have been reported earlier (e.g. Leuschner & Hertel 2003, Finér et al. 2007, Kirfel et al. 2019). This can be interpreted as the extensive strategy, and a flexible response of resource allocation patterns to nutrient deficiency, stimulating fine root growth to increase the absorptive capacity for nutrients (and water) at sites with poor availability of N, base cations and other nutrients. Increasing SRL and SRA upon nutrient deficiency is characterized as the 'intensive strategy' to promote nutrient and water uptake (Lõhmus et al. 2006, Ostonen et al. 2007), for which some evidence is provided by our study, as SRL and SRA increased in beech with a decrease in topsoil N_t content. Yet, we have no data on N mineralization rate and thus N supply, and mean fine root diameter increased, and not decreased, with a reduction in pH and base saturation.

It comes as a surprise that none of the investigated climatic and stand structural variables were found to influence FRB, in stark contrast to the soil chemical factors. Earlier studies in beech forests along precipitation gradients found either increases with decreasing mean annual precipitation (Hertel et al. 2013, Meier et al. 2018), or decreases (Leuschner & Hertel 2003, Meier & Leuschner 2008), or no dependence on precipitation (Finér et al. 2007), suggesting that the FRB – precipitation relation depends largely on site conditions, notably nutrient availability. In our beech forests, a FRB increase with increasing precipitation might have been masked by a possible negative effect of stand age on FRB (Leuschner & Hertel 2003, Finér et al. 2007), as MAP and stand age were weakly related to each other (rho = 0.62, P = 0.102). Mean annual temperature has been found to correlate negatively with beech FRB (Leuschner & Hertel 2003, Meier & Leuschner 2008), which is not visible in our data. The lacking dependence of beech FRB and FRP on tree age (variation among sites: 104–195 y), time since last thinning (6–41 y), stem density (103–348 ha^{-1}), basal area (20.8–39.6 m^2 ha^{-1}) and aboveground productivity (5.9–10.3 Mg dry mass ha^{-1} y^{-1}) is remarkable, as it indicates that the by far most important determinant of FRB and FRP on these nutrient-poor sandy soils is deprivation of soil N and/or base cations, which may have masked the influence of other environmental and stand structural factors.

The fine root system of pine, in contrast, appears to be more strongly dependent on climatic and stand structural factors, while soil chemistry seems to be of minor importance, matching earlier observations (Finér et al. 2007, Ostonen et al. 2007). We found a FRB increase with decreasing mean annual or summer precipitation, which is opposite to findings of Leuschner & Hertel (2003), Vanguelova et al. (2005) and Brunner et al. (2019). The negative effect of summer precipitation and positive influence of summer temperature on FRB (but not FRP) in our study may be interpreted as an acclimative response of the pine root system to cope with drier summers by increasing standing FRB to meet the higher evaporative demand. This would be in accordance with the prediction of optimal partitioning theory that plants allocate more C to root growth when soil resources are short in supply (Bloom et al. 1985), which is characterized as the 'extensive strategy'. FRP in pine was apparently stimulated by deprivation of base cations in the soil, while N deficiency seemed not to be influential. In correspondence to the observed low morphological plasticity of pine fine roots between organic layer and mineral soil, we found pine root morphology to be relatively unaffected by edaphic and stand structural factors. In contrast, RTD decreased and consequently RTF, SRA and SRL increased with precipitation and decreased with summer temperature, indicating that pine may form more robust fine roots with smaller absorptive surface area upon climate warming and drying. This is opposite to what would be expected for the intensive root adaptation strategy.

Conifer fine roots have repeatedly been characterized as having a lower SRL than broadleaf tree fine roots (Reich et al. 1998, Pregitzer et al. 2002, Ostonen et al. 2007, Alvarez-Uria & Körner 2011). In correspondence, Bauhus & Messier (1999) found a larger mean fine root diameter in boreal conifers than in broadleaf tree species, which was interpreted as a more conservative root growth strategy. This is also valid for our beech-pine comparison, but the SRL difference was insignificant and SRA was greater in pine than beech (significant in the mineral soil), contradicting this picture.

The contrasting belowground response to environmental variation of beech and pine raises the question, how the plasticity of the fine root systems may affect the overall performance of the trees. Both species grow in Central Europe on soils varying from alkaline base-rich to acidic base-poor and in climates varying from moist to moderately dry, suggesting that the species must be able to adapt or acclimate to variation in soil chemical conditions and soil moisture regimes. That beech adjusted neither FRB nor fine root morphology in response to a precipitation decrease from 813 to 567 mm y^{-1} in our study, might point at lacking flexibility in allocation patterns and root morphology. However, beech is well capable of modifying FRB and fine root morphology in response to unfavorable soil chemical conditions to increase resource uptake capacity, as is demonstrated by the increase in SRA and root tip abundance with a decrease in soil N_t content and base cation concentration (or CECe) in our study. One thus might conclude from the root data that nutrient shortage (N, basic cations) is more critical for beech on these Pleistocene soils than water deficiency. However, a more plausible explanation is that a relatively drought-

sensitive tree species such as beech (Leuschner 2020) will not increase its drought tolerance by increasing FRB in the upper soil and/or developing finer roots to increase water uptake in dry soil, while a corresponding response may well be advantageous to cope with nutrient shortage. In contrast, Scots pine is assumed to be more drought-tolerant than beech (Niinemets & Valladares 2006, Leuschner & Ellenberg 2017), as it usually develops a few deep-reaching taproots that may access soil water also in dry periods (Polomski & Kuhn 1998). According to our data, pine seems to acclimate to a drier and warmer climate by increasing FRB, while forming more robust roots with fewer root tips and thus reduced uptake capacity. On the other hand, undemanding pine seems to endure nutrient deprivation quite well, rendering root system modification less advantageous in this case. Nevertheless, it appears that Scots pine is sensitive to heat and it is questionable whether this predominantly boreal species is well adapted to a hotter and drier climate in the temperate zone. Droughts have caused widespread Scots pine dieback in Spain and central Switzerland (Rigling et al. 2013, Guada et al. 2016) and during the 2018/2019 drought also in Germany and elsewhere (Schuldt et al. 2020). In direct comparison to beech, Anders et al. (2005) found a faster growth decline in pine than in beech upon drought in northeastern Germany, which they attributed to the rather shallow fine root system of pine.

We have no information on shifts in the community composition of the mycorrhizal assemblages of beech and pine along the studied environmental gradients. Root morphological changes in response to soil chemical gradients, as observed in beech, or as a reaction to climate gradients, as in pine, might lead to shifts in the mycorrhizal assemblages and related changes in root nutrient acquisition (Teissier du Cros 1981, Leberecht et al. 2016, Valverde-Barrantes et al. 2016). Analyzing changes in root functioning along the climatic and edaphic gradients of our study would require investigating the fungal partners as well.

While the pairwise comparison of beech and pine forests on similar parent material is a strength of our study, we emphasize that we compared different forest types with specific management history and not the tree species per se. Even though we did not detect effects of management or stand age on FRB, FRP and root morphology, such effects cannot be fully ruled out. Further, our results are valid for sandy soils, which dominate the northern German lowlands and are the typical sites on which pine forests have been established. Other parent materials may lead to different outcomes.

3.4.4 Conclusion

Our comparison of beech forests and nearby planted pine forests on similar parent material contributes to a better understanding of the belowground consequences of a conversion of natural beech to pine forests. We demonstrate large species differences in FRB, and in the responsiveness of FRB and FRP to variation in climate, soil and stand structure. Species differences in fine root morphology were only moderate, as beech fine root morphology varied more between the soil horizons than it differed from pine. The fine root system of beech responded with considerable plasticity to variation in soil acidity and

soil fertility and to the contrasting growing conditions in organic layer and mineral soil, but was not responsive to the climatic gradient. In contrast, pine modified FRB and root morphology in response to precipitation and temperature, but did not respond to soil chemistry and fertility. These differences, together with a much higher FRB of beech, indicate contrasting belowground resource foraging strategies of beech and pine. Further investigations are needed to better understand species- specific belowground adaptations to soil chemical and climatic variation and their relatedness to the aboveground performance of the trees. This will help to predict tree species responses to climatic and soil chemical stresses and contribute to better-informed silvicultural decisions.

CRediT authorship contribution statement

Agnes Förster: Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Dietrich Hertel:** Conceptualization, Methodology, Writing - review & editing, Supervision. **Rebekka Werner:** Investigation, Data curation. **Christoph Leuschner:** Conceptualization, Methodology, Resources, Writing - review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Appendix

Table A3.1. Fine root characteristics of beech and pine used for the differentiation between fine roots of different tree species (Hertel 1999, Hölscher et al. 2002, Becker 1997, complemented by own observations).

	Fagus sylvatica L.	*Pinus sylvestris* L.
Color	Brown-red to dark red, seldom orange-red	White to yellow(-brown)
Surface structure	Rough, with winding longitudinal furrows	Rough, with longitudinal furrows; root tips often flaky, shiny, covered with grey resin
Ramification	Second-order branches evenly ramified into numerous first-order branches, with many root tips	Often long parts of the main branches without ramification, short first-order branches
Elasticity	High	Low

Table A3.2. Results of the linear regression analysis on the relation between fine root necromass from standard analysis and additional analysis. Given are the parameter estimates (a,b), the sample size (N), the correlation coefficient (r) and the p value for the regression equation (y = a + bx).

Forest type	Soil layer	a	b	N	r	p value
NB	Organic layer	0.0038	3.6193	22	0.8301	<0.0001
NB	Mineral soil	0.127	2.3866	20	0.478	<0.05
PP	Organic layer	0.008	3.021	17	0.9092	<0.0001
PP	Mineral soil	0.031	1.3525	18	0.6707	<0.01

Table A3.3. Some climatic, structural and topsoil (0-10 cm) characteristics of the studied forest stands. Test statistics and p-values of Wilcoxon signed rank tests for differences between beech (*Fagus sylvatica* L.) and pine (*Pinus sylvestris* L.) forests are given. Climate data source: DWD CDC (2019).

Main tree species	Weichel Beech	Pine	Lüßberg Beech	Pine	Süsing Beech	Pine	Ewige Route Beech	Pine	Nievoldhagen Beech	Pine	Kaarzer Holz Beech	Pine	Eggesiner Forst Beech	Pine	Ueckermünder Heide Beech	Pine	Mean Beech	Pine	V	p value
Climate																				
Mean annual precipitation (mm yr^{-1})	797	822	813	809	775	799	728	712	624	605	659	657	567	555	571	558	692	690	21	0.742
Mean annual temperature (°C)	9.3	9.1	8.7	8.7	8.9	8.9	8.9	8.9	9.1	9.4	8.8	8.9	8.8	8.8	8.7	8.8	8.9	8.9	6	0.345
Stand structure																				
Stand age (yr)	144	68	195	67	139	64	134	66	124	64	112	68	104	62	150	62	138	65	36	**0.008**
Time since last thinning operation (yr)	29	3	41	0	19	7	19	12	16	4	11	6	6	2	10	7	19	5	36	**0.012**
Mean diameter at breast height (cm)	50.5	23.9	41.6	29	34.8	25.1	37.1	31.2	36.5	23	33.2	24.5	28.8	26.4	55.7	22.9	39.8	25.8	36	**0.008**
Stem density (n ha^{-1})	167	487	163	355	282	452	277	295	348	492	225	578	273	428	103	715	230	475	0	**0.008**
Basal area (m^2 ha^{-1})	37	27.1	23.6	24.9	34.9	25.9	32.5	23.4	39.6	27.1	21.7	29.5	20.8	24.8	25.6	30.8	29.5	26.7	26	0.313
Proportion of beech/pine (% basal area)	87	78	93	100	96	92	92	100	89	73	94	96	92	97	95	100	92	92	17	0.945
Aboveground live tree biomass (Mg dry mass ha^{-1})	422	146	234	127	377	128	321	114	401	136	193	155	163	124	290	150	300	135	36	**0.008**
Aboveground net primary production (Mean 2015 – 2017, Mg dry mass ha^{-1} yr^{-1})	9.2	7.2	5.9	5.9	9.4	6.6	8.8	5.5	8.6	6.1	9.6	7.6	6.2	5.5	10.3	5.1	8.5	6.2	35	**0.016**

Main tree species	Weichel		Lüßberg		Süsing		Ewige Route		Nievoldhagen		Kaarzer Holz		Eggesiner Forst		Ueckermünder Heide		Mean		Wilcoxon test	
	Beech	Pine	Beech	Pine	Beech	Pine	Beech	Pine	Beech	Pine	Beech	Pine	Beech	Pine	Beech	Pine	Beech	Pine	V	p value
Topsoil characteristics																				
$pH(H_2O)$	4.2	3.7	3.7	4.1	4.1	4.1	4.2	4.4	4.5	4.1	4.2	3.8	4	3.7	4.4	3.8	4.1	4	28	0.195
Soil organic carbon (mg g^{-1})	20.5	53.4	135.5	72.2	43.6	28	22.5	35.3	21.4	76.2	28.6	47.7	40.5	37	15.6	52.5	41	50.3	12	0.461
N_t (mg g^{-1})	1.15	1.84	5.11	3.2	2.11	1.24	1.2	1.67	1.53	3.21	1.36	2.23	1.6	1.27	0.88	2.16	1.87	2.1	13	0.547
P_{resin} (µg g^{-1})	1.66	1.59	1.64	2.13	6.47	1.63	2.82	1.24	2.36	1.81	9.59	10.28	5.42	6.66	7.6	5.26	4.69	3.82	25	0.383
C/N ratio (g g^{-1})	18.9	29.6	26.1	21.9	19.9	23	18.6	20.6	14.5	23.8	19.3	20.6	23.3	28.9	17.8	24	19.8	24.1	4	0.055
N/P ratio (g g^{-1})	1036	1325	1375	1540	446	846	737	1514	550	1886	198	221	502	527	222	514	633	1047	0	**0.008**
Effective cation exchange capacity (µmol$_c$ g^{-1})	32.6	67.3	126.7	91.7	53.6	45.4	39.1	45.1	90.5	102.3	39.3	61.5	56.8	45.2	25.2	56.7	58	64.4	13	0.547
Exchangeable base cation concentration (µmol$_c$ g^{-1})	8.7	7.8	8.3	33.3	6.7	6.8	5.7	11.8	33.2	36.4	4.6	8.3	5.6	3.1	3.3	3.3	9.5	13.9	8	0.195
Base saturation (%)	26.2	11.2	5.5	28.1	12.9	16.9	14.1	24.8	33.8	36.3	10.4	12.1	7.2	4.6	13	4.8	15.4	17.4	15	0.742
Organic layer depth (cm)	4.1	7.9	6.2	6	5.9	4.8	5.3	6.4	2.9	6.8	5.3	5.4	4.6	7.8	3.7	4.8	4.8	6.2	6.5	0.107

Table A3.4. Results of the Principal Component Analysis of the circle plots in beech and pine forests (n = 96). Given are the Eigenvalues, the (cumulative) proportion of variance explained and the loadings of the variables of the first three principal components. The most important variables of the principal components according to their loadings (> 0.3) are printed in bold.

	PC1	PC2	PC3
Eigenvalues	4.561	3.032	1.510
Proportion of Variance	0.326	0.217	0.108
Cumulative Proportion	0.326	0.542	0.650
Fine root biomass	**0.335**	0.253	-0.046
Fine root necromass	0.254	**0.386**	-0.123
Fine root productivity	0.171	0.286	-0.210
Mean annual precipitation	0.087	-0.093	**0.563**
Mean annual temperature	-0.004	**-0.366**	0.217
Stand age	**0.437**	0.111	0.094
Stem density	**-0.339**	-0.079	0.093
Basal area	0.172	**-0.353**	0.232
Time since last thinning operation	**0.371**	0.066	**0.308**
Aboveground live tree biomass	**0.394**	-0.219	0.102
Aboveground net primary productivity	0.295	-0.210	-0.055
pH($H_2$0)	0.135	**-0.326**	**-0.476**
C/N ratio	-0.230	0.292	**0.383**
Base saturation	0.012	**-0.363**	-0.146

References

Aber, J.D., Melillo, J.M., Nadelhoffer, K.J., McClaugherty, C.A., Pastor, J., 1985. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods. Oecologia 66, 317–321.

Alvarez-Uria, P., Körner, C., 2011. Fine root traits in adult trees of evergreen and deciduous taxa from low and high elevation in the Alps. Alp. Botany 121, 107–112.

Anders, S., Beck, W., Hornschuch, F., Müller, J., Steiner, A., 2005. Zur Zukunftsfähigkeit des Kiefern-Buchen-Mischbestandes – ökologische Voraussetzungen, forstliche Steuerungsmöglichkeiten, waldwachstumskundliche und umweltrelevante Wirkungen. In: Ministerium für Ländliche Entwicklung, Umwelt und Verbraucherschutz des Landes Brandenburg, Landesforstanstalt Eberswalde, editors. Ökologischer Waldumbau im nordostdeutschen Tiefland. Eberswalder Forstliche Schriftenreihe, Vol. XXIII: 12-32.

Bauhus, J., Bartsch, N., 1996. Fine-root growth in beech (*Fagus sylvatica*) forest gaps. Can. J. For. Res. 26, 2153–2159.

Bauhus, J., Messier, C., 1999. Soil exploitation strategies of fine roots in different tree species of the southern boreal forest of eastern Canada. Can. J. For. Res. 29, 260–273.

Bardgett, R.D., Mommer, L., De Vries, F.T., 2014. Going underground: root traits as drivers of ecosystem processes. Trends Ecol. Evol. 29, 692–699.

Becker, C., 1997. Das Feinwurzelsystem von Birke, Kiefer und Drahtschmiele in Konkurrenzsituation in einem Mischbestand. Diploma thesis, University of Göttingen, Göttingen, 1-58 pp.

Bloom, A., Chapin III, F.S., Mooney, H.A., 1985. Resource limitation in plants – an economic analogue. Annu. Rev. Ecol. Syst. 16, 363–392.

Bork, H.-R., 2001. Landnutzung in Deutschland. Petermanns Geogr. Mitt. 145, 36–37.

Brunner, I., Herzog, C., Galiano, L., Gessler, A., 2019. Plasticity of fine-root traits under long-term irrigation of a water-limited Scots pine forest. Front. Plant Sci. 10, 701.

BfN (Bundesamt für Naturschutz), 2010. Karte der potentiellen natürlichen Vegetation Deutschlands. Maßstab 1:500.000. Bonn-Bad Godesberg, Germany.

Burk, D., 2006. Physiologische, anatomische und chemische Aspekte der Regulation der Wurzelwasseraufnahme bei Rotbuche, Kiefer und Birke auf zwei unterschiedlich wasserversorgten Standorten. PhD thesis. University of Göttingen, Germany.

Clemmensen, K.E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., et al., 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science 339, 1615–1618.

Diers, M., Weigel, R., Culmsee, H., Leuschner, C. (submitted). Soil carbon and nutrient stocks under Scots pine plantation in comparison to European beech forests: A paired-plot study across forests with different management history and precipitation regimes.

DWD CDC (Deutscher Wetterdienst Climate Data Center), 2019. Grids of climate data over Germany. https://opendata.dwd.de/climate_environment/CDC/grids_ge rmany/. (Access: 07.2019).

Eissenstat, D.M., Yanai, R.D., 1997. The ecology of root life span. Adv. Ecol. Res. 27, 1–60.

Eissenstat, D.M., Wells, C.E., Yanai, R.D., Whitbeck, J.L., 2000. Building roots in a changing environment: implications for root longevity. New Phytol. 147, 33–42.

Finér, L., Helmisaari, H.-S., Lõhmus, K., Majdi, H., Brunner, I., Børja, I., et al., 2007. Variation in fine root biomass of three European tree species: Beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* L. Karst.), and Scots pine (*Pinus sylvestris* L.). Plant Biosyst. 141, 394–405.

Finér, L., Ohashi, M., Noguchi, K., Hirano, Y., 2011a. Factors causing variation in fine root biomass in forest ecosystems. For. Ecol. Manage. 261, 265–277.

Finér, L., Ohashi, M., Noguchi, K., Hirano, Y., 2011b. Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. For. Ecol. Manage. 262, 2008–2023.

Förster, A., Culmsee, H., Leuschner, C., 2021. Thinned northern German Scots pine forests have a low carbon storage and uptake potential in comparison to naturally developing beech forests. For. Ecol. Manage. 479, 118575.

