Comparing northern German Scots pine plantations with natural beech forests: Soil carbon pools and growth dynamics

Dissertation
zur Erlangung des mathematisch-naturwissenschaftlichen Doktorgrades
„**Doctor rerum naturalium**“
der Georg-August-Universität Göttingen

im Promotionsprogramm
Biologie
der Georg-August-University School of Science (GAUSS)

vorgelegt von
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aus
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Göttingen, 2022

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Tag der mündlichen Prüfung: 24.03.2022

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Summary

Forestry in the North German Lowlands has been historically characterized by pine in particular. Apart from pine, beech is one of the most important deciduous tree species in this region and would naturally also be the predominant species. The intensive cultivation of pine in the North German Lowlands evolved due to demographic changes and beginning of industrialization in the 18th century. Due to its low site requirements and fast growth, pine was considered the optimal tree species for the already nutrient-poor sandy soils degraded by partly intensive use as forest pasture or litter raking.

The large-scale cultivation has been affecting landscape structure, biodiversity, soil, macro-, and microclimate until today, and will probably do so in the future. As climate change progressed over the last decades, more and more disadvantages of monocultures became apparent. From this followed a rethinking in forestry towards more site-appropriate mixed stands.

Restructuring forests is important so they can form stable ecosystems for the future climate and thus continue to perform or provide their ecosystem functions and services. Particularly important functions regarding the ongoing climate change are the storage of carbon to mitigate climate change and provision of drinking water.

There has been much debate among experts about which tree species or mixed stands will form the forests of the future in northern Germany. If one follows the potential natural vegetation, it would be beech forests in large parts of the lowlands. However, with reference to climate change and the associated shift of species ranges, a rethinking of the approach is necessary.

This dissertation thesis aims to contribute to the decision process between tree species for future cultivation by analyzing paired beech forests with pine plantations in terms of their soil carbon storage and their climate sensitivity and growth behavior.

Data were collected in 10 pairs of pine and beech stands in the North German Lowlands along a climatic gradient. In each stand, 10 soil profiles were established for the analysis of soil data. Soil samples were taken from four soil depths, up to 60 cm depth and the organic layer. For the dendrochronological investigations, cores of 20 trees per stand were taken and analyzed in the laboratory and correlated with climate data.

While the organic layer on average stored about 80 % more C under pine than beech, the pools of soil oranic carbon (SOC) and total N in the total profile (organic layer plus mineral soil measured to 60 cm and extrapolated to 100 cm) were greater under pine by about 40 % and 20 %, respectively. Besides tree species, neither precipitation nor temperature influenced the SOC pool for this data set. An extended data set (which included additional pine stands established more recently on former agricultural soil) revealed that, besides tree species

identity, forest continuity is an important factor determining the SOC and nutrient pools of these stands.

In the majority of beech stands, basal area increment (BAI) has lost its positive trend since the 1980s or growth declined since then, while the BAI of pine has continually increased. Long-term change in June precipitation is a more important determinant of beech growth trends in the study region than the amount of mean annual precipitation (MAP), while pine growth is largely dependent on the warmth of February/March. Yet, pine growth is also sensitive to low precipitation and high climatic aridity in midsummer, with sensitivity increasing toward low MAP. Until recently, the negative impact of increasingly warm summers on growth has been compensated by the positive effect of late-winter warming, resulting in stable (or increasing) growth trends. Climate sensitivity of growth has significantly declined since the 1980s in beech, while no such trend could be observed in pine, even in regions with declining June precipitation.

In light of existing research, the results of this study suggest that neither pine nor beech forests are unconditionally sustainable forest communities for future forestry in the North German Lowlands. From the current perspective, it will probably come down to a compromise in the choice of sustainable tree species, where a balance between climate sensitivity and productivity should be the goal. In this context, further research is needed on which tree species – and, in particular, which mix of species – can meet both the demands of future forest ecosystems and show possible adaptation potential.

CHAPTER 1

General introduction

1.1 Forestry in the North German Lowlands

Forests are the basis of existence for a large number of living creatures worldwide. They are of great ecological, economic and social importance. Ecosystem services such as climate protection, wood as a raw material and the supply of drinking water are particularly important for humans. With 11.4 million hectares of forest, Germany is one of the most densely forested countries in Europe (BMEL, 2021). The local forests are mainly characterized by spruce (25%), pine (22%), beech (15%) and oak (10%) (Thünen-Institut, 2022a). The forestry in northern Germany is particularly characterized by conifers, especially Scots pine.

The coniferous wood supply of the managed forest in the federal states of Brandenburg, Mecklenburg-Western Pomerania, Lower Saxony, Saxony-Anhalt and Schleswig-Holstein amounts to roughly 11 million m^3 yr^{-1}. In comparison, the hardwood supply is about 4 million m^3 yr^{-1}. Pine species (>7 million m^3 yr^{-1}) and spruce (>3 million m^3 yr^{-1}) have the largest share, as well as beech (>2 million m^3 yr^{-1}) and oak species (>70 thousand m^3 yr^{-1}). Lower Saxony is the federal state with the largest total wood supply (>6 million m^3 yr^{-1}) in northern Germany (Thünen-Institut, 2022b).

Scots pine (*Pinus sylvestris*, L.) and European beech (*Fagus sylvatica*, L.) are two of the most important tree species for forestry in the North German Lowlands (Leuschner, 2020; Müller, 2007). More than half of the forest area is covered by pine-dominated forests (53.2 %), although it would naturally occur on only about 2.3 % of the area (Leuschner et al., 2022). In comparison, beech forest, which naturally occurs on 48.6 %, does only occur on 6.6 % of the recent forest area in the North German Lowlands (Leuschner et al., 2022).

Pine was predominant in the Alleröd (Weichselian glacial period, Pleistocene) 10,000 years ago (Milnik, 2007). Since around 6200 BC in the Holocene, beech recolonized Europe. During this time, oak forests mixed with several tree species were already present in large areas of Central Europe. Since the last 4000 years, beech became predominant (Lang, 1994 in Leuschner and Ellenberg, 2017).

The intensive cultivation of pine in the northeast German lowlands evolved due to demographic changes and beginning of industrialization in the 18th century. It was primarily achieved to meet the demand for construction and firewood (Milnik, 2007). Due to the largely unregulated intense timber use and litter ranking, soil degradation occurred (Milnik, 2007). Therefore, pine with its low habitat requirements and excellent growth performance, was a particularly well suited species to meet the increasing demand for wood. With shares in forest areas of 70.1% in Brandenburg, 36.7% in Mecklenburg-Western Pomerania, 28.6% in Lower-Saxony, and 42.6% in Saxony-Anhalt, pine is still an important timber species today. In Brandenburg, it is even considered as a “bread tree” (Müller, 2007; Thünen-Institut, 2022b).

However, it has been shown that pine forests store less carbon than beech forests, and groundwater recharge is lower under pine- compared to beech stands (Leuschner et al., 2022). This lowered groundwater recharge can be partly attributed to higher transpiration and evaporation rates of pine stands (see review by Leuschner et al., 2022). In addition, studies from southern Europe showed that pine trees experience growth declines and dieback processes in excessively dry climates (Etzold et al., 2019; Matías et al., 2017). Despite the advantages of beech over pine in terms of water balance and C sink strength, beech as drought-sensitive tree species is probably only suitable to a limited extent in a drier climate (Scharnweber et al., 2011; Stolz et al., 2021). Therefore, it is questionable whether pine or beech can still be considered as sustainable tree species in the north German Lowland. Changes in forestry policy have led to a decline in the proportion of pine and an increase in the establishment of mixed and deciduous forest stands (Bauhus et al., 2021).

1.2 Climate change

The global temperature rose steadily every year for the last four decades (IPCC, 2021). Global surface temperature between 2011 and 2020 was 1.09 K higher than the reference period (1850-1900). Over land, this increased temperature was even higher at 1.59 K (IPCC, 2021). Depending on the scenario, global annual temperature is predicted to increase until 2100 between 1.0 and 5.7K above the reference period (IPCC, 2021).