Freschet, G. T., Roumet, C., Comas, L. H., Weemstra, M., Bengough, A. G., Rewald, B., et al., 2021. Root traits as drivers of plant and ecosystem functioning: Current understanding, pitfalls and future research needs. New Phytol. https://doi.org/ 10.1111/nph.17072.

Fuchs, S., Hertel, D., Schuldt, B., Leuschner, C., 2020. Effects of Summer Drought on the Fine Root System of Five Broadleaf Tree Species along a Precipitation Gradient. Forests 11, 289.

Guada, G., Camarero, J.J., Sánchez-Salguero, R., Navarro Cerrillo, R.M., 2016. Limited growth recovery after drought-induced forest dieback in very defoliated trees of two pine species. Front. Plant Sci. 7, 418.

Helmisaari, H.-S., Derome, J., Nöjd, P., Kukkola, M., 2007. Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands. Tree Physiol. 27, 1493–1504.

Hertel, D., 1999. Das Feinwurzelsystem von Rein- und Mischbeständen der Rotbuche: Struktur, Dynamik und interspezifische Konkurrenz. Stuttgart: Dissert. Bot. 317, 1- 190 pp.

Hertel, D., Leuschner, C., 2002. A comparison of four different fine root production estimates with ecosystem carbon balance data in a *Fagus-Quercus* mixed forest. Plant Soil 239, 237–251.

Hertel, D., Strecker, T., Müller-Haubold, H., Leuschner, C., 2013. Fine root biomass and dynamics in beech forests across a precipitation gradient – is optimal resource partitioning theory applicable to water-limited mature trees? J. Ecol. 101, 1183–1200.

Hölscher D., Hertel D., Leuschner C., Hottkowitz, M., 2002. Tree species diversity and soil patchiness in a temperate broad-leaved forest with limited rooting space. Flora 197, 118–25.

Janssens, I.A., Sampson, D.A., Curiel-Yuste, J., Carrara, A., Ceulemans, R., 2002. The carbon cost of fine root turnover in a Scots pine forest. For. Ecol. Manage. 168, 231–240.

Kalhoff, M., 2000. Das Feinwurzelsystem in einem Kiefern-Eichen-Mischbestand. Struktur, Dynamik und Interaktion. Stuttgart: Dissert. Bot. 332, 1–199.

Kalyn, A.L., Van Rees, K.C.J., 2006. Contribution of fine roots to ecosystem biomass and net primary production in black spruce, aspen, and jack pine forests in Saskatchewan. Agric. For. Meteorol. 140, 236–243.

Kirfel, K., Heinze, S., Hertel, D., Leuschner, C., 2019. Effects of bedrock type and soil chemistry on the fine roots of European beech – A study on the belowground plasticity of trees. For. Ecol. Manage. 444, 256–268.

Klingenberg, E., Leuschner, C., 2018. A belowground perspective of temperate old- growth forests: Fine root system structure in beech primeval and production forests. For. Ecol. Manage. 425, 68–74.

Konôpka, B., Yuste, J.C., Janssens, I.A., Ceulemans, R., 2005. Comparison of fine root dynamics in Scots pine and Pedunculate oak in sandy soil. Plant Soil 276, 33–45.

Kremser, W., 1990. Niedersächsische Forstgeschichte. Heimatbund Rotenburg/Wümme.

Leberecht, M., Tu, J., Polle, A., 2016. Acid and calcareous soils affect nitrogen nutrition and organic nitrogen uptake by beech seedlings (*Fagus sylvatica* L.) under drought, and their ectomycorrhizal community structure. Plant Soil 409, 143–157.

Leuschner, C., 2002. Forest succession and water resources: soil hydrology and ecosystem water turnover in early, mid and late stages of a 300-yr-long chronosequence on sandy soil. In: Dohrenbusch, A., Bartsch, N. (Eds.), Forest Development, Succession, Environmental Stress and Forest Management. Springer, Berlin, Germany, pp. 1–68.

Leuschner, C., 2020. Drought response of European beech (*Fagus sylvatica* L.) — A review. Perspect. Plant Ecol. Evol. Syst. 47, 125576.

Leuschner, C., Ellenberg, H., 2017. Ecology of Central European Forests: Vegetation Ecology of Central Europe, Vol. I. Springer, Cham, Switzerland.

Leuschner, C., Hertel, D., 2003. Fine root biomass of temperate forests in relation to soil acidity and fertility, climate, age and species. Prog. Bot. 64, 405–438.

Leuschner, C., Immenroth, J., 1994. Landschaftsveränderungen in der Lüneburger Heide 1770–1985. Dokumentation und Bilanzierung auf der Grundlage historischer Karten. Arch. Nat.schutz Landsch.forsch. 33, 35–139.

Leuschner, C., Rode, M.W., 1999. The role of plant resources in forest succession: changes in radiation, water and nutrient fluxes, and plant productivity over a 300-yr- long chronosequence in NW-Germany. Perspect. Plant Ecol. Evol. Syst. 2, 103–147.

Leuschner, C., Wulf, M., Bäuchler, P., Hertel, D., 2013. Soil C and nutrient stores under Scots pine afforestations compared to ancient beech forests in the German Pleistocene: The role of tree species and forest history. For. Ecol. Manage. 310, 405–415.

Lõhmus, K., Truu, J., Truu, M., Kaar, E., Ostonen, I., Alama, S., et al., 2006. Black alder as a promising deciduous species for the reclaiming of oil shale mining areas. WIT Trans. Ecol. Environ. 94, 87–97.

Lust, N., Geudens, G., Olsthoorn, A.F.M., 2000. Scots pine in Belgium and the Netherlands. Investig. Agrar.: Sist. Recur. For. 9, 213–231.

MacQueen, D.R., 1968. The quantitative distribution of absorbing roots of *Pinus sylvestris* and *Fagus sylvatica* in a forest succession. Oecol. Plant. 3, 83–99.

Mainiero, R., Kazda, M., 2006. Depth-related fine root dynamics of *Fagus sylvatica* during exceptional drought. For. Ecol. Manage. 237, 135–142.

Majdi, H., 1996. Root sampling methods — applications and limitations of the minirhizotron technique. Plant Soil 185, 255–258.

Makkonen, K., Helmisaari, H.-S., 1998. Seasonal and yearly variations of fine-root biomass and necromass in a Scots pine (*Pinus sylvestris* L.) stand. For. Ecol. Manage. 102, 283–290.

Makkonen, K., Helmisaari, H.S., 2001. Fine root biomass and production in Scots pine stands in relation to stand age. Tree Physiol. 21, 193–198.

McCormack, M.L., Adams, T.S., Smithwick, E.A.H., Eissenstat, D.M., 2012. Predicting fine root lifespan from plant functional traits in temperate trees. New Phytol. 195, 823–831.

McCormack, M.L., Dickie, I.A., Eissenstat, D.M., Fahey, T.J., Fernandez, C.W., Guo, D., et al., 2015. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. New Phytol. 207, 505–518.

Meier, I.C., Brunner, I., Godbold, D.L., Helmisaari, H.-S., Ostonen, I., Soudzilovskaia, N. A., Prescott, C.E., 2019. Roots and rhizospheres in forest ecosystems: Recent advances and future challenges. For. Ecol. Manage. 431, 1–5.

Meier, I.C., Knutzen, F., Eder, L.M., Müller-Haubold, H., Goebel, M.-O., Bachmann, J., et al., 2018. The deep root system of *Fagus sylvatica* on sandy soil: structure and variation across a precipitation gradient. Ecosystems 21, 280–296.

Meier, I.C., Leuschner, C., 2008. Belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. Glob. Chang. Biol. 14, 2081–2095.

Meinen, C., Hertel, D., Leuschner, C., 2009. Root growth and recovery in temperate broad-leaved forest stands differing in tree species diversity. Ecosystems 12, 1103–1116.

Milnik, A., 2007. Zur Geschichte der Kiefernwirtschaft in Nordostdeutschland. In: Ministerium für Ländliche Entwicklung, Umwelt und Verbraucherschutz des Landes Brandenburg, Landesforstanstalt Eberswalde, editors. Die Kiefer im nordostdeutschen Tiefland – Ökologie und Bewirtschaftung. Eberswalder Forstliche Schriftenreihe, Vol. XXXII: 14-21.

MLUR Brandenburg (Ministerium für Landwirtschaft, Umweltschutz und Raumordnung des Landes Brandenburg), editor. 2004. Waldbau-Richtlinie 2004. "Grüner Ordner" der Landesforstverwaltung Brandenburg. Sonderdruck. Ministerium für Landwirtschaft, Umweltschutz und Raumordnung.

Majunke, C., Dreger, F., Schulz, U., Rös, M., Torkler, F., 2005. Zur Bedeutung des Waldumbaus für die Erhöhung von Biodiversität und der Selbstregulation – Potenziale in kieferndominierten Waldbeständen. In: Ministerium für Ländliche Entwicklung, Umwelt und Verbraucherschutz des Landes Brandenburg, Landesforstanstalt Eberswalde, editors. Ökologischer Waldumbau im nordostdeutschen Tiefland. Eberswalder Forstliche Schriftenreihe, Vol. XXIII: 121- 138.

Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. Ecol. Monogr. 76, 521–547.

NLF (Niedersachsische Landesforsten) editor. 2011. Das LÖWE-Programm. 20 Jahre Langfristige Ökologische Waldentwicklung. Niedersächsische Landesforsten, Braunschweig, Germany.

Ostonen, I., Lõhmus, K., Helmisaari, H.-S., Truu, J., Meel, S., 2007. Fine root morphological adaptations in Scots pine, Norway spruce and silver birch along a latitudinal gradient in boreal forests. Tree Physiol. 27, 1627–1634.

Persson, H., 1980. Fine-root dynamics in a Scots pine stand with and without near- optimum nutrient and water regimes. Acta Phytogeogr. Suec. 68, 101–110.

Polomski, J., Kuhn, N., 1998. Wurzelsysteme. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft, Birmensdorf. Paul Haupt, Bern, Switzerland, pp. 1–290.

Poschlod, P., 2017. Geschichte der Kulturlandschaft: Entstehungsursachen und Steuerungsfaktoren der Entwicklung der Kulturlandschaft. Lebensraum- und Artenvielfalt in Mitteleuropa, Ulmer, Stuttgart, Germany.

Pregitzer, K.S., DeForest, J.L., Burton, A.J., Allen, M.F., Ruess, R.W., Hendrick, R.L., 2002. Fine root architecture of nine North American trees. Ecol. Monogr. 72, 293–309.

R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org/.

Reich, P.B., Walters, M.B., Tjoelker, M.G., Vanderklein, D., Buschena, C., 1998. Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. Funct. Ecol. 12, 395–405.

Riek, W., Strohbach, B., Kallweit, R., 2007. Bodenzustand und Stoffhaushalt von Kiefernbeständen in Brandenburg. In: Ministerium für Ländliche Entwicklung, Umwelt und Verbraucherschutz des Landes Brandenburg, Landesforstanstalt Eberswalde, editors. Die Kiefer im nordostdeutschen Tiefland – Ökologie und Bewirtschaftung. Eberswalder Forstliche Schriftenreihe, Vol. XXXII: 54-63.

Rigling, A., Bigler, C., Eilmann, B., Feldmeyer-Christe, E., Gimmi, U., Ginzler, C., et al., 2013. Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. Glob. Chang. Biol. 19, 229–240.

Scherfose, V., 1990. Feinwurzelverteilung und Mykorrhizatypen von *Pinus sylvestris* in verschiedenen Bodentypen. Ber. Forsch.zentr. Waldökosysteme Univ. Göttingen. 62, 1–166.

Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., et al., 2020. A first assessment of the impact of the extreme 2018 summer drought on Central European forests. Basic Appl. Ecol. 45, 86–103.

Tefs, C., Gleixner, G., 2012. Importance of root derived carbon for soil organic matter storage in a temperate old-growth beech forest – Evidence from C, N and ^{14}C content. For. Ecol. Manage. 263, 131–137.

Teissier du Cros, E., editor. 1981. Le Hêtre. INRA, Paris, France. 1-613 pp.

TI (Thünen-Institut), 2015. Dritte Bundeswaldinventur - Basisdaten (Stand 20.03.2015). https://bwi.info/Download/de/BWI-Basisdaten/ACCESS2003/bwi20150320_alle_ daten2012.zip.

Valverde-Barrantes, O.J., Horning, A.L., Smemo, K.A., Blackwood, C.B., 2016. Phylogenetically structured traits in root systems influence arbuscular mycorrhizal colonization in woody angiosperms. Plant Soil 404, 1–12.

Vanguelova, E.I., Nortcliff, S., Moffat, A.J., Kennedy, F., 2005. Morphology, biomass and nutrient status of fine roots of Scots pine (*Pinus sylvestris*) as influenced by seasonal fluctuations in soil moisture and soil solution chemistry. Plant Soil 270, 233–247.

Van Praag, H.J., Sougnez-Remy, S., Weissen, F., Carletti, G., 1988. Root turnover in a beech and a spruce stand of the Belgian Ardennes. Plant Soil 105, 87–103.

Vogt, K.A., Vogt, D.J., Palmiotto, P.A., Boon, P., O'Hara, J., Asbjornsen, H., 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 187, 159–219.

Weemstra, M., Mommer, L., Visser, E.J., van Ruijven, J., Kuyper, T.W., Mohren, G.M.J., Sterck, F.J., 2016. Towards a multidimensional root trait framework: a tree root review. New Phytol. 211, 1159–1169.

Weemstra, M., Sterck, F.J., Visser, E.J., Kuyper, T.W., Goudzwaard, L., Mommer, L., 2017. Fine-root trait plasticity of beech (*Fagus sylvatica*) and spruce (*Picea abies*) forests on two contrasting soils. Plant Soil 415, 175–188.

Yuan, Z.Y., Chen, H.Y., 2010. Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: literature review and meta-analyses. Crit. Rev. Plant Sci. 29, 204–221.

Železnik, P., Vilhar, U., Starr, M., de Groot, M., Kraigher, H., 2016. Fine root dynamics in Slovenian beech forests in relation to soil temperature and water availability. Trees 30, 375–384.

Chapter 4

Are northern German Scots pine plantations climate smart? The impact of large-scale conifer planting on climate, soil and the water cycle

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Abstract

Increasing temperatures and rising atmospheric vapor pressure deficits are exposing forests around the globe to increasing drought and heat stress, demanding a shift to climate-smart forestry for increasing the stress resistance and resilience of production forests and to enhance their climate change mitigation potential. Based on measurements in paired pine and beech forests and the review of literature data, we analyse the biophysical consequences and the carbon cycle impact of large-scale Scots pine (*Pinus sylvestris* L.) plantations in northern Germany in the face of a warming and aridifying climate. We quantified canopy surface albedo and surface temperature, evapotranspiration and deep seepage, carbon (C) storage in biomass and soil and annual C sequestration, and soil acidification of pine plantations in comparison to beech forests (*Fagus sylvatica* L.), the natural forest vegetation. We find that near-infrared (NIR, 700–3000 nm) canopy surface albedo is higher by 5.2 percentage points during summer over beech as compared to pine forest, resulting in a 9 % higher net radiation and a 0.6 K higher surface temperature of the pine canopy. Deep seepage is on average by 68 mm yr^{-1} smaller under pine than beech forest (66 mm yr^{-1} vs. 134 mm yr^{-1}) due to the higher evapotranspiration of pine. C storage in biomass and soil is by ~ 48 Mg C ha^{-1} higher in beech than pine forests, reflecting the higher productivity of beech, demonstrating an unfavorably low C sequestration potential of Scots pine plantations. We conclude that the large-scale Scots pine plantations in northern Germany (>1.7 million ha) are neither environmental-friendly nor climate smart, given their enhancement of climate-warming, low climate change mitigation potential, and negative effect on groundwater recharge. Replacing pine plantations by beech (or other hardwood) forests in northern

Germany and adjacent regions is urgently needed for achieving the goals of climate-smart forestry.

Keywords: Canopy albedo, Canopy temperature, Carbon sequestration, Deep seepage, Evapotranspiration, Fagus sylvatica, Paired plots, Pinus sylvestris, Soil acidification, Soil moisture

4.1 Introduction

Climate-smart forestry (CSF) is a forest management concept developed in the face of climate change with the objectives (i) to adapt forests to upcoming climate-related stresses and increase tree resistance and resilience, (ii) to secure (or even increase) forest productivity and incomes, and (iii) to reduce or remove greenhouse gas emissions (Yousefpour et al. 2018, Verkerk et al. 2020, FAO 2021). With rapidly increasing temperatures and atmospheric saturation deficits and regionally decreasing summer precipitation, many forests have been exposed to increasing drought and heat stress in the last decades (Allen et al. 2010), which requires management decisions and often a shift in tree species composition in production forests in order to meet the three objectives outlined above. The urgency for action has recently been demonstrated by the severe 2018–2020 drought episode in Central Europe, probably the worst for 2000 years (Büntgen et al. 2021), which left large areas of planted conifer forest, but also some broadleaf forests, damaged or dead (Braun et al. 2020, Schuldt et al. 2020). One consequence of this increasing pressure on forests is that silvicultural concepts and tree species selection have to be scrutinized in the context of current and expected climatic conditions, but also in order to meet changing societal demand for roundwood and other environmental services provided by forests. Due to their large influence on the carbon cycle, forests have been placed at the forefront of action to mitigate climate warming, either through carbon sequestration and storage in biomass and soil, or through the use of wood products for material and energy substitution (Harmon 2019, Hudiburg et al. 2019). This is why CSF concepts mostly focus on enhancing the climate change mitigation role of forests and seek to increase timber production, while other environmental services are less often addressed, even though they should by definition also be targeted by CSF strategies (Bowditch et al. 2020).

In a warming and aridifying climate, the impact of forests on the water cycle is crucial, as surface flow and groundwater recharge depend on tree species and forest structure (Chang 2012). In many industrialized regions, water scarcity is a problem even in humid climates, when the demand for agriculture, industries and public use is high (European Commission 2012). It may be necessary to opt for tree species with lower water consumption, when competition for water is fierce among different users.

Large parts of the lowlands of northern Germany and Poland, and of the Netherlands are covered by planted Scots pine (*Pinus sylvestris* L.) forests that stock on Pleistocene

unconsolidated substrates and replace the former temperate broadleaf forests mostly of European beech (*Fagus sylvatica* L.) and oak species (*Quercus petraea* (Matt.) Liebl and *Q. robur* L.). After the original broadleaf forest had widely been cleared for agriculture or was devastated through wood pasturing and litter raking during the Middle Ages or in earlier times, Scots pine was introduced from the 18th century onwards to tackle severe timber shortages. Pine was a suitable choice for reafforestation, as the species is undemanding and thus copes well with the mostly nutrient-poor soils, and is easy to establish through seeding or planting on bare soil. In many regions of this former broadleaf forest landscape, pine is nowadays the dominant tree species with a share of up to 75 % of total forest cover (e.g. in Brandenburg in eastern Germany and in western Poland; Hofmann et al. 2000). In many regions of the northern German and Polish lowlands, wood industries based on pine are important elements of the local economy, producing wood for construction and pulp (Bilke & Noack 2007). In 2017 (the last year before the severe 2018–2020 drought), about 7.2 million m^3 of pine roundwood (without bark) have been harvested in the North German lowlands (including a small fraction of larch wood; DESTATIS 2017), which is roughly 10 percent of Germany's annual wood harvest.

Large-scale replacement of temperate broadleaf forest by conifer plantations may have consequences for many ecosystem properties and functions, notably the carbon, water and nutrient cycles, soil chemistry, microclimate, and biodiversity, as the phenology, foliar stoichiometry and stand structure of this mainly boreal conifer species is largely different to that of temperate broadleaf trees. While much information exists about the occurrence of pest organisms and the fire regime of Central European pine plantations (Ebert 1968, Schlick & Möller 2007, BLE 2020), only few studies have directly compared Central European Scots pine to broadleaf forests for differences in microclimate and biogeochemical cycles. Some comprehensive studies have been conducted in adjacent pine and beech stands on sandy soil in north-eastern Germany examining microclimate, soil chemistry, productivity, rooting patterns, and water turnover (e.g. Anders et al. 2004, Müller 2009, Müller & Bolte 2009). A few studies exist that systematically compared soil carbon pools under pine and broadleaf (mostly beech) stands in the Pleistocene lowlands of northern Germany and the Netherlands (Fischer et al. 2002, Heinsdorf 2002, Schulp et al. 2008, Leuschner et al. 2013, Diers et al. 2021). Anders et al. (2004) and Förster et al. (2021a) compared the biomass and net primary productivity of matching pine and beech stands on similar soil, and Anders et al. (2005) and Förster et al. (2021b) studied fine root biomass and productivity. However, a comprehensive assessment of the biogeochemical and biophysical consequences of replacing beech by Scots pine on sandy soils is lacking. Given the vast extension of Scots pine plantations in northern Central Europe (>1.7 million ha in the northern German lowlands alone) and the velocity of recent climate warming, a critical assessment of the impact of current silvicultural schemes on climate, soils and biogeochemical cycles in this region is needed.