Precipitation has increased on a global scale since 1950, and particularly rapidly since the 1980s (IPCC, 2021). For Germany, a seasonal shift in precipitation was observed. Summer precipitation decreased, whereas winter precipitation increased, so that mean annual precipitation remained roughly constant (DWD, 2020). As a consequence of the shifts in precipitation and increase in temperature, soil moisture changed and will continue to change in the future (IPCC, 2021).

1.3 Climate change and forests

A strong reduction of greenhouse gas (GHG) emissions is essential to achieve climate change mitigation goals (IPCC, 2021; Streck and Scholz, 2006). In this matter forestry plays an important role, as it must provide sustainable forests that can fulfill their ecosystem services for human well-being even under changing climate conditions (Bauhus et al., 2021; Millennium Ecosystem Assessment (Program), 2005). On the one hand, forests which are able to cope with the projected climate changes and associated abiotic and biotic influences are needed. On the other hand, these forests should sequester sufficient C, both in the soil and in the biomass, promote groundwater recharge and maintain or increase timber yield. Combining and maximizing all these ecosystem services is challenging, as negative linkages between individual ecosystem services have also been observed (e.g., Brockerhoff et al., 2017; van der Plas et al., 2018, 2016). Climate change will have an influence on plant communities and their distribution range. A poleward shift in climate zones has been observed globally since 1970, with a lengthening of the growing season since the 1950s (northern hemisphere, extratropics) (IPCC, 2021). If the global temperature will reach the 1.5 °C point, climate projections suggest that 8% of the plants worldwide could lose half of their climatically defined habitat range until 2100 (Warren et al., 2018). For forest species in Europe, a northward shift and losses of present distribution ranges are predicted due to changes in climate conditions (Hanewinkel et al., 2013).

In conjunction with the described alterations in climate, observations of vitality losses as well as dieback of trees increase (Allen et al., 2010; Carnicer et al., 2011; van Mantgem et al., 2009). Extreme weathers in Central Europe like drought events in 2003, 2015 and 2018/2019 caused reductions in primary production and a dieback of trees in temperate forests (Braun et al., 2020; Ciais et al., 2005; Obladen et al., 2021; Schuldt et al., 2020; Senf et al., 2020; Yuan et al., 2019). Further on, the impact of drought stress on tree health likely causes higher vulnerability of trees towards insect and pest attacks (McDowell et al., 2008; Schuldt et al., 2020). In addition, warmer winter temperatures promote the survival of insects facilitating expansions of insect pest outbreaks (Pureswaran et al., 2018). Forest devastation by wind, bark beetles and forest fires has increased during the 20th century. It is assumed that the forest destruction by disturbance agents is greater than the biomass increase from climate change (Reyer et al., 2017; Schelhaas et al., 2003).

1.4 Carbon storage and climate change

The proportion of CO_2 that can be sequestered in terrestrial and aquatic ecosystems will likely decrease with increasing cumulative CO_2 emissions (depending on the scenario) (IPCC, 2021). Previous studies showed that the carbon sink strength of terrestrial ecosystems has increased in the past with increasing anthropogenic CO_2 emissions, but due to environmental and climate changes this will not continue at this rate in the future (Ballantyne et al., 2012; Walker et al., 2021). Forests are considered as one of the largest carbon sinks in the context of mitigating climate change by storing a large amount of carbon in their biomass and soil (Pan et al., 2011; Whitehead, 2011). Forest soils as an important element of the global carbon cycle by sequestration of carbon as stable organic matter, store one third of the organic carbon (Lal, 2005; Price et al., 2012; Spalding et al., 2012). Particular importance is attributed to the northern hemisphere as carbon sink (Ciais et al., 2019). The increased atmospheric CO_2 concentration resulted in an increase in photosynthesis and led to an increase in C sequestration in forests but there are uncertainties about climate change-carbon cycle feedback so that the future climate services of forests are very obscure (Bonan, 2008; Fernández-Martínez et al., 2019, 2017; Smith and Fang, 2010).

The carbon sequestration is affected by several variables, like climate, soil, air chemistry and forest management (Leuschner and Ellenberg, 2017). The atmospheric CO_2 increase itself affects tree growth. In turn climate and its change (temperature and water availability) influence the effect of higher CO_2 concentration on forest growth and the mineralization of organic matter, and thus the carbon pool (Fekete et al., 2021; Fernández-Martínez et al., 2019, 2017; Grüneberg et al., 2019; Lorenz and Lal, 2010; Walker et al., 2021). There are predictions that a growth period characterized by CO_2 fertilization will now be followed by a period affected by climate change, which will be dominated by heat and drought, thus eliminating the positive CO_2 effect (Peñuelas et al., 2017). It is expected that rising temperatures will lead to an increased decomposition rate in the soil, leading to a reduction in the soil organic carbon (SOC) pool (Kasper et al., 2021; Melillo et al., 2017).

In addition to CO_2 increase, anthropogenically induced N deposition also has an impact on growth and the carbon pool. The N deposition increased the sequestration capacity of CO_2 from the atmosphere in the northern hemisphere (Jandl et al., 2007; Zak et al., 2019).

Moreover, the tree species influence the carbon sequestration (Grüneberg et al., 2019; Jandl et al., 2007). The litter quality, e.g., chemical foliage composition, the litter quantity and differences in (fine) root biomass as well as occurrence within the soil profile, affect soil carbon content (Förster et al., 2021; Leuschner and Ellenberg, 2017). Coniferous litter, which is usually more difficult to decompose due to higher amounts of lignin and cutin (Leuschner and Ellenberg, 2017), leads to a higher carbon content in the organic layer, which is usually thicker than in deciduous forests (Grüneberg et al., 2019). In addition, shallow-rooted conifers add carbon through decaying root biomass (Grüneberg et al., 2019). In the case of deciduous trees, on the other hand, larger carbon stocks in the mineral soil are generally assumed (Grüneberg et al., 2019; Jandl et al., 2007).

In order to mitigate climate change and create climate-stable forests, the information reported above should be taken into account when making changes in forest management. In sum, any change can significantly affect the carbon sequestration potential (Griscom et al., 2017; Leuschner and Ellenberg, 2017).

1.5 Study sites

The present study took place in the North German Lowlands, which extend from the Netherlands in the west, along the North Sea and Baltic Sea coasts to the Polish border and are bounded to the south by the low mountain range (Figure 1). The landscape was formed in the Pleistocene mainly by the Weichselian, Saalian and Elsterian glaciations. The study took place in 10 pairs (9 pairs in Chapter 2) of European beech (*Fagus sylvatica*, L.) and Scots pine (*P. sylvestris* L.) stands (Table 1, Figure 1). The forest stands are located in the states of Lower Saxony, Mecklenburg-Western Pomerania, Saxony-Anhalt, and Brandenburg. All forest stands of the study are located in the native range of the two tree species (San-Miguel-Ayanz et al., 2016, Figure 1, small map).

All stands, except beech stand no. 10, are developed in glacial sandy to sandy-loamy deposits from ground and end moraine (Saalian and Elsterian glaciation) as well as flats and Pleistocene watercourse (Weichselian glaciation) (BGR, 2022a, 2022b). Beech stand no 10 is on Triassic sandstone (BGR, 2022a, 2022b). Due to the parent material and pedogenesis these soils are very clayey and nutrient rich compared to the other more nutrient poor sandy to sandy-loamy soils.

The studied stands are located along a climate gradient ranging from a cool-temperate oceanic climate near the North Sea coast in the west to a cool-temperate subcontinental climate in the east of northern Germany. The mean annual temperature (30-year average, 1988-2017, MAT) ranges from 9.0 °C in the West to 9.7 °C in the continental east. The west-east precipitation gradient decreased from 823 mm yr^{-1} to 564 mm yr^{-1} (30-year average, 1988-2017, MAP).