Here, we present a review of empirical data on the microclimate, soil acidity, soil and biomass carbon storage, productivity, soil moisture regimes, and water consumption of

paired Scots pine and European beech stands on Pleistocene sandy to sandy-loamy soil in various regions of northern Germany with the objective to assess the effects of replacing broadleaf by conifer forests in a cool-temperate climate. A focus is on ecosystem services that likely will play a crucial role in future silvicultural and landscape management schemes in a warmer and drier climate. These services must be a key element of climate-smart forestry, notably carbon sequestration in biomass and soil, groundwater recharge, and the feedback of forests on the regional climate. Our analysis bases on three data sets from pine and beech stands on similar soil, the first covering 13 sites spread over a large part of northern Germany, the second referring to 9 sites in the Prignitz region (western Brandenburg, NE Germany), and the third consisting of a detailed comparison of the biogeochemistry of a pine and a beech stand in the Lüneburg Heath region (Lower Saxony, NW Germany). In addition, published data from pine and beech stands on Pleistocene sandy to sandy-loamy soils in northern Germany are included in the analysis, notably several studies on paired pine-beech stands in NE Germany (near Eberswalde, Brandenburg).

4.2 Materials and methods

4.2.1 Determining the Scots pine plantation area

For our analysis, we considered the entire North German lowland area between the Dutch border in the west and river Oder in the east, covering the federal states (or part of) North Rhine-Westphalia, Lower Saxony, Schleswig-Holstein, Saxony-Anhalt, Mecklenburg-Western Pomerania, Brandenburg, Saxony, and the city-states Bremen, Hamburg and Berlin (Fig. A4.1). Seven forest growth regions were distinguished in the lowlands according to climate (oceanic to sub- continental) and age of the glacial substrate (last and penultimate Ice Age), summarizing forest growth areas as defined by Gauer and Kroiher (2012). We first mapped the potential natural forest vegetation for the time prior to human colonization according to the reconstruction by BfN (2010) for the lowland area (data basis: Thünen-Institut) using the software ArcGIS (ESRI Inc.). We subsequently determined the natural extension of (1) beech and beech-oak forest (phytosociological alliance Fagion sylvaticae), (2) natural Scots pine forests (Dicrano-Pinion alliance), and (3) other natural forest communities ('Other', which includes, amongst others, the alliances Carpinion betuli [oak-hornbeam forests] and Quercion roboris [oak forests on acid soils], and floodplain and swamp forests).

For determining the recent extension of Scots pine plantations in northern Germany, we analyzed data provided by the third German National Forest Inventory 2011–2012 (BWI[3], TI 2015), adopting the methodology described in Riedel et al. (2017). Data collection in the frame of BWI[3] was conducted in sampling grids of 16 km^2 mesh width (Hamburg, Lower Saxony, Bremen, North Rhine-Westphalia, Berlin, Brandenburg), 8 km^2 width (Lower Saxony, Saxony), or 4 km^2 width (Schleswig-Holstein, Mecklenburg-Western Pomerania, Saxony-Anhalt). We estimated the forest area ('real forest area' as derived from the share of

forested tract corners in the total number of tract corners) in the North German lowlands, based on stocked and accessible forest land, excluding gaps in the main stand. In a first step, we determined the natural extension of the different forest types (beech and beech-oak forests, Scots pine forest, 'Other') in the recent forest area. In a second step, estimated forest areas once covered by a given natural vegetation type in the North German lowlands were linked to the recent stocking type (pure and mixed stands dominated by (1) beech (*Fagus sylvatica* L.), (2) pine (*Pinus* spp., mainly *P. sylvestris*), or (3) other tree species) in these areas.

4.2.2 Study sites

The forests investigated for microclimatic, hydrological and biogeochemical characteristics were mature Scots pine and European beech stands stocking on unconsolidated sandy to sandy-loamy fluvio- glacial deposits or moraine material of the penultimate (Saalian) or last (Weichselian) glaciation in northern Germany between Cologne in the west and river Oder in the east (federal states of Lower Saxony, Mecklenburg-Western Pomerania, Brandenburg and North Rhine- Westphalia). Data from the following three field studies were included in the analysis: (1) A paired-plot study at 13 sites (of which subsets were used for the different analyses) located between Cologne in the west and river Oder in the east (soil and biomass carbon stocks, productivity, soil acidity), (2) a comparative study in 9 pine stands and 9 beech stands on similar soil in NE Germany (Prignitz region in the state of Brandenburg) (soil carbon stocks, soil acidity), and (3) an in-depth study of a pine and a nearby beech stand in NW Germany (Unterlüss/Eimke, Lüneburg Heath, state of Lower Saxony) (microclimate, water fluxes). In addition, published data on water fluxes in beech and pine stands on Pleistocene substrates in other regions of northern Germany were considered for comparison, notably the study of a pine and a nearby beech stand in Kahlenberg near Eberswalde (NE Germany, state of Brandenburg; Müller & Bolte 2009).

The climate in the study region is cool-temperate with mean annual temperatures (MAT) between 8.6 and 10.3 °C and mean annual precipitation (MAP) varying between 555 and 884 mm. MAP and climate oceanity decrease from the west to the east across the study region (DWD CDC 2019). The natural forest vegetation is in most of the region beech or beech-oak forest on acid soil, in the east locally also oak-pine forest (BfN 2010). The studied pine and beech stands developed from seed or were planted and thus represent age cohorts, as is characteristic for most of the managed forests in northern Germany. All stands have been subjected to regular thinning operations according to local silvicultural schemes. Some of the beech forests have recently been taken out of management for nature conservation purposes, but the forest structure clearly mirrors management history. As pine is harvested at somewhat younger age (typically at 80–120 years in the study region) than beech (120–140 years; Beinhofer & Knoke 2009), the selected pine stands were in most cases (40)60–80 years and the beech stands 100–140 years old. Correspondingly, tree height was greater (25–33 m) in the beech than the pine stands (12–28 m), and stem density higher in

the pine stands, while stand basal area was more or less similar. Stand structural data for data set (1) are given in Förster et al. (2021a), for data set (2) in Leuschner et al. (2013), and for data set (3) in Leuschner (2002).

4.2.3 Soil chemical analyses

In each nine paired pine and beech stands of study (1) (i.e. a subset of the 13 sites) with usually not>5 km distance to each other, each ten soil pits were dug to 60 cm depth at random positions in the stand. Soil samples of 100 cm³ volume were extracted with a steel corer at 0–10 cm, 10–20 cm, 20–40 cm, and 40–60 cm depth and in the organic layer on the forest floor (each three replicate samples that were mixed in the analysis). In study (2), each nine pine and beech stands on similar soil were sampled in a comparable manner, but with five (instead of 10) pits per stand. In the ground and dried soil material, C concentrations were determined by gas chromatography (vario EL III, elementar, Hanau, Germany). While all C in the organic layer was assumed to be organic C, inorganic C was determined in the mineral soil as the difference between gas chromatographic C analyses before (total C) and after combustion at 640 °C (inorganic C). For obtaining the SOC pool for a standard 1-m soil profile, we fitted a Michaelis-Menten curve to the SOC pools of the 0–10, 10–20, 20–40, and 40–60 cm layers and extrapolated the pools down to a depth of 1 m based on the obtained concentration-depth curve fitted for each soil plot.

The pH was measured in a suspension of 10 g fresh sieved soil (or 2.5 g of organic layer material) in 25 ml deionized water (pH(H_2O)) or in 1 M KCl (pH(KCl)). We report only pH (KCl) values here, which represent the potential acidity of the soil.

4.2.4 Biomass and productivity measurements

Coarse wood biomass (live trees >7 cm diameter at breast height, saplings and deadwood) was computed in the paired pine and beech stands at 13 sites of study (1) from inventory data collected in each ten 0.1 ha-plots using allometric regressions for pine and beech (Förster et al. 2021a). Aboveground net primary productivity (ANPP) was measured in 2015–2017 at 11 sites of study (1) in the paired pine and beech stands with each six 0.1 ha-plots investigated. Coarse wood production was derived from repeated reading of dendrometer tapes mounted at 15 trees per plot, and litter production was measured with one litter trap per plot (i.e. 6 replicate traps per stand; for details see Förster et al. 2021a). We further conducted two fine root inventories in spring 2015 and 2017 at eight sites of study (1) in the paired pine and beech stands with six plots per stand investigated. Pine and beech fine root bio- and necromass were determined in the organic layer and the top 20 cm of the mineral soil from 10 replicate samples per stand (one sample per plot; for details see Förster et al. 2021b).

4.2.5 Microclimatological and hydrological measurements

Microclimatological and water flux measurements in a pine and a nearby beech stand were conducted in 1991 and 1992 from scaffolding towers in the frame of study (3) at the Unterlüss/Eimke sites in the Lüneburger Heath region (NW Germany). Net radiation above the canopy was measured continuously with ventilated Schulze-type net radiation sensors (Fa. Lange, Berlin, Germany), downward and upward short-wave radiation (300–3000 nm) with CM5 and CM7 solarimeters (Kipp & Zonen, Delft, The Netherlands), and downward and upward fluxes of photosynthetically-active radiation (PAR, 300–700 nm) with LI-190SA quantum sensors (LICOR, Lincoln, NE, USA) at 1–2 m height above the beech and pine canopies. Near-infrared radiation (NIR, 700–3000 nm) was obtained as the difference between short-wave radiation and PAR. Canopy surface temperature was computed from the flux density of upward long-wave terrestrial radiation, obtained by subtracting reflected short-wave radiation from outgoing total radiation.

Soil moisture variation was determined gravimetrically at weekly intervals in 1991 and 1992 in the Unterlüss/Eimke stands by soil coring at 0–5 cm, 10–15 cm and 55–60 cm depth and in the organic layer (3–5 replicate samples). The data was used to calculate the variation in water storage in the profile to a depth of 70 cm. The amount of plant-available water (water held between –300 hPa and −1.5 MPa) was computed for different mineral soil depths and the organic layer material from water retention curves established in intact 250 cm^3-soil cores through desorption in the laboratory.

The water vapour flux with transpiration (dry canopy) and evapotranspiration (ET, wet canopy) was determined for the beech forest of study (3) with the Bowen ratio energy balance approach from continuously measured temperature and air humidity gradients above the canopy (Leuschner 2002). In case of the pine forest, the fetch did not allow gradient measurements above the canopy, and ET was estimated with the big leaf formulation of the Penman-Monteith equation based on continuous net radiation, temperature and air humidity measurements above the canopy. Canopy and aerodynamic resistances (r_c and r_a) were derived from micrometeorological profile measurements conducted above a nearby pine forest of similar structure (Fuhrberg site, Flüggen 1991). To estimate deep seepage under the beech and pine forests, simple water balance calculations at the ecosystem level were conducted for the year 1991 using precipitation and ET data and seasonal change in soil water storage. For measuring details see Leuschner (2002). Literature data on stand transpiration and evapotranspiration of beech and pine stands on Pleistocene substrates in northern Germany measured either with the microclimatological gradient approach, the ecosystem water balance approach or stem sapflux sensors were compiled in order to compare the two species on a broader data basis.

The hydrological fluxes in mature beech and pine forests near Eberswalde (state of Brandenburg) were approximated from above- and below-canopy precipitation measurements, continuous soil moisture measurements, and estimation of

evapotranspiration based on local climate data (Lützke & Simon 1972; Lützke 1991). Deep seepage data were checked against measurements with small and large weighable/non-weighable lysimeters planted with pine or beech (Müller & Bolte 2009).

4.2.6 Statistical analyses

Data analysis was conducted with R software, version 3.6.3 (R Core Team 2020). In the paired plot studies, we tested for significantly different pine and beech forest means of aboveground biomass carbon stocks (n = 13), ANPP (n = 11) and fine root mass (n = 8) with Wilcoxon signed-rank tests for paired samples. To test for differences between tree species in SOC stocks and soil acidity (pH KCl), we applied ANOVAs (F-test) and included study site (9 sites), soil depth level and the interaction between tree species and soil depth as additional model variables. Soil depth level(s) with a significant effect of tree species were identified with Tukey's HSD tests. We pooled our own transpiration, evapotranspiration and seepage data of study (3) with published data on canopy T, ET and seepage and tested for normal distribution of the data with a Shapiro-wilk test and analysed differences between beech and pine forest means with two-sided or one-sided t tests. In case of the microclimatological data, testing for significantly different means was not possible due to n = 1. Linear regressions of stand transpiration and evapotranspiration on precipitation were calculated with the software Xact (SciLab, Hamburg, Germany). A significance level of α = 0.05 was used throughout the study.

4.3 Results

4.3.1 Extent of pine plantation area

While Scots pine forests likely contributed with only 2.3 % to the natural forest area of the North German lowlands before anthropogenic forest destruction, mostly in the more continental east, 53.2 % of the recent forest area refers to pine stands (which includes a small proportion of other introduced pine species such as *P. nigra*) (Table 4.1). Beech forests, which once potentially contributed 48.6 % of the natural forest area, are currently found on only 6.6 % of the recent forest area (Table 4.1). Across the North German lowlands, pine plantations today extend over 1.75 million ha, while beech occurs on only 0.22 million ha (Table 4.2). The large-scale replacement of potential natural beech forests by Scots pine plantations is also evident, when tracking the forest conversion in the area that would naturally be stocked with beech: Of the 1.72 million ha of current forest stocking on former beech forest soils, only 10.5 % (0.18 million ha) are today beech forest, while 50 % refers to pine stands and another 39.5 % to other planted forests, notably Norway spruce, oak, larch and other species. Even larger is the species replacement in the area that was once covered by 'Other forest communities', i.e. mostly oak-hornbeam forests and oak forests on acid soil, where 54 % of the area is now covered by Scots pine with an area of 0.78 million ha (Table 4.2). The pine dominance is highest in the Saalian moraine region (east) with a share of 75.4 % in the current forest area, but is also high in the Weichselian moraine region

(50.1 %), the Saalian moraine region (west) (48.6 %), and the eastern coastal region (42.4 %, Table 4.1).

4.3.2 Microclimate

Neighboring pine and beech forests at the Lüneburg Heath site (Eimke/Unterlüss; study (3)) differed largely in their canopy short-wave reflectivity during summer (May 15 – September 15). In the 300–3000 nm wave-length range, the beech forest canopy had a by 3.7 percentage points higher reflectivity than the pine forest (13.9 % vs. 10.2 %, average of two summers; Table 4.3). This difference was even larger in the NIR range (700–3000 nm) with 5.2 percentage points (20.4 vs. 15.2 %). While beech and pine canopies differed substantially in the leafy period of beech, reflectivities were more similar in the leafless period (Fig. 4.1). Consequently, above-canopy net radiation between May and September was on average by 17 W m^{-2} (+9 %) higher over pine than beech (average of two summers; Fig. 4.2). This corresponded to a mean canopy surface temperature that is by 0.6 K higher in the pine forest during summer (18.60 vs. 17.96 $^{\circ}$C; Table 4.3).

Table 4.1. Potential natural forest cover (all forest types), and potential cover of natural European beech and natural Scots pine forest (in percent of potential natural forest area) prior to human forest destruction, and recent forest cover (all forest types), and recent extent of beech and pine forests (in percent of recent stocked and accessible forest area) in the seven climatically and geologically defined sub-regions of the North German lowlands. The figures for the total lowland area are also given (in bold). Numbers in brackets refer to the stocked and accessible forest area, which is somewhat less than total forest area. Based on a GIS analysis of the map of the natural vegetation of Germany after BfN (2010), assigned to forest growth regions adapted from Gauer and Kroiher (2012), and on data on recent forest area after TI (2015).

Region	Natural forest cover (%)	Area naturally covered by beech forests (%)	Area naturally covered by pine forests (%)	Recent forest cover (%)	Recent beech forest cover (%)	Recent pine forest cover (%)
Western coastal region	95.4	13.0	0.0	9.8 (9.1)	5.9	16.5
Central coastal region	94.2	61.8	0.0	10.8 (10.3)	22.4	6.4
Eastern coastal region	97.1	81.6	1.0	25.4 (23.4)	12.1	42.4
Weichselian moraine region	96.5	74.6	0.7	27.0 (25.4)	11.5	50.1
Lower Rhine and Westphalian Bay	99.6	54.8	0.0	15.4 (14.7)	15.3	17.8
Saalian moraine region (west)	99.4	46.4	0.0	28.1 (26.6)	2.8	48.6
Saalian moraine region (east)	95.6	30.5	8.2	37.4 (35.0)	1.7	75.4
Total: North German lowlands	**96.8**	**48.6**	**2.3**	**24.9 (23.4)**	**6.6**	**53.2**

Table 4.2. Extension of current beech forests, pine forests, and other forest types on area assignable to former natural beech (or beech-oak) forest, natural pine forest, or other natural forest types, given in their absolute size (ha) and in % of the area of that natural forest category extension in the lowlands. In the last column, the extension of current beech forests, pine forests and other forests assignable to the three different natural forest categories is expressed in percent of the total current forest area in the North German lowlands. The lowermost four rows give the extension of beech, pine and other forest types in the whole N German lowland region. For forest area, the standard error (SE) of the size estimate is additionally given, as caused by the grid size of forest data from BWI[3].

Area assignable to natural forest category:	Current stocking type	Size of current forest area (ha)	Share of current forest area (%) in natural forest category	Share of current forest area (%) in the North German lowlands
Natural beech (and beech-oak) forests	Beech forests	181,188 ± 8,898	10.5	5.5
	Pine forests	860,820 ± 23,957	50.0	26.2
	Other	679,126 ± 17,029	39.5	20.7
	Sum	1,721,332 ± 32,373	100	52.4
Natural pine forests	Beech forests	199 ± 141	0.2	0
	Pine forests	108,756 ± 10,076	88.7	3.3
	Other	13,675 ± 2,993	11.2	0.4
	Sum	122,630 ± 10,848	100	3.7
Other natural forest types	Beech forests	36,684 ± 4,007	2.5	1.1
	Pine forests	781,268 ± 24,897	54.1	23.8
	Other	626,270 ± 17,931	43.4	19.0
	Sum	1,444,322 ± 31,925	100	43.9
Current forest area in the N German lowlands	Beech forests	218,072 ± 9,832	-	6.6
	Pine forests	1,750,843 ± 3,3715	-	53.2
	Other	1,319,070 ± 24,668	-	40.1
	Sum	3,287,985	-	100

Table 4.3. Canopy reflectivity for short-wave radiation (300–3000 nm) and NIR (700–3000 nm), net radiation above the canopy, and canopy surface temperature as calculated from long-wave radiation flux density for the pine forest BP3 and the beech forest OB5 in the Lüneburg Heath region (study (3)) during the summer period (May 15 – September 15), averaged over 1991 and 1992.