The selected 20 forests are mature stands which had been managed in the past by regular thinning. The beech stands had an age of 95 to 195 years, the pine stands of 55 to 74 years. In the beech stands, the last thinning operations took place 6 to 43 years ago, while the pine stands were last thinned roughly 2-14 years ago.

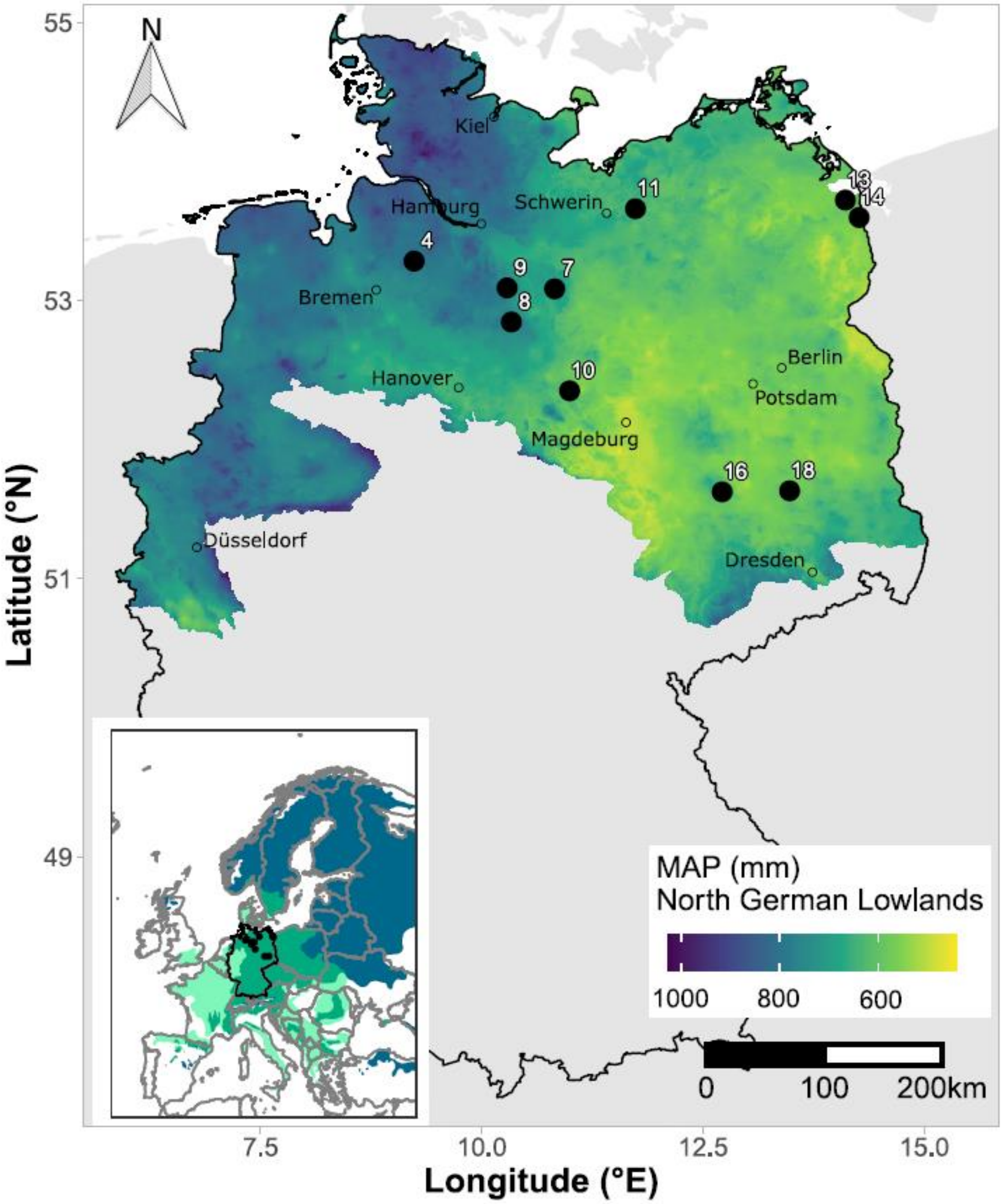

Figure 1. Large Map: Map of Germany with the 10 study sites (black dots) in the North German Lowlands colored by mean annual precipitation (MAP, 1991-2020, DWD Climate Data Center (CDC), 2022). Small map: Location of Germany in Europe with study sites (black dots) and distribution of Scots pine (dark blue) and European beech (light green) in Europe. The area where both species occur is marked dark green (source: Caudullo et al., 2021).