	Unit	Pine forest	Beech forest
Short-wave reflectivity	%	10.2	13.9
NIR reflectivity	%	15.2	20.4
Net radiation	W m^{-2}	215	198
Canopy surface temperature	°C	18.60	17.96
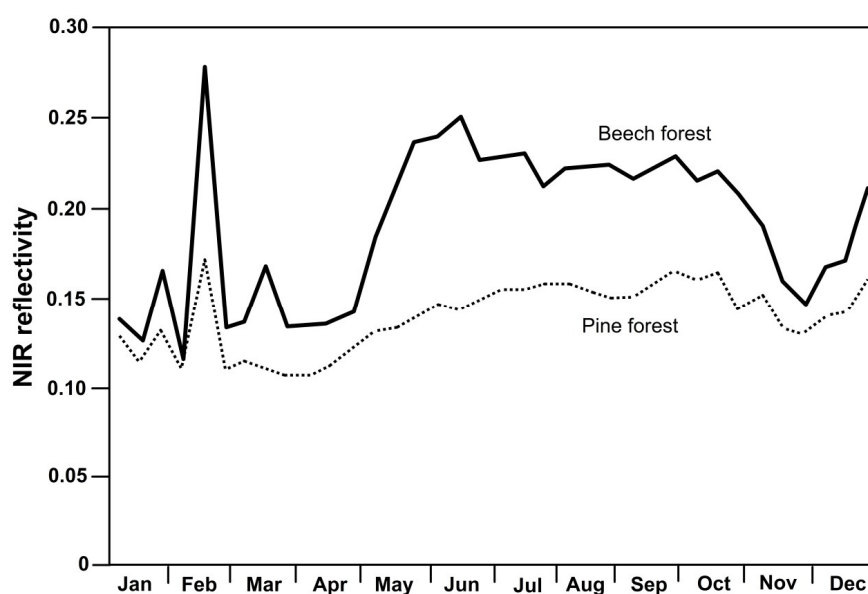
Figure 4.1. Canopy reflectivity in the NIR range (700–3000 nm) of the beech forest OB5 and the pine forest BP3 in the Lüneburg Heath region (study (3)) during the year 1992. Only values recorded at highest sun angles (10 a.m. – 2p.m.) are considered.
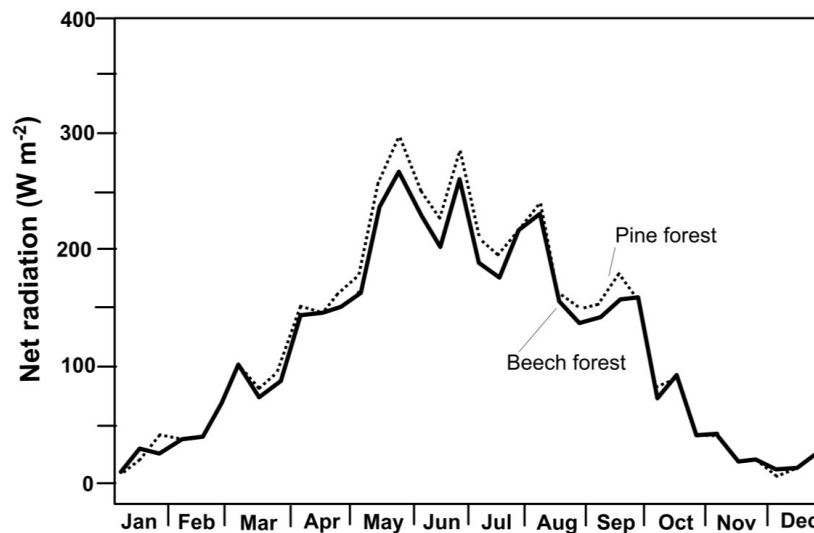
91

Figure 4.2. Seasonal course of net radiation above the canopy of the beech forest OB5 and the pine forest BP3 in the Lüneburg Heath region (study (3)) over the year 1992.

4.3.3 Soil moisture regime

Both the mineral soil profile to 70 cm depth and the organic layer were moister under the beech forest than the pine forest at the Lüneburg Heath site (study (3)) throughout the two study years. Volumetric soil water content (θ) was in all investigated horizons generally 30–70 % higher in the beech forest soil than under pine (Table 4.4) and approached the lower moisture levels of the pine forest soil only during short periods, e.g. in September/October 1991 and 1992 (Figs. 4.3 and 4.4). In correspondence, the storage of plant-available soil water was on average during summer by 20 mm larger under the beech forest than the pine forest (Table 4.4, Fig. 4.5); this difference was smaller (about 10 mm) in the winter months. During periods of highest drought intensity as in September 1991 and July 1992, soil moisture was more depleted under the pine than the beech stand (Fig. 4.5). Even though organic layer depth was similar in both forest types (85 and 80 mm under pine and beech, respectively), the beech layer contained much more plant-available water than the pine layer (1.7 vs. 10.1 mm for pine and beech during summer on average, Table 4.4). In correspondence, the water potential-water content curve of organic layer material was shifted toward lower θ values for pine litter, indicating a smaller capacity to adsorb and store water as compared to beech litter (Fig. A4.3).

Table 4.4. Mean volumetric soil water content and mean storage of plant-available water in the organic layer and mineral soil of the pine forest BP3 and the beech forest OB5 at Eimke/Unterlüss (Lüneburg Heath region, study (3)) in the summers (May 15 – September 20) and full years of 1991 and 1992. Pine forest – normal fonts, beech forest – fonts in italics. The storage is given for water held in the potential range −300 hPa to −1.5 MPa.

|		1991		1992	
		Summer	Year	Summer	Year
SOIL WATER CONTENT (vol. %)					
Organic layer	Pine	15.5	-	9.0	14.1
	Beech	*28.1*	*-*	*17.8*	*23.6*
0-5 cm	Pine	10.3	15.2	15.1	22.4
	Beech	*18.9*	*23.4*	*24.7*	*28.1*
10-15 cm	Pine	8.7	12.5	8.7	16.0
	Beech	*13.5*	*17.5*	*13.5*	*22.5*
55-60 cm	Pine	3.3	4.3	3.7	6.3
	Beech	*5.0*	*6.9*	*5.3*	*8.8*
WATER STORAGE (mm)					
Organic layer	Pine	1.6	-	1.8	5.7
	Beech	*12.1*	*-*	*8.2*	*9.7*
Mineral soil (0-70 cm)	Pine	23.3	39.7	37.8	76.8
	Beech	*33.0*	*50.7*	*52.1*	*84.6*
Total profile	Pine	24.6	-	39.6	82.5
	Beech	*45.1*	*-*	*60.3*	*94.3*
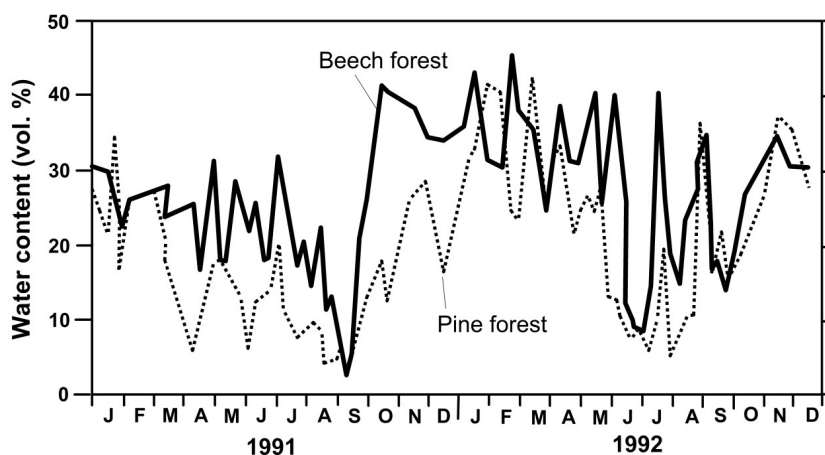
Figure 4.3. Seasonal course of soil water content in the mineral topsoil (0-5 cm) under the beech forest OB5 and the pine forest BP3 in the Lüneburg Heath region (study (3)) in the years 1991 and 1992.
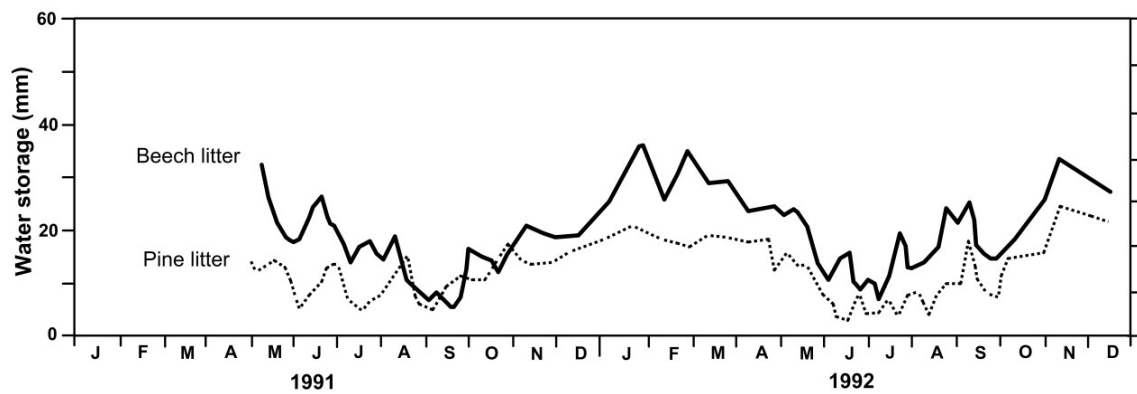
Figure 4.4. Seasonal course of water storage in the organic layer (L, F and O layers) of beech forest OB5 and pine forest BP3 in the Lüneburg Heath region (study (3)) from May 1991 to December 1992.
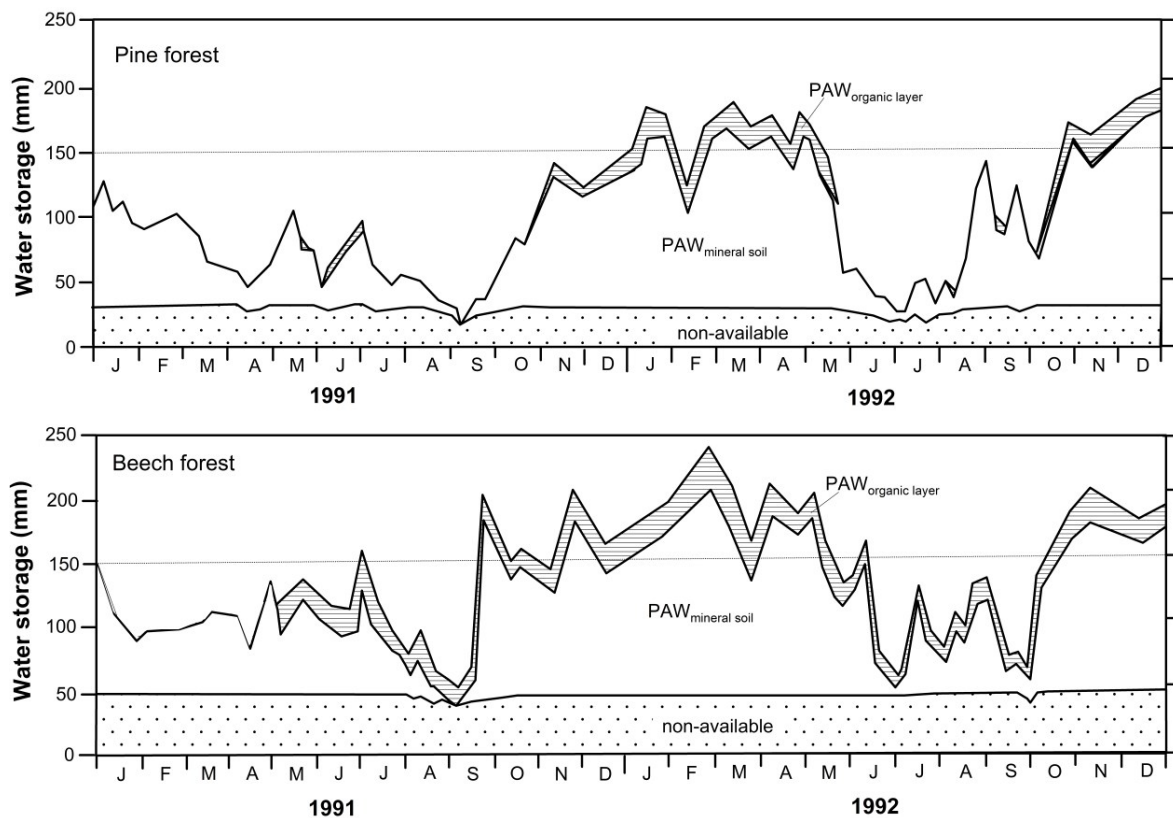

Figure 4.5. Seasonal course of soil water storage in the soil profile to 70 cm depth under pine forest BP3 (upper panel) and beech forest OB5 (lower panel) in the Lüneburg Heath region (study (3)) in 1991 and 1992. Indicated are non-available water (held at $\psi_{soil} < -1.5$ MPa) and plant-available water (PAW, -300 hPa $>$PAW $>$-1.5 MPa), and the storage in the mineral soil and in the organic layer. Note that organic layer data are lacking for the period January – April 1991. The dotted line at 150 mm is depicted to facilitate comparison.

4.3.4 Water consumption and seepage

Evapotranspiration data from six northern German pine and beech sites on Pleistocene substrates (including our study (3)) gave a mean annual canopy transpiration rate for the pine and beech stands of 320 mm and 304 mm, respectively (species difference not significant; t test: $t = 0.32$, $p = 0.76$, Table 4.5). However, direct comparison of the neighboring pine/beech stands at the Eimke/Unterlüss site showed a by 30–80 mm higher annual transpiration of pine than beech (Table 4.6). The species difference was larger for mean annual evapotranspiration (ET, transpiration and canopy interception), which averaged at 582 mm in the pine stands compared to 496 mm in the beech stands (difference significant; t test: $t = 2.55$, $p = 0.04$, Fig. 4.6). In correspondence, annual ET was markedly higher in the pine as compared to the beech stands in the paired-plot studies at Eimke/Unterlüss (NW Germany) and Kahlenberg (NE Germany).

The annual amount of deep seepage ranged from 15 to 88 mm under the pine stands (mean 66 mm), and from 100 to 273 mm (mean 134 mm) under the beech stands (difference significant; t test: $t = -2.07$, $p = 0.04$), which equals 2–13 % and 15–31 % of precipitation in the pine and beech stands, respectively (Table 4.5).

4.3.5 Carbon stocks in biomass and soil

The 13 beech forests of study (1) stored more than twice as much C in aboveground live tree biomass (including young trees) than the nearby pine forests (155.4 vs. 69.7 Mg C ha^{-1}; Wilcoxon test, $V = 91$, $p<0.001$). In contrast, the pine stands had larger SOC stores in both the organic layer (52.0 vs. 28.6 Mg C ha^{-1}) and the mineral soil to 1 m (89.1 vs. 70.4 Mg C ha^{-1} in pine and beech, respectively; ANOVA, $p<0.05$). The C storage in deadwood (1.8 vs. 4.1 Mg C ha^{-1}; Wilcoxon test, $V = 84$, $p<0.01$) and fine root mass (1.1 vs. 3.3 Mg C ha^{-1}; Wilcoxon test, $V = 36$, $p<0.01$) was marginal, but larger in the beech forests (Fig. 4.7). The ecosystem C pool (biomass and soil but without coarse root biomass) amounted to 213.6 Mg C ha^{-1} in the pine forests and to 261.7 Mg C ha^{-1} in the beech forests of study (1), i.e. the beech stands exceeded the pine stands by 48.2 Mg C ha^{-1} (+22.5 %).

4.3.6 C sequestration with productivity

Mean aboveground productivity (ANPP; coarse wood production and aboveground litter production) was 3.30 Mg C ha^{-1} yr^{-1} in the pine and 4.49 Mg C ha^{-1} yr^{-1} in the beech forests of study (1), which is an on average 1.19 Mg C ha^{-1} yr^{-1} greater ANPP value in the beech stands (Wilcoxon test, $V = 66$, $p<0.001$). The higher beech ANPP resulted mainly from a higher litter (foliage, fruits) production, while coarse wood production did not differ significantly between the species.

Table 4.5. Water consumption (canopy transpiration and evapotranspiration) and deep seepage of Scots pine and beech forests in northern Germany on Pleistocene soils (mostly sandy) (annual rates in mm). Given are precipitation, canopy transpiration (T), evapotranspiration (ET, including canopy interception), and seepage in absolute and relative terms (in % of precipitation). The pine/beech stands at Eimke/Unterlüss (study (3)) and at Kahlenberg occur on similar soil in close distance to each other. Method of T and ET determination: MCL – microclimatic profile/Bowen ratio approach, SAF – sap flux measurement, WBA – stand water balance approach with ET estimation based on local climate data.

	Region	Year	Precipitation	Method	Transpiration	Evapotranspiration	Seepage	Seepage in % of P	Author
PINE FORESTS									
Eimke, Lüneburg Heath	NW Germany	1991	638	MCL	325	588	15	2	Leuschner 1994
Eimke, Lüneburg Heath	NW Germany	1992	815	MCL	409	654	88	11	Leuschner 1994
Liepe, Eberswalde	NE Germany	5 years	627	WBA	227	545	82	13	Lützke 1991
Kahlenberg, Eberswalde	NE Germany	4 years	620	WBA		542	78	12	Müller & Bolte 2009
BEECH FORESTS									
Unterlüss, Lüneburg Heath	NW Germany	1991	669	MCL	288	475	100	15	Leuschner 1994
Unterlüss, Lüneburg Heath	NW Germany	1992	883	MCL	331	557	273	31	Leuschner 1994
Unterlüss, Lüneburg Heath	NW Germany	1996	584	SAF	272				Schipka 2002
Beerenbusch, Rheinsberg	NE Germany	4 years	642	SAF	241	437			Lüttschwager & Jochheim
Bornhöved, Plön	NW Germany	4 years	743	MCL	389				Herbst et al. 1999
Kahlenberg, Eberswalde	NE Germany	4 years	620	WBA		491	129	21	Müller & Bolte 2009

Table 4.6. Water fluxes (in mm) in neighboring Scots pine and beech stands in Eimke/Unterlüss in the Lüneburg Heath region (study (3)) in the growing season and the full years of 1991 and 1992.

		1991		1992	
		Growing season	Year	Growing season	Year
Precipitation	Pine	392	638	413	815
	Beech	*393*	*669*	*422*	*883*
Canopy interception	Pine	123	198	134	245
	Beech	*122*	*187*	*124*	*226*
Canopy transpiration	Pine	321	325	404	409
	Beech	*288*	*288*	*331*	*331*
Soil evaporation	Pine	52	65	72	84
	Beech	*44*	*64*	*34*	*52*
Total evapotranspiration	Pine	496	588	610	738
	Beech	*454*	*639*	*489*	*609*
Change in soil water storage	Pine	-104	+35	-197	-11
	Beech	*-61*	*+30*	*-67*	*+1*
Deep seepage	Pine	0	15	0	88
	Beech	*0*	*100*	*0*	*273*
Seepage in % of precipitation	Pine	0	2	0	11
	Beech	*0*	*15*	*0*	*31*

4.3.7 Soil acidification

Soil acidity differed between the nine paired pine and beech stands of study (1) only in the organic layer, while the pH in the mineral soil was largely similar (Fig. A4.4). Pine litter led to a by 0.5 units lower pH (measured in KCl) in the organic layer as compared to beech (3.1 vs. 3.6; ANOVA, $p < 0.05$). Soil acidity was slightly (but not significantly) higher in the subsoil (50 cm depth) under beech than under pine. A similar result was obtained in the each nine pine and beech stands of the Prignitz region (NE Germany; study (2)).
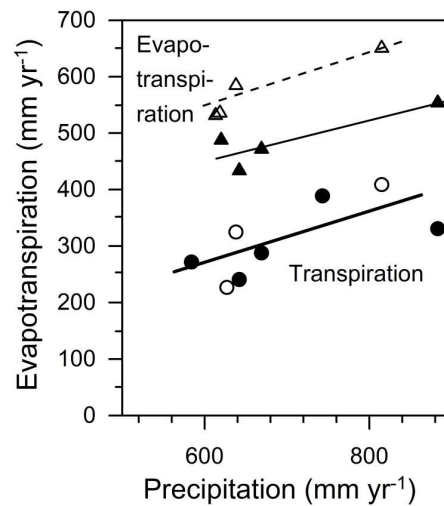
Figure 4.6. Dependence of annual transpiration (circles) and evapotranspiration (triangles) of North German pine (open symbols) and beech forests (filled symbols) on annual precipitation. While transpiration differs only slightly between the forest types (and the data are pooled in the analysis), evapotranspiration was higher in the pine stands (dotted line) than the beech stands (continuous line). Transpiration pine & beech: $y = 5.83 + 0.43 \ x$, $p = 0.03$, $r = 0.69$; ET pine: $y = 227 + 0.53 \ x$, $p = 0.03$, $r = 0.94$; ET beech: $y = 240 + 0.36 \ x$, $p = 0.07$, $r = 0.86$. For data sources see Table 4.5.
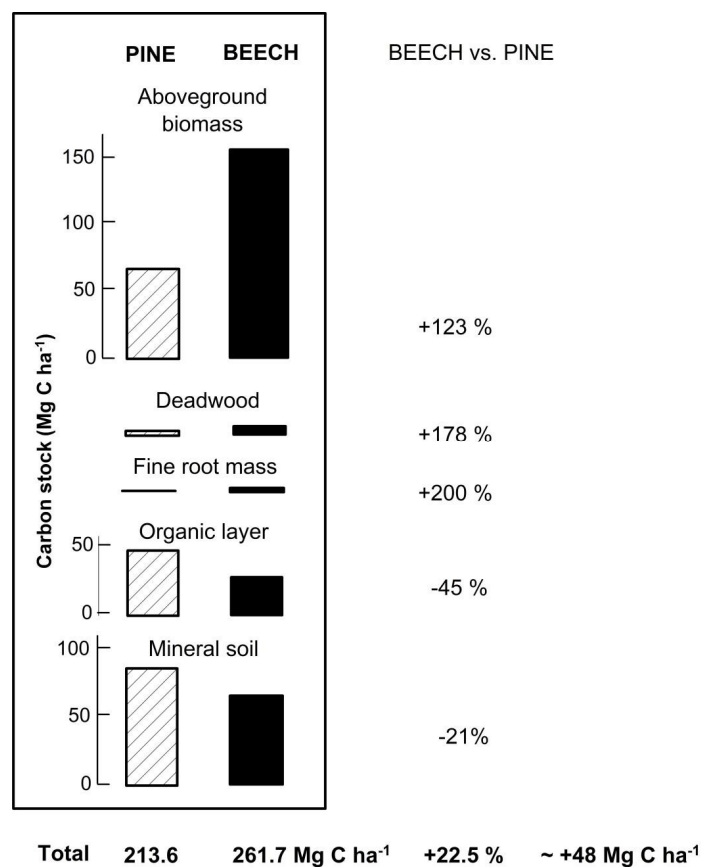
Figure 4.7. Ecosystem carbon storage in the beech and pine forests of study (1) (mean of each 9 stands; in Mg C ha^{-1}). Given is also the difference in C storage in beech relative to the pine forests.