Table 1. Study sites. Species: Be = Beech, Pi = Pine, Age = Stand age, MAP = mean annual precipitation (30 year average, 1988-2017), MAT = mean annual temperature (30 year average, 1988-2017)

Site	Name	Species	Latitude (°N)	Longitude (°E)	Altitude (m)	MAP (mm)	MAT (°C)	Age (yr)
4	Weichel	Be	53.13756	9.399531	62	779	9.7	144
		Pi	53.2841	9.234567	62	823	9.5	68
7	Ewige Route	Be	53.12415	10.89294	118	725	9.2	134
		Pi	53.08472	10.82287	93	712	9.2	66
8	Lüssberg	Be	52.83756	10.33114	129	805	9.0	195
		Pi	52.84641	10.33369	126	801	9.1	66-68
9	Süsing	Be	53.1049	10.36403	123	771	9.3	139
		Pi	53.09167	10.28569	113	794	9.2	58-69
10	Nievoldhagen	Be	52.29464	11.13858	162	613	9.5	124
		Pi	52.35144	10.99112	118	601	9.7	64
11	Kaarzer Holz	Be	53.67275	11.73467	75	657	9.2	112
		Pi	53.66076	11.73564	71	654	9.2	60-74
13	Eggesiner Forst	Be	53.71144	14.13436	28	578	9.2	95-115
		Pi	53.72342	14.10779	30	569	9.1	62
14	Ueckermünder Heide	Be	53.57152	14.27635	58	577	9.1	147-152
		Pi	53.59773	14.26387	19	564	9.2	62
16	Authausener Wald	Be	51.64038	12.74352	146	653	9.6	166
		Pi	51.62486	12.71552	140	644	9.7	55
18	Weißhaus	Be	51.63212	13.45511	140	617	9.6	146
		Pi	51.63282	13.47791	145	623	9.5	62

1.6 Methodological approach

Paired natural beech stands and even-aged pine plantations were compared in soil carbon pool and climate-growth relations along a gradient from an oceanic to a sub-continental climate. The methodological approach of this study can be summarized for each chapter as follows:

i) We determined the stocks of SOC and macro-nutrients (nitrogen, phosphorus, calcium, potassium and magnesium) in nine paired European beech/Scots pine stands on similar Pleistocene sandy substrates across a precipitation gradient

(560–820mm·yr^{-1}) in northern Germany and explored the influence of tree species, forest history, climate, and soil pH on SOC and nutrient pools.

ii) We studied the radial growth patterns of Scots pine over the last 60 years at ten sites along a precipitation gradient (823–564 mm mean annual precipitation), analyzing the spatial and temporal variability of the climate sensitivity of growth in order to identify limits of the drought and heat tolerance of the species by means of linear mixed models.

iii) We employed dendrochronology to investigate the climate sensitivity of growth and long-term growth trends of beech and pine in ten pairs of forests along a precipitation gradient (823 to 564 mm mean annual precipitation, MAP) in the North German Lowlands with the aim to compare the species' climate sensitivity and to search for species-specific climatic thresholds.

1.7 Main study objectives

The overall objective of this study was to obtain more information on soil chemical properties and growth behavior of pine plantations widely distributed in the north German Lowlands compared to naturally growing beech stands in this region. The studied stands were selected along a precipitation gradient so that conclusions could be drawn for different regions.

The study is divided into three chapters focusing on differences in soil chemical properties between tree species (Chapter 2), drivers of radial growth in Scots pine (Chapter 3) and differences in climate related growth trends in Scots pine and European beech in northern Germany (Chapter 4).