4.4 Discussion

The establishment of about 1.75 million ha of pine plantations in the North German lowlands in a natural broadleaf forest landscape represents one of the world's largest forest conversions to conifer plantations, the dimension of which comes close to a biome shift from temperate broadleaf to temperate (or boreal) coniferous. The consequences of this man-made transformation are far-reaching, ranging from biophysical to socio-economic impacts, and include effects on regional climate, soil, forest biota, fire and pest/pathogen infection risks, and the recreational value of the forest. Our analysis focuses on several key ecosystem services, notably climate regulation, carbon sequestration, the provision of groundwater, and soil fertility, while ignoring other aspects.

4.4.1 Feedback on climate

The lower short-wave albedo of conifer forests compared to temperate broadleaf forest canopies by about 4–6 percentage points is well recognized (Gates 1980, Stewart 1971, Stoutjesdijk & Barkman 2015). Our comparison of a pine and a beech stand in the Lüneburg Heath region yielded a by 4 percentage points lower reflectance of the pine canopy in summer, which seems to be caused by both differences in foliage optical properties and canopy roughness. The brighter pigments of beech leaves, the more level leaf orientation, and the usually lower canopy roughness of the concave beech crown surfaces all tend to increase the short-wave albedo and thus reduce the radiation load to the canopy. Our data show that the species difference is even larger in the NIR range (20 vs. 15 % reflectance in the beech and pine stands, respectively), causing more pronounced heating of the pine canopy during summer, as net radiation input was 9 % greater and mean canopy surface temperature 0.6 K higher than in the beech canopy. Elevated canopy temperatures may stimulate leaf physiological activity in the cool boreal environment, the core region of Scots pine distribution, but pine stands in the warmer Central European climate might well experience heat stress during summer periods, especially when it is coupled to drought stress (Rehschuh & Ruehr 2021). If not consumed by evapotranspiration, the excess energy available in the heated canopy will increase the heating of the well-mixed atmospheric boundary layer through enhanced fluxes of sensible heat and long-wave upward radiation (Teuling et al. 2017), thereby amplifying regional climate warming. The warming effect of forest on the atmospheric boundery layer is particularly strong during heat waves due to the sensible stomatal response of trees to the atmospheric vapour pressure deficit (Teuling et al. 2010; Lansu et al. 2020). Our microclimate data suggest that the establishment of large-scale Scots pine plantations has reinforced regional climate warming through the elevated net radiation input to pine canopies compared to beech canopies, the natural forest vegetation in most of the study region. The higher canopy temperatures of the pine canopy in summer develop despite a somewhat higher evapotranspiration, which counteracts the heating through evaporative cooling.

4.4.2 Effects on the water cycle

Soil moisture content was higher under beech than pine from the organic layer to the subsoil at 60 cm depth, and moisture reserves were exhausted to a greater extent under beech than pine in the Lüneburger Heath stands, matching observations in other pine/beech comparisons on sandy to sandy/loamy soil (Anders et al. 2004). Various factors are contributing to the greater soil moisture depletion under pine, notably the higher canopy interception loss under evergreen pine (in our stands + 10–20 mm), which reduces throughfall and infiltration into the soil. A slightly higher canopy transpiration of pine, as observed in the Lüneburg Heath stands, may enhance this effect. Further, the higher light transmissivity of the pine canopy increases net radiation at the forest floor, which enhances soil evaporation and the transpiration of the usually dense herb layer. Finally, laboratory measurements show that organic layer and mineral soil material under pine is less wettable than soil under beech with larger contact angles of the liquid phase to the mineral surfaces (J. Bachmann, unpubl.), which is reflected in the shift of the water content-matric potential relationship of pine litter material to lower moisture contents (Fig. A4.3). Thus, less rainfall infiltrates into the soil and more water is extracted under pine, with the consequence that, in the Lüneburg Heath stands, seepage to groundwater layers was on average by 135 mm yr^{-1} lower under the pine than the beech stand.

This in line with results from another study on pine and beech forests near Eberswalde (NE Germany), where a mean difference of 93 mm yr^{-1} was found between pine (mean: 47 mm yr^{-1}, range: 0 – 120 mm yr^{-1}) and beech (mean: 140 mm yr^{-1}, range: 100–180 mm yr^{-1}) (Anders et al. 2005). Müller & Bolte (2009) reported in the Kahlenberg pine and beech forests (also near Eberswalde) averaged over five years a 51 mm yr^{-1} higher seepage under beech than pine. For the eastern German state of Brandenburg, Riek & Müller (2007) gave an average groundwater recharge under pine of only 30 mm yr^{-1}, with many pine stands having no seepage at all. Averaged over all studies compiled in Table 4.5, we found a mean difference of 68 mm yr^{-1} in annual seepage between pine (mean: 66 mm yr^{-1}) and beech stands (134 mm yr^{-1}). A simple extrapolation to the 1.75 million ha of pine forest area in northern Germany gives ~ 1.2 billion m^3 of groundwater recharge lost, which equals 20 % of the annual groundwater volume used in Germany (5.95 billion m^3, BGR 2021). It should be noted that this rough calculation considers mature forests; the seepage difference between pine and beech forests is certainly smaller in younger forests (Teuling & Hoek van Dijke 2020).

Given that large parts of the eastern German lowlands receive <600 mm yr^{-1} of precipitation, it is obvious that the large pine plantations in this region are an important driver of water scarcity in summer, as they reduce groundwater recharge by 50–90 mm yr^{-1} on average compared to beech forests. Water shortages will increase in future with climate warming and the rise in atmorpheric evaporative demand. Morover, parts of eastern Germany have experienced reductions in summer precipitation during the 20th century

(Schönwiese & Janoschitz 2008; Banzragch et al., submitted), increasing the threat of summer droughts especially in the state of Brandenburg, and partly also in Saxony-Anhalt, Saxony, Mecklenburg-Western Pomerania and eastern Lower Saxony. Modelling studies predict that much of the arable land on sandy soils in this region will require irrigation with advancing climate warming (Anter et al. 2009, Riediger et al. 2014, Gutzler et al. 2015, UBA 2021), increasingly competing with public water use and demand for industries. It is especially the negative impact on groundwater recharge that is disqualifying the future establishment and maintenance of large Scots pine plantations in northern German regions with water scarcity.

Enhanced topsoil drying under pine is a major reason for the high fire risk in Scots pine plantations especially in the more continental east of Germany, a threat that will increase with ongoing warming (Schlick & Möller 2007). Fires are promoted in pine stands by the hydrophobicity of the rapidly drying pine litter and the warmer soil in the stand interior in comparison to beech and other hardwood stands. Further, pine stands with their small leaf area index (2–3 vs. 5–8 in beech forests; Leuschner & Ellenberg 2017) facilitate the influx of drier and warmer air masses into the stand interior, while beech stands are characterized by relatively cool and moist air underneath the canopy, which effectively reduces the risk of ignition. Haesen et al. (2021) compiled a data base that may allow quantifying the thermal insulation capacity of forest canopies across Europe, which obviously is larger in beech and than pine stands. In correspondence, fires are very rare events in beech forests (Maringer et al. 2020), even in the more continental climate of eastern Germany.

4.4.3 Carbon sequestration potential

Forestry and wood industry can contribute to the goal of carbon dioxide sequestration through four pathways, (1) by increasing the long- term storage of C in biomass and soil, (2) by increasing the storage of long-lived wood products, (3) by producing wood that substitutes energy-intensive construction materials such as concrete and steel, or (4) by substituting fossil fuels by wood that is burnt to produce heat and/or energy (Taroe et al. 2017, Harmon 2019, Hudiburg et al. 2019). While it is feasible to compare the C accumulation in biomass and soil (pathway (1)) using the inventory data of mature pine and beech stands, quantifying the other three pathways is much more difficult and subject to dispute. Controversial positions exist especially with respect to the validity of greenhouse gas displacement factors of harvested wood products, which relate the emission reduction to the carbon mass contained in the wood, the longevity of wood products, and the climate change mitigation potential of using forest biomass for bioenergy (Harmon 2019, Leturcq 2020, Pomponi et al. 2020).

Due to the uncertainties in calculating the pathways (2) – (4), we focus on the biomass and soil C stores of pine and beech forests on sandy to sandy-loamy soils. The much larger aboveground live tree biomass C storage found in the beech forests of study (1) (difference 85.7 Mg C ha^{-1}; +123 %) matches the prediction of pine and beech yield tables for NE

Germany, which give a by 50–61 % higher aboveground coarse wood mass production at the age of 100 years for closed stands of beech as compared to pine on poor to moderately fertile soils (yield classes 2 to 3.5, Table A4.1; Dittmar et al. 1986, Lembcke et al. 2000). The difference is smaller when wood production is calculated on a volume basis (493 – 752 m^3 ha^{-1} and 622 – 875 m^3 ha^{-1} for pine and beech at age 100 years in the yield classes 2 to 3.5, respectively; cf. also BWI[3]). The yield table calculations were made for managed pine and beech age-class stands that are thinned at regular intervals according to conventional management schemes, with 48–49 % (pine) and 45–48 % (beech) of total aboveground biomass production being harvested until the age of 100 years (Dittmar et al. 1986, Lembcke et al. 2000). The higher biomass accumulation in the beech stands corresponds to a higher net primary productivity and thus actual carbon sequestration rate, with beech ANPP exceeding that of pine by 36.4 % at maturity according to the study (1) results.

The ecosystem carbon pool (live and dead biomass plus soil) was by 48.2 Mg C ha^{-1} larger in the beech than the pine forests. This difference rose to about 65 Mg C ha^{-1}, when the aboveground live tree biomass estimate was increased by 20 % to account for coarse root biomass. Since both the amount of cumulative harvested wood (+144 to + 163 % in the yield classes 2 to 3.5) and the size of the remaining biomass stock (+161 to + 186 %) were considerably larger in the beech than in the pine forests, the northern German Scots pine plantations have a much smaller climate change mitigation potential than beech forests, in case the harvested wood were primarly used for product substitution and the fabrication of long-lived wood products. Replacing pine forests by beech (or other hardwoods) would thus be an important step toward the creation of climate-smart forests in northern Germany, as both the harvestable amount of roundwood and the standing stock of biomass carbon are higher in beech stands over a 100-yr time horizon, which is critical for tackling climate warming.

Large-scale conversion of pine stands to broadleaf forests is primarily hindered by the structure of wood markets that actually face a much higher demand for conifer wood than for hardwood timber. Currently, about 64 % of the hardwood timber harvest in Germany is burnt, with the largest part being beech wood (FNR 2019). This is not effective with respect to climate change mitigation, as forest biomass burning for bioenergy is far from being carbon–neutral (Ter-Mikaelian et al. 2015, Norton et al. 2019). Thus, a massive shift from conifer wood to hardwood timber in the construction sector and the wood composite products industry would be needed in order to increase the demand for durable hardwood timbers and to reduce the consumption of conifer wood.

4.4.4 Soil acidification

Even though soil acidification by conifer litter is a well understood phenomenon (Bublinec 1974, Hornung 2007), the acidifying potential of Scots pine on soils developed from Pleistocene substrates in northern Germany is more difficult to assess. Centuries to

millenia of forest destruction and litter raking until the mid 20th century in combination with atmospheric deposition of nitrogen compounds and strong acids, but locally also of basic dusts, have impacted on the soil chemistry in this region, modifying and overlaying the acidifying effect of pine litter (Riek et al. 2007). Direct comparison of soil profiles under nearby pine and beech stands on similar geological substrate may allow at least a relative assessment of the acidifying potential of pine in comparison to the natural forest vegetation in this region. In our study (1) of nine paired pine/beech stands, a significantly higher acidity (pH(KCl)) under pine as compared to beech was only found in the organic layer and the mineral topsoil to 10 cm depth, while deeper horizons exhibited similar acidity under the two tree species. Similar results were reported in the comparison of each nine pine and beech stands in the Prignitz region (Brandenburg, northern Germany; study (2)) and in a paired pine/beech forest study near Eberswalde (NE Germany, Anders et al. 2005). However, in a common garden study with 22-yr old planted beech and Scots pine stands on sandy glacial soil in central Poland, pine caused lower pH(H2O) values than under beech not only in the organic layer and the mineral topsoil (difference 0.13 to 0.45 units), but also in deeper layers (20–40 cm; difference 0.26 units; Hobbie et al. 2006). It appears that, other than beech, Scots pine is unable to mobilize base cations, in particular Ca, from the subsoil, which increases soil biological activity (Anders et al. 2005, Reich et al. 2005) and may counteract the acidifying effect of pine litter. In addition, Scots pine appears to inhibit larger earthworms such as *Lumbricus terrestris* (Meentemeyer & Berg 1986), thereby reducing bioturbation. Thus, the low pH, base saturation and soil biological activity in the topsoil of Scots pine stands on glacial deposits in northern Germany are partly a consequence of the litter chemistry of this species, but are certainly enhanced by widespread base cation extraction with litter raking in the past and the deposition of acidifying substances in more recent time.

4.5 Conclusions

The rationale behind planting Scots pine in large areas of the lowlands of northern Germany, Poland and beyond is mainly economic, driven by an expanding market for conifer wood in Central Europe and globally (Mantau 2012). Pine wood is the most important timber by volume in the study region with most of it used for construction and as industrial wood (Weimar 2018). Even though productivity is lower than of beech, Norway spruce and other timbers, it is widely preferred by foresters due to its tolerance of infertile and drought-prone sites and because of relatively low costs of planting, stand maintenance and harvesting. In fact, Scots pine plantations are usually profitable in Central Europe (Kroth 1983), except for very infertile sites and for episodes, when stands are destabilized by extreme biotic and climatic hazards as during the 2018–2020 drought. Pine forestry thus represents an important source of income in many rural areas of northern Germany, as in Brandenburg (eastern Germany) (Bilke & Noack 2007).

On the other hand, if the negative effects of pine plantations on groundwater yield, soil fertility and acidity, and the regional climate would be monetarized, the balance sheet of

economic costs and benefits will certainly be highly negative, with the costs of deteriorated ecosystem services loaded onto society. Since our evaluation does not quantify the higher risk of fire and insect/pathogen infestation of pine stands (Möller et al. 2007), the costs are likely even higher. Thus, Scots pine plantations are in this region neither environmental-friendly nor climate-smart, given their low climate change mitigation potential relative to that of natural beech forests. Our compilation of environmental effects and climate feedbacks of Scots pine plantations urges forestry planning to speed-up transformation of pine plantations to broadleaf forests on sites that are suitable for growing beech, oak or other more drought-tolerant hardwoods. In fact, if maximizing CO_2 sequestration is to become a main goal of forest policy, the relatively unproductive Scots pine plantations should be replaced by beech (or other hardwood) forests, wherever possible. Establishing mixed pine-beech stands has been found to be a promising option in certain regions of NE Germany (Anders et al. 2004), as it may allow combining positive effects of beech on carbon sequestration and hydrology with the option to continue harvesting pine wood.

A shift in forest management from conifer-dominated to hardwood-dominated silvicultural systems will only be successful, if the utilization of durable hardwood products can be greatly increased in Central Europe and elsewhere. This requires policy incentives to foster the use of hardwood timbers in the construction sector, to promote the development of a broader spectrum of engineered hardwood timber products, and to support forest owners in the establishment of broadleaf forests. Our analysis of important biophysical consequences of plantation forestry further suggests that the concept of climate-smart forestry, which most often addresses only the climate change mitigation potential and timber production, needs broadening to address other important ecosystem services as well, notably biophysical feedbacks on climate and the water cycle.