The study was guided by the following main research questions:

i) How do tree species, stand history, and climate influence the soil C stock? (Chapter 2)

ii) Which factors influence the growth of Scots pine most and are there differences along the climate gradient? (Chapter 3)

iii) What are the differences between beech and pine in their climatic sensitivity, how has climate sensitivity changed during the last decades in the two species, and do climate sensitivity and growth trends vary regionally and along the climate continentality gradient? (Chapter 4)

The overarching hypothesis of this study was that old beech stands store more soil carbon compared to younger pine stands, but in the context of climate change, pine shows better growth trends than beech due to its large climatic and edaphic amplitude.

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CHAPTER 2

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

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Published in Forest Ecosystems (2021) 8:47

Abstract

Organic carbon stored in forest soils (SOC) represents an important element of the global C cycle. It is thought that the C storage capacity of the stable pool can be enhanced by increasing forest productivity, but empirical evidence in support of this assumption from forests differing in tree species and productivity, while stocking on similar substrate, is scarce. We determined the stocks of SOC and macro-nutrients (nitrogen, phosphorus, calcium, potassium and magnesium) in nine paired European beech/Scots pine stands on similar Pleistocene sandy substrates across a precipitation gradient (560–820 mm yr^{-1}) in northern Germany and explored the influence of tree species, forest history, climate, and soil pH on SOC and nutrient pools. While the organic layer stored on average about 80 % more C under pine than beech, the pools of SOC and total N in the total profile (organic layer plus mineral soil measured to 60 cm and extrapolated to 100 cm) were greater under pine by about 40 % and 20 %, respectively. This contrasts with a higher annual production of foliar litter and a much higher fine root biomass in beech stands, indicating that soil C sequestration is unrelated to the production of leaf litter and fine roots in these stands on Pleistocene sandy soils. The pools of available P and basic cations tended to be higher under beech. Neither precipitation nor temperature influenced the SOC pool, whereas tree species was a key driver. An extended data set (which included additional pine stands established more recently on former agricultural soil) revealed

that, besides tree species identity, forest continuity is an important factor determining the SOC and nutrient pools of these stands. We conclude that tree species identity can exert a considerable influence on the stocks of SOC and macronutrients, which may be unrelated to productivity but closely linked to species-specific forest management histories, thus masking weaker climate and soil chemistry effects on pool sizes.

2.1 Introduction

The sequestration of atmospheric carbon dioxide in soils as stable organic matter is discussed as a means of mitigating anthropogenic climate warming (Spalding et al. 2012). Forest soils store one third (c. 720 Pg) of the global organic carbon (C) (Schlesinger 1991, Price et al. 2012) and thus are an important element of the global C cycle (Lal 2005). Soil organic C (SOC) storage depends not only on climate (Lorenz & Lal 2010) and mineral properties, notably the potential of soils to stabilize organic C on reactive mineral surfaces (Vogel et al. 2015), but it may also be influenced by tree species identity and forest management (Binkley & Giardina 1998, Jandl et al. 2007, Grüneberg et al. 2019). Tree species influence the C input to the soil by differences in the amounts of aboveground litter (leaves, fruits, coarse woody debris) and root litter (Roy et al. 2001, Finér et al. 2011, Schlesinger & Bernhardt 2013) as well as in root exudation rates and carbohydrate transfer to the mycorrhiza (Godbold et al. 2006, Pausch & Kuzyakov 2018, Akatsuki & Makita 2020). Litter chemistry, notably the content of lignin, nitrogen (N) and calcium (Ca) (and possibly exudate chemistry) are additional important factors that affect C turnover in the soil (Berg & McClaugherty 2003, Reich et al. 2005).