CRediT authorship contribution statement

Christoph Leuschner: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Project administration, Supervision. **Agnes Förster:** Data curation, Formal analysis, Investigation. **Marco Diers:** Data curation, Formal analysis, Investigation. **Heike Culmsee:** Funding acquisition, Project administration, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

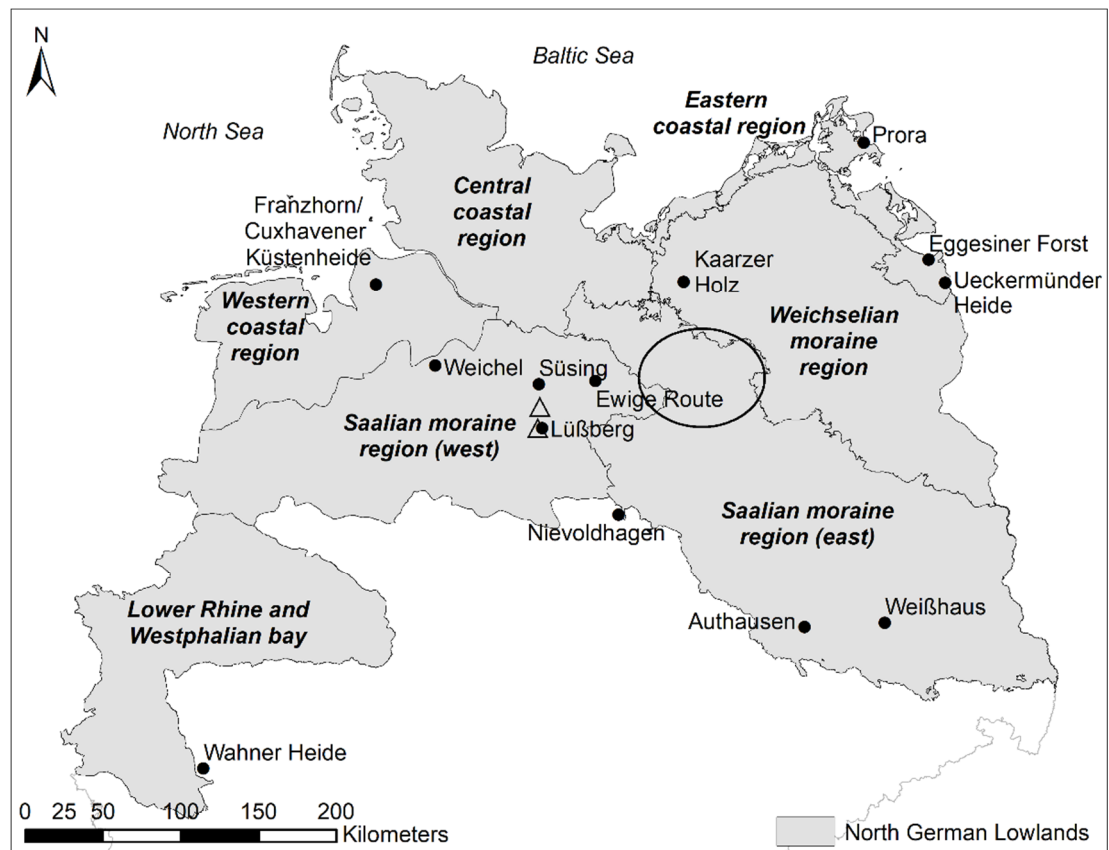## Acknowledgements

Appendix

Figure A4.1. Map of the North German lowlands with the seven subregions recognized here, and the location of study sites in the studies (1, black dots), (2, encircled area) and (3, open triangels: site Unterlüss/Eimke). Based on a map provided by Thünen-Institut.
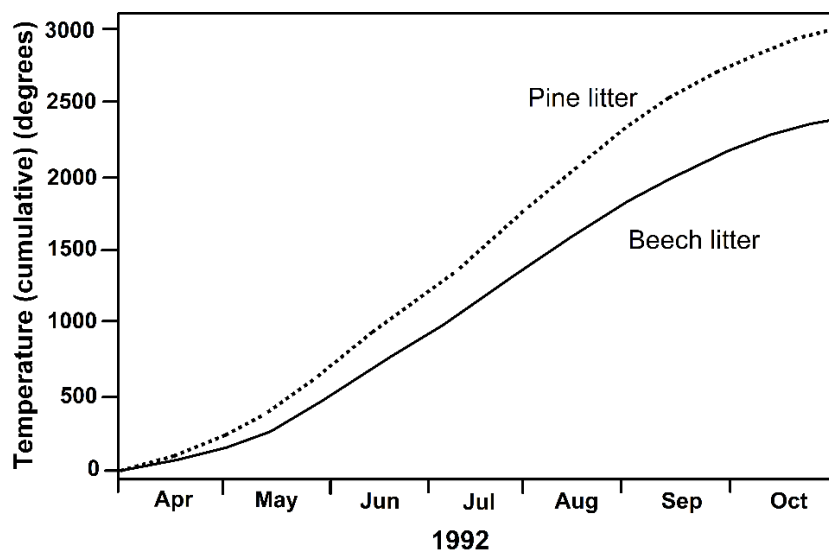

Figure A4.2. Cumulative temperatures in the litter layer of the pine and the beech stand in Eimke/Unterlüss (Lüneburg Heath region, study (3)) in the growing season 1992 (April – October). The daily temperature means are cumulated to display the heating up of the organic layers.
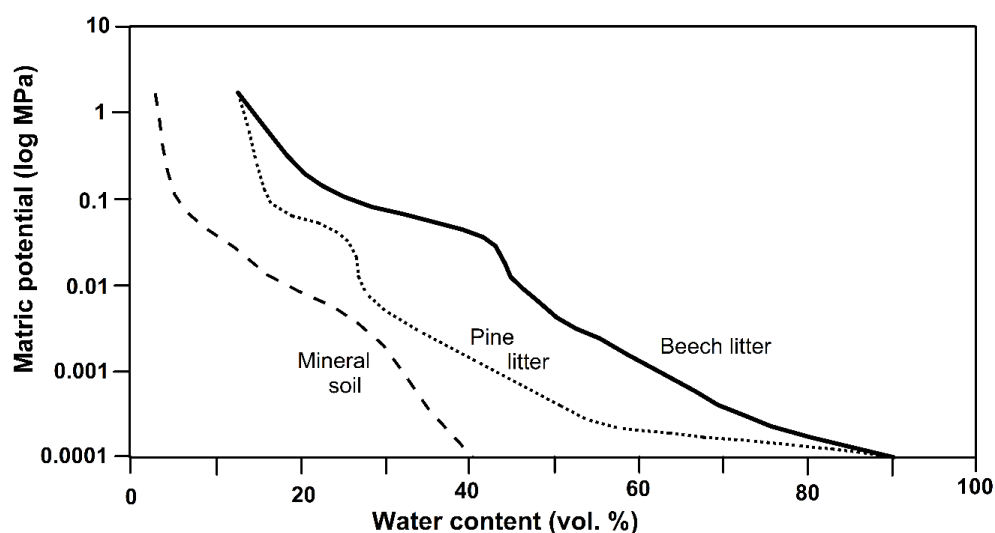
Figure A4.3. Relationship between volumetric water content and matric potential of organic layer material under beech and pine at the sites Eimke/Unterlüss (Lüneburg Heath region, study (3)) in comparison to the corresponding relationship in the mineral topsoil.
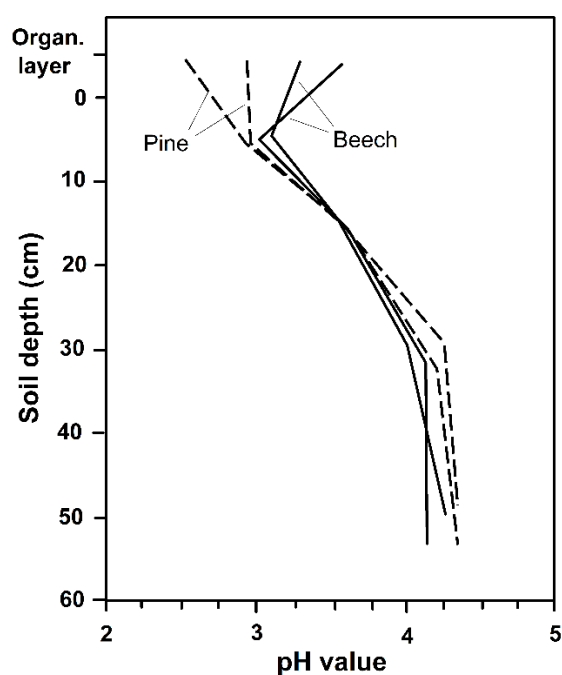

Figure A4.4. Soil depth dependence of pH measured in 1 M KCl (potential acidity) in soil profiles under paired beech and pine forests on Pleistocene substrates in northern Germany according to two studies with each 9 stand pairs (study (1): entire northern Germany, and study (2): Prignitz region, NE Germany). Significant differences between pine and beech existed only in the organic layers.

Table A4.1. Production of coarse wood volume (total volume production) and total aboveground biomass (coarse wood, branches, foliage) in closed monospecific pine and beech stands at age 100 years, and cumulative wood harvest and remaining coarse wood at age 100 years according to the pine and beech yield tables for north-east Germany (Dittmar et al. 1986, Lembcke et al. 2000). The productivity classes ('Höhenbonität', classes after Kraft) refer to soils of decreasing fertility (2.0 moderately fertile, 3.5 poor). Wood mass was calculated from wood volume with the density values given in the Global wood density data base (Scots pine: 0.422 g cm^{-3}, beech 0.585 g cm^{-3}). Total biomass was derived from Pretzsch (2019, p. 443) who gives a factor of F = 0.78 for transforming standing wood volume (in m^3) into total tree biomass (including branches, foliage and roots; in Mg ha^{-1}) for pine, and of F = 1.004 for beech.

Productivity class	Total volume production m^3 ha^{-1}			Total biomass production Mg ha^{-1}			Cumulative harvested wood until age 100 Mg ha^{-1}			Remaining wood biomass at age 100 Mg ha^{-1}		
	Pine	Beech	*%*	Pine	Beech	*%*	Pine	Beech	*%*	Pine	Beech	*%*
2.0	752	875	*116*	587	879	*150*	171	246	*144*	165	266	*161*
2.5	661	790	*120*	516	793	*154*	137	219	*160*	142	243	*171*
3.0	575	707	*123*	449	710	*158*	119	192	*161*	119	222	*187*
3.5	493	622	*126*	385	625	*161*	100	163	*163*	108	201	*186*

References

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

Anders, S., Beck, W., Hornschuch, F., Müller, J., Steiner, A. 2004. Vom Kiefern-Reinbestand zum Kiefern-Buchen-Mischbestand – ökologische Veränderungen, waldwachstumskundliche und landschaftsökologische Folgen sowie waldbaulichpraktische Empfehlungen. Beitr. Forstwirtsch. u. Landsch.ökol. 38: 55-67.

Anders, S., Beck, W., Hornschuch, F., Müller, J., Steiner, A. 2005. Zur Zukunftsfähigkeit des Kiefern-Buchen-Mischbestandes – ökologische Voraussetzungen, forstliche Steuerungsmöglichkeiten, waldwachstumskundliche und umweltrelevante Wirkungen. Eberswalder Forstlicher Schriftenreihe Bd. XXIII: 12-32.

Anter, J., Gömann, H., Kreins, P., Richmann, A. 2009. Einfluss sich wandelnder ökonomischer Rahmenbedingungen auf die Beregnung landwirtschaftlicher Kulturen in Deutschland. Landbauforschung – Sonderheft 329: 21-28.

Banzragch, B.-E., E., Weigel, R., Leuschner, C. 2022. Changes in the thermal and hydrometeorological forest growth climate during 1948-2017 in northern Germany. Front. For. Glob. Change (in revision).

Beinhofer, B., Knoke, T. 2009. Ansatzpunkte einer finanziellen Optimierung der Kiefernbewirtschaftung. Forst und Holz 64: 12-16.

BfN (Bundesamt für Naturschutz) 2010. Karte der potentiellen natürlichen Vegetation Deutschlands. Maßstab 1:500.000. Bonn-Bad Godesberg, Germany.

BGR 2021. Die Grundwasservorkommen von Deutschland. https://www.bgr.bund.de/DE/Gemeinsames/UeberUns/ueberuns_node.html;jsessionid=5B7ED5F8F5DC7FE5B43625712626F550.1_cid321, accessed July 17, 2021.

Bilke, G., Noack, T. 2007. Nutzung der Kiefern in Brandenburg – Entwicklung der Sortenstruktur und der Preise in der Landesforstverwaltung Brandenburg von 1993 bis 2006. Eberswalder Forstlicher Schriftenreihe Bd. XXXII: 505-509.

BLE 2020. Waldbrandstatistik der Bundesrepublik Deutschland für das Jahr 2019. Bundesanstalt für Landwirtschaft und Ernährung. https://www.ble.de/SharedDocs/Downloads/DE/BZL/Daten-Berichte/Waldbrandstatistik/Waldbrandstatistik-2019.pdf?__blob=publicationFile&v=4, accessed July 15, 2021.

Bowditch, E., Santopuoli, G., Binder, F., del Río, M., La Porta, N., Kluvankova, T., et al. 2020. What is climate-smart forestry? A definition from a multinational collaborative process focused on mountain regions of Europe. Ecosyst. Serv. 43: 101113.

Braun, S., de Witte, L.C., Hopf, S.E. 2020. Auswirkungen des Trockensommers 2018 auf Flächen der interkantonalen Walddauerbeobachtung. Schweiz. Z. Forstwes. 171: 270280.

Bublinec, E. 1974. Bodenpodsolierung unter Kiefernbeständen. Nanka o Zemi VIII, Pedologica, Bratislava, 8: 1-222.

Büntgen, U., Urban, O., Krusic, P.J., Rybnicek, M., Kolar, T., Kyncl, T., et al. 2021. Recent European drought extremes beyond Common Era background variability. Nat. Geosci. 14: 190-196.

BWI[3]. Die dritte Bundeswaldinventur. BWI 2012. German Ministry for Nutrition and Agriculture (BMEL), Berlin.

Chang, M. 2012. Forest Hydrology. 3rd ed. CRC Press, Boca Raton.

DESTATIS 2017. Statistisches Bundesamt, Fachserie 3, Reihe 3.3.1, Holzeinschlag 2017. Wiesbaden. Accessed July 10, 2021.

Diers, M., Weigel, R., Culmsee, H., Leuschner, C. 2021. Soil carbon and nutrient stocks under Scots pine plantations in comparison to European beech forests: A paired-plot study across forests with different management history and precipitation regimes. For. Ecosyst. 8, 1-16.

Dittmar, O., Knapp, E., Lembcke, G. 1986. DDR-Buchenertragstafel 1983. Inst. f. Forstwiss. Eberswalde. IFE-Berichte aus Forschung u. Entwicklung 4.

DWD CDC (Deutscher Wetterdienst Climate Data Center) 2019. Grids of climate data over Germany. https://opendata.dwd.de/climate_environment/CDC/grids_germany/. Accessed July 5, 2019.

Ebert, W. 1968. Die Schadgebiete unserer wichtigsten Kiefernbestandesschädlinge im Tiefland der DDR. Archiv f. Forstwes. 17: 125-144.

European Commission 2012. Report on the review of the European water scarcity and droughts policy. Brussels, 4.11.2012. COM(2012) 672 final.

FAO (Food and Agriculture Organization) 2021. Climate-smart forestry in practice. http://www.fao.org/climate-smarthttp://www.fao.org/climate-smart-agriculture-sourcebook/production-resources/module-b3-forestry/chapter-b3-3/en/agriculture-sourcebook/production-resources/module-b3-forestry/chapter-b3-3/en/

Fischer, H., Bens, O., Hüttl, R.F. 2002. Changes in humus form, humus stock and soil organic matter distribution caused by forest transformation in the North-eastern lowlands of Germany. Forstwiss. Centralbl. 121: 322-334.

Flüggen, C. 1991. Die Evaporation von Kiefern unter Berücksichtigung des Grundwasserabstandes. Ber. Inst. Meteorol. Klimat. Univ. Hannover, Bd. 39.

FNR 2019. Charta für Holz 2.0. Kennzahlenbericht 2019 Forst & Holz. Fachagentur für Nachwachsende Rohstoffe. Gülzow.

Förster, A., Culmsee, H., Leuschner, C. 2021a. Thinned northern German Scots pine forests have a low carbon storage and uptake potential in comparison to naturally developing beech forests. For. Ecol. Manage. 479: 118575.

Förster, A., Werner R, Hertel D, Leuschner C 2021b. Belowground consequences of converting broadleaf to conifer forest: Comparing the fine root systems of European beech and Scots pine. For. Ecol. Manage. 496: 119457.

Gates, D.M. 1980. Biophysical Ecology. Springer, New York, Heidelberg.

Gauer, J., Kroiher, F. 2012. Waldökologische Naturräume Deutschlands – Forstliche Wuchsgebiete und Wuchsbezirke: Digitale topographische Grundlagen. Neubearbeitung Stand 2011. Landbauforschung Völkenrode, Sonderheft 359

Gutzler, C., Helming, K., Balla, D., Dannowski, R., Deumlich, D., Glemnitz, M., et al. 2015. Agricultural land use changes – a scenario-based sustainability impact assessment for Brandenburg, Germany. Ecol. Ind. 48: 505-517.

Haesen, S., Lembrechts, J.J., De Frenne, P., Lenoir, J., Aalto, J., Ashcroft, M.B., et al. 2021. ForestTemp – Sub-canopy microclimate temperatures of European forests. Glob. Chang. Biol. 27, 6307-6319.

Harmon, M.E. 2019. Have product substitution carbon benefits been overestimated? A sensitivity analysis of key assumptions. Environ. Res. Lett. 14: 065008.

Heinsdorf, D. 2002. Einfluss der Bewirtschaftung auf den Kohlenstoffhaushalt von Forstökosystemen im nordostdeutschen Tiefland. Beitr. Forstwirtsch. u. Landsch.ökol. 36: 168-174.

Hobbie, S.A., Reich, P.B., Oleksyn, J., Ogdahl, M., Zytkowiak, R., Hale, C., Karolewski, P. 2006. Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87: 2288-2297.

Hofmann, G., Anders, S., Matthes, B. 2000. Das potenziell natürliche und derzeitige Waldbild in den ostdeutschen Ländern. Mitt. Bundesforschungsanst. f. Forst- u. Holzwirtsch. Hamburg No. 196. Hamburg, Germany. 93 p.

Hornung, M. 1985. Acidification of soils by trees and forests. Soil Use and Managem. 1: 24-27.

Hudiburg, T.W., Law, B.E., Moomaw, W.R., Harmon, M.E., Stenzel, J.E. 2019. Meeting GHG reduction targets requires accounting for all forest sector emissions. Env. Res. Lett. 14: 095005.

Kroth, W. 1983. Economical aspects of Scotch pine forestry. Forstwiss. Cbl. 102: 36-50.

Lansu, E.M., van Heerwaarden, C.C., Stegehuis, A.I., Teuling, A.J., 2020. Atmospheric aridity and apparent soil moisture drought in European forest during heat waves. Geophys. Res. Lett. 47: e2020GL087091.

Lembcke, G., Knapp, E., Dittmar, O., Lockow, K.-W. 2000. Ertragstafel für die Kiefer (*Pinus sylvestris* L.) im nordostdeutschen Tiefland. Landesforstanstalt Eberswalde. Germany.

Leturcq, P. 2020. GHG displacement factors of harvested wood products: the myth of substitution. Sci. Rep. 10: 1-9.

Leuschner, C. 2002. Forest succession and water resources: soil hydrology and ecosystem water turnover in early, mid and late stages of a 300-yr-long chronosequence on sandy soil. In: Dohrenbusch, A. Bartsch, N. (eds.) Forest Development. Succession, Environmental Stress and Forest Management. Springer, Berlin, pp. 1-68.

Leuschner, C., Ellenberg, H. 2017. Ecology of Central European Forests, Vol. I. SpringerNature, Cham.

Leuschner C., Bäuchler P., Wulf M., Hertel D. 2013. Soil C and nutrient stores under Scots pine afforestations compared to ancient beech forests in the German Pleistocene: the role of tree species and forest history. For. Ecol. Manage. 310: 405-415.

Lüttschwager, D., Jochheim, H. 2020. Drought primarily reduces canopy transpiration of exposed beech trees and decreases the share of water uptake from deeper soil layers. Forests 11: 537.

Lützke, R. 1991. Bestandesklima und Wasserhaushalt in Kiefernbeständen des nordostdeutschen Tieflandes. Berichte aus Forschung u. Entwicklung (Eberswalde) 25: 4-20.

Lützke, R., Simon, K.-H., 1972. Hydrologische Untersuchungen zur Bilanzierung des Wasserhaushalts von Kiefernbeständen im norddeutschen Flachland. Arch. f. Naturschutz u. Landschaftsforsch. 12: 13–36.

Mantau, U. 2012. Holzrohstoffbilanz Deutschland. Entwicklungen und Szenarien des Holzaufkommens und der Holzverwendung von 1987 bis 2015. Universität Hamburg. 65 p.

Maringer, J., Ascoli, D., Gehring, E., Wohlgemuth, T., Schwarz, M., Conedera, M. 2020. Feuerökologie montaner Buchenwälder. Waldleistungen und waldbauliche Massnahmen nach Waldbrand. WSL, Birmensdorf. Merkbl. Prax. 65. 12 S.

Meentemeyer, V., Berg, B. 1986. Regional variation in rate of mass loss of *Pinus sylvestris* needle litter in Swedish pine forests as influenced by climate and litter quality. Scand. J. For. Res. 1: 167-180.

Möller, K., Walter, C., Engelmann, A., Hielscher, K. 2007. Die Gefährdung der Gemeinen Kiefer durch Insekten. Eberswalder Forstliche Schriftenreihe Bd. XXXII: 245-257.

Müller, J. 2009. Der Einsatz von Lysimetern in der forsthydrologischen Forschung im nordostdeutschen Tiefland. 13. Gumpensteiner Lysimetertagung 2009: 47-54.

Müller, J., Bolte, A. 2009. The use of lysimeters in forest hydrology research in north-east Germany. Landbauforschung – vTI Agric. For. Res. 1 (59): 1-10.

Norton, M., Baldi, A., Buda, V., Carli, B., Cudlin, P., Jones, M.B., et al. 2019. Serious mismatches continue between science and policy in forest bioenergy. GCB Bioenergy 11: 1256-1263.

Pomponi, F., Hart, J., Arehart, J.H., D'Amico, B. 2020. Buildings as a global carbon sink? A reality check on feasibility limits. One Earth 3: 157-161.

R Core Team 2020. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rehschuh, R., Ruehr, N. 2021. Unrevealing water and carbon relations during and after heat and hot drought stress in *Pinus sylvestris*. BioRxiv, https://doi.org/10.1101/2021.06.29.450316.

Reich, P.B., Oleksyn, J., Modrzynski, J., Mrozinski, P., Hobbie, S.E., Eissenstat, D.M., et al. 2005. Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. Ecol. Lett. 8: 811-818.

Riedel, T., Hennig, P., Kroiher, F., Polley, H., Schmitz, F., Schwitzgebel, F. 2017: Die dritte Bundeswaldinventur (BWI 2012). Inventur- und Auswertemethoden, 124 S.

Riediger, J., Breckling, B., Nuske, R., Schröder, W. 2014. Will climate change increase irrigation requirements in agriculture of Central Europe? A simulation study for Northern Germany. Environ. Sci. Europe 26: 18.

Riek, W., Müller, J. 2007. Modellierung von Wasserhaushaltskennwerten unter dem Aspekt der Bewertung der wasserwirtschaftlichen Leistung der Wälder und Auswirkungen von Klimaänderungen. Eberswalder Forstliche Schriftenreihe Bd. XXXII: 238-244.

Riek, W., Strohbach, B., Kallweit, R. 2007. Bodenzustand und Stoffhaushalt von Kiefernbeständen in Brandenburg. Eberswalder Forstliche Schriftenreihe Bd. XXXII: 54-63.

Schlick, R., Möller, K. 2007. Waldbrandrisiko und Waldbrandschutz in Brandenburg. Eberswalder Forstliche Schriftenreihe Bd. XXXII: 305-310.

Schönwiese, C.-D., Janoschitz, R. 2008. Klima-Trendatlas Deutschland 1901-2000. 2nd ed. Inst. Atmosph. u. Umwelt, Univ. Frankfurt/M., No. 4. Frankfurt/M.

Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., et al. 2020. A first assessment of the impact of the extreme 2018 summer drought on Central European forests. Basic Appl. Ecol. 45: 86103.

Schulp, C.J.E., Nabuurs, G.-J., Verburg, P.H., de Waal, R.W. 2008. Effect of tree species on carbon stocks in forest floor and mineral soil and implications for soil carbon inventories. For. Ecol. Manage. 256: 482-490.

Stewart, J.B. 1971. The albedo of a pine forest. Quart. J. Roy. Meteorol. Soc. 97: 561-564.

Stoutjesdijk, P., Barkmann, J.J. 2015. Microclimate, Vegetation and Fauna. 1st rev. ed. KNNV Publishers.

Taroe, A., Mustapha, W.F., Stupak, I., Raulund-Rasmussen, K. 2017. Do forests best mitigate CO_2 emissions to the atmosphere by setting them aside for maximization of carbon storage or by management for fossil fuel substitution? J. Env. Manage. 197: 117129.

Ter-Mikaelian, M.T., Colombo, S.J., Chen, J. 2015. The burning question: Does forest bioenergy reduce carbon emission? A review of common misconceptions about forest carbon accounting. J. For. 113: 57-68.

Teuling, A.J., Hoek van Dijke, A.J., 2020. Forest age and water yield. Nature 578, E16–E18.

Teuling, A.J., Seneviratne, S.I., Stöckli, R., Reichstein, M., Moors, E., Ciais, P., et al. 2010. Contrasting response of European forest and grassland energy exchange to heatwaves. Nat. Geosci. 3: 722-727.

Teuling, A.J., Taylor, C.M., Meirink, J.F., Melsen, L.A., Miralles, D.G., van Heerwaarden, C.C., et al. 2017. Observational evidence for cloud cover enhancement over western European forests. Nat. Commun. 8 : 1-7.

TI (Thünen-Institut) 2015. Dritte Bundeswaldinventur - Basisdaten (Stand 20.03.2015). https://bwi.info/Download/de/BWI-Basisdaten/ACCESS2003/bwi20150320_alle_ daten2012.zip.

UBA 2021. Klimawirkungs- und Risikoanalyse 2021 für Deutschland. Climate Change 26/2021. Umweltbundesamt Dessau. https://www.umweltbundesamt.de/sites/ default/files/medien/5750/publikationen/2021-06-10_cc_262021_kwra2021_kurzfassung.pdf. Accessed July 5, 2021.

Verkerk, P.J., Costanza, R., Hetemäki, L., Kubiszewski, L., Leskinen, P., Naaburs, G.J., et al. 2020. Climate-smart Forestry: The missing link. J. For. Econ. 115: 102164.

Weimar, H. 2018. Holzbilanzen 2015 bis 2017 für die Bundesrepublik Deutschland und Neuberechnung der Zeitreihe der Gesamtholzbilanz seit 1995. Thünen Working Paper 101. Hamburg.

Yousefpour, R., Augustynczik, A.L.D., Reyer, C.P.O., Lasch-Born, P., Suckow, F., Hanewinkel, M. 2018. Realizing mitigation efficiency of European commercial forests by climate smart forestry. Sci. Rep. 8: 1-11.

Chapter 5

Synopsis

Scots pine stands currently dominate the forests of the northern German lowlands, which is the result of a long history of forest degradation or deforestation and subsequent afforestation in the region (TI 2015, Leuschner & Ellenberg 2017, Poschlod 2017). The mostly pure and even-aged pine forests replace a natural vegetation that consisted mainly of broadleaf beech or beech-oak forests (BfN 2010, Leuschner & Ellenberg 2017). This shift from temperate broadleaf forests to a predominantly boreal coniferous tree species represents a strong interference with the forest ecosystem as a whole and affects its biodiversity, structure and functioning (Meyer et al. 2020).

Forests play a key role in the efforts to mitigate climate warming due to their ability to store and sequester carbon from the atmosphere (Ashton et al. 2012). This thesis therefore aimed to evaluate the climate change mitigation potential of Scots pine in comparison to European beech forests, by determining the above- and belowground (fine root) biomass C pools and sequestration. The study was conducted at 16 sites distributed throughout the northern German lowlands, covering a climate continentality gradient from west to east. This was complemented by an estimation of the extent of forest conversion in the study area, combined with a comparative analysis of forest functioning (ecosystem C pool, hydrology, microclimate, soil acidity) in beech and pine forests. The following section summarizes the main findings of this thesis and elucidates the prospects for climate change mitigation of Scots pine and European beech forests in the northern German lowlands.

5.1 Functional differences between Scots pine and European beech forests

5.1.1 Carbon pools and sequestration

Carbon stocks in the aboveground biomass were determined at 16 study sites in forests of the potential natural vegetation type (mostly beech forests) and with natural development (ND), in planted, monospecific, young pine forests (YP) and in the transitional stage of pine forests to (mixed) broadleaf stands (OP). In a subset of eight sites, tree fine root biomass was determined in paired naturally developing beech (ND) and YP forests. In confirmation of hypotheses (i) and (ii), carbon stocks in both, the aboveground and belowground (fine root) tree biomass were higher in the investigated ND forests than in YP forests.

With on average 147 Mg C ha^{-1}, the naturally developing (mostly) broadleaf forests (ND) stored about double the amount of carbon in the aboveground biomass than the young pine forests (YP), which stored on average 72 Mg C ha^{-1} (chapter 2). Carbon stocks in the OP stands (86.8 Mg C ha^{-1} on average) did not significantly exceed the ones in YP stands. A linear mixed-effects model clearly revealed that the tree species was the most important factor for explaining the differences in aboveground biomass carbon stocks between forest types, while stand age was not influential. This is surprising, as the stands covered an age span of roughly 100 years for both, beech (103 – 195 years old) and pine forests (55 – 155 years old). The regular biomass extraction through thinning is certainly one reason, and especially in the OP stands, a considerable biomass fraction must have been already removed. For both, beech and pine forests, the here determined carbon stocks are within the range reported from other stands of similar age (Burschel et al. 1993, Xiao et al. 2003, Rademacher et al. 2009).

Correspondingly, fine root biomass was 6.5 times higher and necromass was 2.4 times higher in the naturally developing beech forests than in the managed pine forests (biomass: 237 vs. 37 g m^{-2}, necromass: 420 vs. 175 g m^{-2}, respectively; chapter 3). Due to the relatively shallow sampling in this study (organic layer plus the top 20 cm of the mineral soil), differences in depth distributions between species would have been missed. Therefore, fine root biomass was extrapolated to 60 cm soil depth, based on fine root biomass-soil depth functions that were established from large data sets of our study region (Scherfose 1990, Meier et al. 2018). These extrapolations suggest that differences between species would have even increased with deeper sampling. While fine root biomass in the here studied beech forests was in the lower range of values reported elsewhere (range: 118–960 g m^{-2} at a mean sampling depth of 49 cm, Leuschner & Hertel 2003), fine root biomass in pine forests was particularly low compared to other studies (range: 237–725 g m^{-2} at a mean sampling depth of 74 cm, Leuschner & Hertel 2003). The relation between fine root biomass and stand age for both species observed in this and other studies (Leuschner & Hertel 2003, Finér et al. 2007) does not suggest that values would have converged in stands of more similar age. The main reason for the low fine root biomass in the here investigated YP stands, and thus for the large beech-pine difference, is probably the often dense herbaceous and dwarf shrub layer in pine forests (Leuschner & Ellenberg 2017), that competes for space and resources in the soil.

The lower biomass accumulation of YP stands was also demonstrated by their about 25 % lower ANPP compared to ND stands (3.27 vs. 4.33 Mg C ha^{-1} yr^{-1}, chapter 2) averaged over the recorded years (2015-2017), supporting hypothesis (iii). The average ANPP of 4.5 Mg C ha^{-1} yr^{-1} measured in the 13 beech forests of this study was slightly lower than the average of 5.3 Mg C ha^{-1} yr^{-1} for beech forests in Central Europe reported by Leuschner & Ellenberg (2017), which agrees with the relatively low fertility at our study sites. For pine forests, values reported in other studies range between 3.95 and 11.0 Mg C ha^{-1} yr^{-1} from stands somewhat younger than in this study (35 – 55 years) and with comparably high stem

density and basal area. Since the biomass accumulation curve of pine levels off at an age of 60-80 years (Burschel et al. 1993), stand age is likely a contributing factor for the relatively low values measured in the here studied pine forests (65 years old on average), besides low stem density and basal area. In line with this, Anders et al. (2005) measured only 3.2 Mg C ha^{-1} yr^{-1} in an 84-year-old pine stand in northeastern Germany. The higher ANPP in ND compared to YP forests does not result from differences in basal area, which was similar in the two forest types (28.1 vs. 29.1 m^2 ha^{-1} in YP and ND stands, respectively). It is rather evidence of the superior carbon gain of beech, resulting from its generally much higher leaf area index (5 – 8.5 m^2 m^{-2}) compared to pine (1.8 – 3 m^2 m^{-2}, Leuschner & Ellenberg 2017).

Fine root productivity was 1.9 times higher in beech than in pine forests (147 vs. 77 g m^{-2} yr^{-1}, respectively), but the difference was only significant in 10-20 cm depth. Thus, hypothesis (iv) could only partly be confirmed. Even though the estimated lifespan for pine fine roots was much shorter than for beech fine roots (4 vs. 13 months), absolute carbon consumption and thus carbon input upon fine root death in beech forests still exceeded the one in pine forests.

It is remarkable that the higher input of aboveground litter and fine roots in the beech stands, which are the most important SOC sources in forests (Davidson & Janssens 2006, Ashton et al. 2012), is not reflected in the SOC pools of these stands, which were in turn higher in the pine stands (Diers et al. 2021). Possible reasons include the species-specific litter quality and the influence of forest management and history (Diers et al. 2021). Nevertheless, the ecosystem C pool (biomass and soil, but without coarse root biomass) of beech forests exceeded the one in pine plantations by 22.5 % (chapter 4).

5.1.2 Microclimate, hydrology and soil acidity

Direct comparisons between neighboring beech and pine forests of northern Germany demonstrated that beech canopies have a higher shortwave and NIR reflectivity than the canopies of pine. Correspondingly, above-canopy net radiation averaged over two summers was 9 % higher, and mean canopy surface temperature was 0.6 K higher over pine than over beech (chapter 4). A literature survey revealed a significantly higher annual evapotranspiration in pine than in beech forests, while the difference in annual transpiration was lower and only significant in direct comparison of the neighboring stands in northern Germany. In the same stands, volumetric soil water content and plant-available soil water were generally lower under pine than under beech, with larger differences in summer than in winter (chapter 4). Deep seepage was more than twice as high in beech as in pine forest (134 vs. 66 mm, respectively). It seems that more severe soil drying under pine than under beech results from a combination of higher canopy interception losses and higher transpiration of the evergreen tree species pine, higher soil evaporation due to higher transmissivity of the pine canopy, and more hydrophobic litter and soil material in pine stands (chapter 4).

The acidifying effect of coniferous tree species is well established (Hornung 1985, Augusto et al. 1998). The effect is however difficult to quantify in the study region, where other factors, namely past litter raking and the deposition of acidifying substances act in synergy. In a direct comparison of the here studied beech and pine forests, soil acidity differed between tree species only in the organic layer (3.1 vs. 3.6 in pine and beech stands, respectively), but was similar in the mineral soil (Diers et al. 2021, chapter 4). The ability of beech to act as a base pump, i.e. to take up base cations from deeper soil horizons in exchange of H^+ and assimilating them into biomass, can well explain this pattern (Anders et al. 2005, Achilles et al. 2021).

5.1.3 Landscape-scale consequences of forest conversion in the northern German lowlands

Beech forests represent the potential natural vegetation at about half of both the potential (48.6 %), and the current forest area (52.4 %) of the northern German lowlands, while pine forests would naturally occur on only a few percent of the forest area (2.3 % and 3.7 % of the potential and current forest area, respectively; chapter 4). The current dominance of pine forests on more than 1.75 million ha (53.2 % of the current forest area), and the small current beech forests area of only 0.22 million ha (6.6 %), clearly demonstrate the extent of historic forest conversion that has happened in the northern German lowlands.

The here presented study provides evidence for the superior above- and belowground carbon storage and sequestration potential of beech forests with natural development compared to pine forests. If we extrapolate the by 48 Mg C ha^{-1} larger ecosystem carbon pools (chapter 4) in native beech forests (ND stands) compared to pine plantations (YP stands) to the more than 1.75 million ha of mostly non-native, planted pine forests of the northern German lowlands, we get an idea of the landscape-scale consequences of past forest conversion. The simple extrapolation suggests that more than 80 Tg C has been lost in the course of forest conversion, which is about 5 times the amount annually sequestered by all German forests (15.8 Tg C, WBAE & WBW 2016). Correspondingly, the average rate of carbon sequestration was higher in beech than in pine forests in all measured compartments, with the largest difference found in litter (1.0 Mg C ha^{-1} yr^{-1}, chapter 2), followed by fine roots (0.4 Mg C ha^{-1} yr^{-1}, chapter 3), while the difference in wood production was not significant (0.1 Mg C ha^{-1} yr^{-1}, chapter 2). This adds up to a by 1.5 Mg C ha^{-1} higher annual productivity in beech than in pine forests. Extrapolated to the current pine forest area, this is more than 2.6 Tg C annually and almost 17 % of the amount annually sequestered by all German forests. Analogously, an extrapolation of the beech-pine difference in deep seepage (68 mm yr^{-1} higher in beech than in pine forests) suggests, that deep seepage is reduced annually by almost 1.2 billion m³ of water (chapter 4). This is 20 % of the annual groundwater volume used in Germany (BGR 2021). Clearly, these are only rough extrapolations with many uncertainties, such as the representativeness of the here studied stands in terms of stand age (see chapter 2.4.4) and structure, soil conditions at the studied

locations or climatic conditions during the study period. Nevertheless, they give an idea of the magnitude of the landscape-scale effects of the historic forest conversion on ecosystem functioning.

The microclimate data presented in chapter 4 furthermore suggest negative feedbacks on the regional climate by Scots pine plantations established to the above described extent, as above canopy temperatures were higher over pine than over beech, despite lower evapotranspiration of the latter.

5.2 Effects of management cessation on carbon pools and sequestration in European beech forests

European beech trees can reach a natural age of 350 years and more, while the age of beech trees at harvesting is in Germany usually around 140 years (Sperber & Hatzfeldt 2007, Glatthorn et al. 2017). Thus, old-growth stages and their characteristic structures are widely lacking in typically managed beech forests (Brunet et al. 2010, Meyer et al. 2021a). In the here investigated 13 beech forests with natural development, management ceased, but the last thinning operations happened 6 to 41 years before data collection (20 years on average). This is only a relatively short period considering the high natural lifespan of the trees, and thus the structure of the investigated stands strongly reflects past management. Accordingly, ANPP, fine root biomass and fine root productivity were unrelated to the time elapsed since the last timber extraction in the here investigated naturally developing beech forests (chapters 2 and 3). Some studies have reported enhanced growth after thinning in beech forests (e.g. Boncina et al. 2007, Bouriaud et al. 2019). However, the results of this thesis agree with observations from direct comparisons between true primary beech and beech production forests in Slovakia, where no significant differences in ANPP or the fine root systems were detected (Glatthorn et al. 2018, Klingenberg & Leuschner 2018).

In contrast, a mixed-effects model revealed a significant positive effect of the time since the last timber extraction on the aboveground biomass carbon pool across all investigated forests (chapter 2). The possible end point of carbon accumulation was estimated by a comparison with three true primary forests in the Slovakian Carpathians, from where comparable data are available (Glatthorn et al. 2018). Aboveground biomass carbon stocks in live trees (including saplings) in the three primary forests exceeded the amounts in the here studied naturally developing beech forests by only 25 % (193 vs. 155 Mg C ha^{-1}, respectively). Furthermore, some of our beech ND stands had even greater carbon stocks in the aboveground biomass of live trees (up to 225 Mg C ha^{-1}) than the primary forest average, while the carbon stocks in coarse deadwood were almost 9 times higher in the primeval forests compared to the beech ND stands (35 vs. 4 Mg C ha^{-1}, respectively). Similarly, Meyer et al. 2021b described biomass C stocks of almost 240 Mg C ha^{-1} in beech forests 50 years after management cessation, which continued to increase linearly.

Thus, management in beech forests seems to affect mostly the aboveground biomass carbon storage, since the otherwise extracted biomass remains in the stand, while aboveground productivity and the fine root system are less affected. It should however be noted that management effects on ANPP and the fine root system in this study cannot be ruled out completely, as these could be masked by other factors with stronger impact. Furthermore, the time elapsed since the last timber extraction gives only restricted information on past management of the forests, as for instance thinning intensity is not considered.

5.3 Climate change mitigation potential of Scots pine and European beech forests

The large differences in carbon stocks and sequestration summarized in section 5.1.1 are clear evidence for an inferior climate change mitigation potential of pine forests compared to the natural beech forests they replace, with additional negative effects on groundwater recharge, the regional climate and soil fertility (section 5.1.2). Yet, for a complete evaluation, the wood products C pool and substitution effects need to be considered as well.

The wood products pool represents only a few percent of the world´s forests biomass C pool, but it is constantly growing and the rate can be influenced by forest management (Pan et al. 2011, Wördehoff et al. 2011, Ashton et al. 2012, Chen et al. 2019). The direct utilization of wood for bioenergy production can substitute fossil fuels. However, positive mitigation effects can lag more than a century, while the initial C balance is usually negative (Ter-Mikaelian et al. 2015). The material substitution effect is generally positive and increases with the lifespan of the product (WBAE & WBW 2016, Leskinen et al. 2018). Cascading use with burning as a last step can considerably enhance the climate change mitigation potential of wood (Bais-Moleman et al. 2018) In Germany, almost two thirds (64 %) of the harvested hardwood is used thermally, while the share of coniferous wood is only 14 % (Purkus et al. 2019). Moreover, coniferous wood is used to a higher share for products with long lifespan than hardwood (WBAE & WBW 2016). Even though quantifying substitution effects is complex and involves many uncertainties (Leskinen et al. 2018, Ter-Mikaelian et al. 2015), the mostly thermal use of beech wood clearly impairs the high climate change mitigation potential of beech in comparison to pine forests. A quantification of these effects would give a more accurate picture on the beech-pine difference in mitigation potential. Still, considering the additional negative effects of pine forests on further forest functions, this would not affect the overall conclusion. It rather stresses the need for changes in the woodworking industry that is focused on the utilization of coniferous wood, especially in the building sector (e.g. Ehrhart et al. 2021, Pečnik et al. 2021). The consequently thigh demand for coniferous wood on the market hinders the successful transition to more broadleaf forests.

The performance of the tree species under future climatic conditions has to be considered as well, when evaluating its relevance for coming management decisions. Surprisingly, the climatic gradient of the study region had only little influence on the results of this study. ANPP of beech and pine did not correlate with precipitation or temperature of the growing season, and similarly, fine root productivity of both tree species was not related to climatic variables either. Similarly, Müller-Haubold et al. (2013) and Hertel et al. (2013) observed only little influence of a precipitation gradient on total net primary productivity (above- and belowground) in beech forests, but rather a shift in allocation with higher fruit and fine root production but lower wood and leaf production towards drier sites. As one exception, the fine root system of pine responded in this study to warmer and drier climatic conditions with increasing fine root biomass and the formation of more robust roots, presumably with a lower uptake capacity. In contrast, the beech fine root system did not respond to climatic variation in our study, but was more responsive to variation in soil acidity and fertility.

Climatic conditions across all study sites varied considerably between years in the study period (2015-2017). Temperature and precipitation of the growing season of 2015 were similar to the multi-annual mean (1981-2010), and therefore the ANPP difference between beech and pine measured in that year is presumably representative for past decades. In the warm and dry growing season of 2016, a beech masting event occurred in most of the investigated beech forests. The high fruit production resulted in an even higher ANPP difference between beech and pine than the year before, even though wood production in beech forests slightly decreased in 2016. In view of increasing frequency of beech masting events in parts of Europe (Nussbaumer et al. 2016), a high fruit production of beech might become the main driver of aboveground carbon sequestration differences between beech and pine. It remains to be verified if these ANPP differences persist under varying climatic conditions.

European beech is known as a relatively drought-sensitive tree species that reduces radial growth in response to dry and warm summers of previous or current years (Leuschner 2020). While beech is well able to recover from moderate drought spells, drought-induced mortality was observed during severe drought events such as the recent dry spell 2018-2020, which are predicted to increase in the future (Schär et al. 2004, Leuschner 2020, Schuldt et al. 2020). The sensitivity of beech to drought and heat impairs its future prospects in silviculture, and modelling approaches have shown that it might not be able to remain vital in part of its current distribution range (Kramer et al. 2010, Walentowski et al. 2017). Scots pine is a predominantly boreal tree species, but it has an extremely wide natural distribution range and also grows in relatively dry Mediterranean regions (Meusel 1965, Leuschner & Ellenberg 2017). Even though it is generally more drought-tolerant than beech (Michelot et al. 2012), tree death in response to drought was recently described not only for dry sites in Spain or inner-alpine valleys, but unexpectedly also on less water-limited sites in Central Europe (Sánchez-Salguero et al. 2012, Rigling et al. 2013, Schuldt et al. 2020). Reich & Oleksyn (2008) demonstrated reduced growth and survival rate of Scots pine in response to

temperature increases in Europe, except for the far North. Accordingly, a modelling approach indicated severe distribution range reductions in Western Europe due to climate warming (Cheaib et al. 2012). Furthermore, pure pine forests are prone to calamities that are likely to increase in the course of climate change (see chapter 1). The surprising tree death of both beech and pine in the severe drought spell of 2018-2020 suggests that the impact of climatic extremes might have been underestimated, with unknown consequences for the species' future performances and viability in the study region (Fuhrer et al. 2006, Schuldt et al. 2020).

The here investigated forests were mostly pure stands (main tree species' share of the basal area: 88 % and 91 % in ND and YP stands, respectively). There is increasing scientific evidence that mixed forests generally are not only more productive, but also provide a higher variety of ecosystem services and are less prone to calamities than pure stands (Ammer et al. 2019, del Río et al. 2021). This might also be valid for forests of European beech, a tree species that naturally forms forests with very low tree species diversity (e.g. Meyer et al. 2021a). For instance, Mölder & Leuschner (2014) observed a lower drought-sensitivity of beech in mixed than in pure stands. Thus, mixed stands will certainly be of great significance in the future, which is already apparent from the increasing dominance of mixed stands in German forests (BMEL 2021). The climate change mitigation potential of forests of European beech and other, less heat and drought-sensitive tree species, especially in mixture, needs to be investigated in future studies, in order to enable well-founded management decisions in the sense of a climate-smart forestry.

5.4 Conclusions

The presented study provides clear evidence that historic forest conversion in the northern German lowlands has resulted in a significant loss of the C storage and sequestration potential in the above- and belowground biomass of the region´s forests. The naturally dominant European beech forests have a considerably higher climate change mitigation potential than the Scots pine forests replacing them, although the high share of beech wood used for the production of bioenergy impairs their potential. In addition, the planted pine forests led to reduced groundwater recharge, higher soil acidity and higher canopy surface temperatures, suggesting warming effects on the regional climate. Our forest types did not only differ in their dominant tree species, but also in terms of stand age and management. Disentangling the effects was only possible for carbon stocks in the aboveground biomass, for which pine forests in transition to mixed broadleaf stands were studied as well. Here, the effect of past thinning was small and stand age was not influential. Comparisons with other studies support the view that the tree species is the most important factor in explaining the observed differences between forest types. The results presented are valid for sandy soils, which dominate the northern German lowlands and on which pine forests were preferably established. The results further reflect past and current climatic conditions, and even though the climatic gradient of the region had only little influence in this study, the performances of

beech and pine under future climatic conditions will certainly affect the functioning of both forest types. The recent severe drought spell in Europe 2018-2020 has demonstrated that both species will suffer from climate change more than previously expected (Schuldt et al. 2020). This further stresses the importance of management decisions that promote forests with a high potential to mitigate climate warming. The results of this thesis therefore strongly suggest that Scots pine is not a suitable choice in a silviculture focusing on the mitigation of, and the resilience against climate change. Wherever climate projections do not argue against it, European beech should be preferred.

References

Achilles, F., Tischer, A., Bernhardt-Römermann, M., Heinze, M., Reinhardt, F., Makeschin, F., Michalzik, B., 2021. European beech leads to more bioactive humus forms but stronger mineral soil acidification as Norway spruce and Scots pine–Results of a repeated site assessment after 63 and 82 years of forest conversion in Central Germany. For. Ecol. Manage. 483, 118769.

Ammer, C., 2019. Diversity and forest productivity in a changing climate. New Phytol. 221, 50-66.

Anders, S., Beck, W., Hornschuch, F., Müller, J., Steiner, A., 2005. Zur Zukunftsfähigkeit des Kiefern-Buchen-Mischbestandes – Ökologische Voraussetzungen, forstliche Steuerungsmöglichkeiten, waldwachstumskundliche und umweltrelevante Wirkungen. In: Ministerium für Ländliche Entwicklung, Umwelt und Verbraucherschutz des Landes Brandenburg, Landesforstanstalt Eberswalde (eds.). Ökologischer Waldumbau im nordostdeutschen Tiefland. Eberswalder Forstliche Schriftenreihe, Vol. XXIII: 12-32.

Ashton, M.S., Tyrrell, M.L., Spalding, D., Gentry, B. (eds.), 2012. Managing forest carbon in a changing climate. Springer, Dordrecht, Netherlands.

Augusto, L., Bonnaud, P., Ranger, J., 1998. Impact of tree species on forest soil acidification. For. Ecol. Manage. 105, 67-78.

Bais-Moleman, A.L., Sikkema, R., Vis, M., Reumerman, P., Theurl, M.C., Erb, K.-H., 2018. Assessing wood use efficiency and greenhouse gas emissions of wood product cascading in the European Union. J. Clean. Prod. 172, 3942-3954.

BfN (Bundesamt für Naturschutz), 2010. Karte der potentiellen natürlichen Vegetation Deutschlands. Maßstab 1:500.000. Bonn-Bad Godesberg, Germany.

BGR (Bundesanstalt für Geowissenschaften und Rohstoffe), 2021. Die Grundwasservorkommen von Deutschland. https://www.bgr.bund.de/DE/Themen/Wasser/grundwasser_deutschland.html?nn=1542268. (Access: 08.08.2021).

BMEL (Bundesministerium für Ernährung und Landwirtschaft), 2021. Waldbericht der Bundesregierung 2021.

Boncina, A., Kadunc, A., Robic, D., 2007. Effects of selective thinning on growth and development of beech (*Fagus sylvatica* L.) forest stands in south-eastern Slovenia. Ann. For. Sci. 64, 47-57.

Bouriaud, O., Don, A., Janssens, I.A., Marin, G., Schulze, E.-D., 2019. Effects of forest management on biomass stocks in Romanian beech forests. For. Ecosyst. 6, 1-15.

Brunet, J., Fritz, Ö., Richnau, G., 2010. Biodiversity in European beech forests – a review with recommendations for sustainable forest management. Ecol. Bull. 53, 77-94.

Burschel, P., Kürsten, E., Larson, B.C., 1993. Die Rolle von Wald- und Forstwirtschaft im Kohlenstoffhaushalt – Eine Betrachtung für die Bundesrepublik Deutschland. Forstl.Forsch.ber. Münch. 126, 1–135.

Cheaib, A., Badeau, V., Boe, J., Chuine, I., Delire, C., Dufrêne, E., et al. 2012. Climate change impacts on tree ranges: model intercomparison facilitates understanding and quantification of uncertainty. Ecol. Lett. 15, 533-544.

Chen, A., Peng, S., Fei, S., 2019. Mapping global forest biomass and its changes over the first decade of the 21st century. Sci. China Earth Sci. 62, 585–594.

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature, 440, 165-173.

Diers, M., Weigel, R., Culmsee, H., Leuschner, C., 2021. Soil carbon and nutrient stocks under Scots pine plantations in comparison to European beech forests: a paired-plot study across forests with different management history and precipitation regimes. For. Ecosyst. 8, 1-16.

Ehrhart, T., Steiger, R., Frangi, A., 2021. Brettschichtholz aus Buche. Bautechnik 98, 1-11.

Finér, L., Helmisaari, H.-S., Lõhmus, K., Majdi, H., Brunner, I., Børja, I., et al., 2007. Variation in fine root biomass of three European tree species: Beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* L. Karst.), and Scots pine (*Pinus sylvestris* L.). Plant Biosyst. 141, 394–405.

Glatthorn, J., Feldmann, E., Pichler, V., Hauck, M., Leuschner, C., 2018. Biomass stock and productivity of primeval and production beech forests: greater canopy structural diversity promotes productivity. Ecosystems 21, 704–722.

Glatthorn, J., Pichler, V., Hauck, M., Leuschner, C., 2017. Effects of forest management on stand leaf area: Comparing beech production and primeval forests in Slovakia. For. Ecol. Manage. 389, 76-85.

Hertel, D., Strecker, T., Müller-Haubold, H., Leuschner, C., 2013. Fine root biomass and dynamics in beech forests across a precipitation gradient–is optimal resource partitioning theory applicable to water-limited mature trees? J. Ecol. 101, 1183–1200.

Hornung, M., 1985. Acidification of soils by trees and forests. Soil use Manag. 1, 24-27.

Klingenberg, E., Leuschner, C., 2018. A belowground perspective of temperate old-growth forests: Fine root system structure in beech primeval and production forests. For. Ecol. Manage. 425, 68-74.

Kramer, K., Degen, B., Buschbom, J., Hickler, T., Thuiller, W., Sykes, M.T., de Winter, W., 2010. Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change – range, abundance, genetic diversity and adaptive response. For. Ecol. Manage. 259, 2213-2222.

Leskinen, P., Cardellini, G., González-García, S., Hurmekoski, E., Sathre, R., Seppälä, J., et al., 2018. Substitution effects of wood-based products in climate change mitigation. From Science to Policy, 7. European Forest Institute.

Leuschner, C., 2020. Drought response of European beech (*Fagus sylvatica* L.) – A review. Perspect. Plant Ecol. Evol. Syst. 47, 125576.

Leuschner, C., Ellenberg, H., 2017. Ecology of Central European Forests: Vegetation Ecology of Central Europe, Vol. I. Springer, Cham, Switzerland.

Leuschner, C., Hertel, D., 2003. Fine root biomass of temperate forests in relation to soil acidity and fertility, climate, age and species. Prog. Bot. 64, 405–438.

Meier, I.C., Knutzen, F., Eder, L.M., Müller-Haubold, H., Goebel, M.-O., Bachmann, J., et al., 2018. The deep root system of *Fagus sylvatica* on sandy soil: structure and variation across a precipitation gradient. Ecosystems 21, 280–296.

Meusel, H., Jäger, E.J., Weinert, E., 1965. Vergleichende Chorologie der zentraleuropäischen Flora. Text und Karten. Band 1. VEB Fischer, Jena, Germany.

Meyer, P., Aljes, M., Culmsee, H., Diers, M., Förster, A., Leuschner, C., Mölder, A., Schneider, H., 2020. Wildnis Naturerbe – Wie können wir Naturnähe im Wald messen? Deutsche Bundestiftung Umwelt (DBU): Osnabrück, Germany. 38 p.

Meyer, P., Aljes, M., Culmsee, H., Feldmann, E., Glatthorn, J., Leuschner, C., Schneider, H., 2021a. Quantifying old-growthness of lowland European beech forests by a multivariate indicator for forest structure. Ecol. Indic., 125, 107575.

Meyer, P., Nagel, R., Feldmann, E., 2021b. Limited sink but large storage: biomass dynamics in naturally developing beech (*Fagus sylvatica*) and oak (*Quercus robur*, *Quercus petraea*) forests of northwestern Germany. J. Ecol.

Michelot, A., Bréda, N., Damesin, C., Dufrêne, E., 2012. Differing growth responses to climatic variations and soil water deficits of *Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris* in a temperate forest. For. Ecol. Manage. 265, 161-171.

Mölder, I., Leuschner, C., 2014. European beech grows better and is less drought sensitive in mixed than in pure stands: tree neighbourhood effects on radial increment. Trees, 28, 777-792.

Müller-Haubold, H., Hertel, D., Seidel, D., Knutzen, F., Leuschner, C., 2013. Climate responses of aboveground productivity and allocation in *Fagus sylvatica*: a transect study in mature forests. Ecosystems 16, 1498–1516.

Nussbaumer, A., Waldner, P., Etzold, S., Gessler, A., Benham, S., Thomsen, I.M., et al., 2016. Patterns of mast fruiting of common beech, sessile and common oak, Norway spruce and Scots pine in Central and Northern Europe. For. Ecol. Manage. 363, 237-251.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., et al., 2011. A large and persistent carbon sink in the world's forests. Science 333, 988–993.

Pečnik, J.G., Kutnar, A., Militz, H., Schwarzkopf, M., Schwager, H., 2021. Fatigue behavior of beech and pine wood modified with low molecular weight phenol-formaldehyde resin. Holzforschung 75, 37-47.

Poschlod, P., 2017: Geschichte der Kulturlandschaft: Entstehungsursachen und Steuerungsfaktoren der Entwicklung der Kulturlandschaft, Lebensraum- und Artenvielfalt in Mitteleuropa. Ulmer, Stuttgart, Germany.

Purkus A., Lüdtke J., Becher G., Jochem D., Polley H., Rüter S., et al., 2019. Charta für Holz 2.0 – Kennzahlenbericht 2019 Forst & Holz. Fachagentur Nachwachsende Rohstoffe e. V. (FNR), Gülzow-Prüzen, Germany. 45 p.

Rademacher, P., Khanna, P.K., Eichhorn, J., Guericke, M., 2009. Tree growth, biomass, and elements in tree components of three beech sites. In: Brumme, R., Khanna, P.K. (eds.), Functioning and management of European beech ecosystems. Springer, Berlin, Germany, pp. 105–136.

Reich, P.B., Oleksyn, J., 2008. Climate warming will reduce growth and survival of Scots pine except in the far north. Ecol. Lett. 11, 588-597.

Rigling, A., Bigler, C., Eilmann, B., Feldmeyer-Christe, E., Gimmi, U., Ginzler, C., et al., 2013. Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. Glob. Chang. Biol. 19, 229-240.

Sánchez-Salguero, R., Navarro-Cerrillo, R. M., Camarero, J. J., Fernández-Cancio, Á., 2012. Selective drought-induced decline of pine species in southeastern Spain. Clim. Chang. 113, 767-785.

Schär, C., Vidale, P.L., Lüthi, D., Frei, C., Häberli, C., Liniger, M.A., Appenzeller, C., 2004. The role of increasing temperature variability in European summer heatwaves. Nature 427, 332–336.

Scherfose, V., 1990. Feinwurzelverteilung und Mykorrhizatypen von *Pinus sylvestris* in verschiedenen Bodentypen. Ber. Forsch.zentr. Waldökosysteme Univ. Göttingen. 62, 1–166.

Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., et al., 2020. A first assessment of the impact of the extreme 2018 summer drought on Central European forests. Basic Appl. Ecol. 45, 86-103.

Sperber, G., Hatzfeldt, H., 2007. Hat die Buche eine forstliche Perspektive in Deutschland?. Nat. Landsch. 82, 436-438.

Ter-Mikaelian, M.T., Colombo, S.J., Chen, J., 2015. The burning question: Does forest bioenergy reduce carbon emissions? A review of common misconceptions about forest carbon accounting. J. For. 113, 57-68.

TI (Thünen-Institut), 2015. Dritte Bundeswaldinventur - Basisdaten (Stand 20.03.2015). https://bwi.info/Download/de/BWI-Basisdaten/ACCESS2003/bwi20150320_alle_ daten2012.zip.

Walentowski, H., Falk, W., Mette, T., Kunz, J., Bräuning, A., Meinardus, C., et al., 2017. Assessing future suitability of tree species under climate change by multiple methods: a case study in southern Germany. Ann. For. Res. 60, 101-126.

WBAE (Wissenschaftlicher Beirat Agrarpolitik, Ernährung und gesundheitlicher Verbraucherschutz) und WBW (Wissenschaftlicher Beirat Waldpolitik) beim BMEL (eds.) 2016: Klimaschutz in der Land- und Forstwirtschaft sowie den nachgelagerten Bereichen Ernährung und Holzverwendung. Gutachten. Berlin, Germany.

Wördehoff R, Spellmann H, Evers J, Nagel J., 2011. Kohlenstoffstudie Forst und Holz Niedersachsen. Nordwestdeutsche Forstliche Versuchsanstalt (ed.) Beiträge aus der Nordwestdeutschen Forstlichen Versuchsanstalt. Vol. 6. Universitätsverlag Göttingen, Göttingen, Germany

Xiao, C.-W., Yuste, J.C., Janssens, I.A., Roskams, P., Nachtergale, L., Carrara, A., et al., 2003. Above-and belowground biomass and net primary production in a 73-year-old Scots pine forest. Tree Physiol. 23, 505–516.

Acknowledgements

Numerous people supported me during the time of my PhD study, and without them this work would not have been possible. First, I want to thank my supervisor Prof. Dr. Christoph Leuschner for providing the opportunity to conduct this exciting study, for valuable advice and for guiding me through the realization of this work. Special thanks go to Dr. Dietrich Hertel, who gave practical guidance, who encouraged me, and whose door was always open to discuss constructively any small or big problem that I had. I am grateful to Prof. Dr. Markus Hauck for supervision and to Prof. Dr. Dirk Hölscher for reviewing this thesis. The technical and student research assistants and gardeners of the department of Plant Ecology and Ecosystems Research were of indispensable help with the practical work of this study, which is gratefully acknowledged.

I further want to thank the entire WiNat-Team, for the fun and constructive teamwork and for being such great colleagues. Special thanks go to Maria Aljes and Dr. Heike Schneider, who also became dear friends of mine during the many days and weeks we spent together in the forests. Rebekka Werner conducted her Master thesis within the WiNat project. She contributed valuable data on fine roots to this work, and was a hard-working and fun companion during field work. Thanks also go to Jonas Glatthorn, Stefan Kaufmann and Eike Feldmann, for listening and joking, and for sharing not only the rare office-time I had, but also their experience.

Finally, the greatest thanks go to my family. Without your endless love, patience and support in every imaginable way, I would never have been able to finish this thesis.

Statutory declaration

I herewith declare that the present dissertation is the result of my own work. I did not use any other than the stated sources and I have marked and listed all material that has been quoted either literally or in content. I have written this dissertation independently, except where jointly-authored publications have been included. My contribution and those of the other authors have been clearly indicated in these publications.

I confirm that this dissertation or parts of it have not been submitted to any other examination board.

I further declare that the printed version is identical to the electronic version of this work.

Göttingen, 07.04.2022 _____

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