Tree species differences in litter properties should be particularly large between angiosperm and gymnosperm trees, as the latter produce needles that are generally poorer in N and Ca than leaves of broad-leaved trees (Berg & McClaugherty 2003, Hobbie et al. 2006), and conifers are often more shallow-rooted than many angiosperm trees (Polomski & Kuhn 1998), with possible consequences for root-borne C input. Species differences in the amount and seasonality of litter production may increase the dissimilarity between these groups. While it is generally agreed that tree species often have a profound effect on the C storage in the organic layer on the forest floor (e.g. Binkley & Valentine 1991, Vesterdal & Raulund-Rasmussen 1998, Fischer et al. 2002), the species effect on mineral soil SOC pools is less clear (e.g. Heinsdorf 2002, Ladegaard-Pedersen et al. 2005, Jandl et al. 2007, Schulp et al. 2008, Grüneberg et al. 2019). Thus, which forest type in general sequesters more SOC cannot be simply be stated, because C sequestration also depends on soil and climate. Hence, with respect to current efforts of quantifying C stock changes in forests and their development under altered climatic conditions, a better understanding of how the forest type and the forest composition influence C sequestration is needed. In the debate about how temperate production forests of the future should look like, this understanding is particularly needed for comparing the impact of conifers, which are widely planted in monocultures and valued in forestry for their timber productivity and economic value, and native hardwood trees, which may have advantages in terms of biodiversity conservation, lower soil acidification potential and lower susceptibility to insect attack (Ammer et al. 2008; Gessler et al. 2006).

In the past, Scots pine (*Pinus sylvestris* L.) plantations have widely replaced the natural broadleaf forests in the lowlands of northern Central Europe, i.e. in the north of the Netherlands, Germany and Poland. At least in Germany and the Netherlands, most of the pine stands have been planted during the last 250 years on soils that once were stocked with European beech (*Fagus sylvatica* L.) and oak forests (*Quercus petraea* Matt. Liebl and *Q. robur* L.) (Kremser 1990, Milnik 2007). Pine-dominated stands nowadays cover 52.1 % of the current forest area in the northern German lowlands (deviating from the region defined as North German Plain Fig.1), while the natural occurrence of Scots pine is only estimated at 2.1 % of the area (Förtser et al. 2021). In absolute terms, a rough calculation of the current pine forest area gives for Poland c. 6.5 Mio ha (1990), for Germany about 2.4 Mio ha (2012), and for the Netherlands c. 0.2 Mio ha (Kuusela 1994, Leuschner et al. 2013, BMEL 2020). These numbers demonstrate the enormous extension of pine plantations in this region. However, while Scots pine is valued as a fast-growing, non-demanding timber species, it has several disadvantages, notably a high susceptibility to fire and pathogen attack, the build-up of a relatively dry and infertile organic layer, and the tendency to acidify the soil (Bublinec 1974, Reich et al. 2005, Prietzel et al. 2006). In terms of C sequestration in the soil, it is not fully clear, how such pine plantations differ from the naturally prevailing beech forests in this area.

Several regional studies that compared Scots pine and the natural broad-leaved forests (beech) on similar soil found in most cases larger organic layer SOC stocks under pine (Fischer et al. 2002, Leuschner et al. 2013), while the information for the mineral soil is contradictory (e.g. Heinsdorf 2002, Jandl et al. 2007, Schulp et al. 2008, Leuschner et al. 2013). The nation-wide Forest Soil Inventory (NFSI) of Germany, which analyzed data from 1900 soil pits, gave roughly three times lager C stores in the organic layer for pine stands (mostly Scots pine) than for beech stands, while the mineral soil SOC pool was significantly smaller than under beech (Grüneberg et al. 2019). Regional studies from northern Germany also found larger C pools in the organic layer and lower pools in the mineral soil under pine compared to beech (e.g. Wördehoff et al. 2017a, 2017b). However, the tree species effect is in these large-scale inventories overlaid by variation in geological substrate, topography, and soil moisture regimes. Moreover, stand history, which can strongly influence SOC pools (Compton and Boone 2000), was not considered in these inventories. Many pine plantations in the lowlands of northern Germany have been established on soils that were heathlands or arable fields for long periods, which may imprint on soil C storage (von Oheimb et al. 2008, Laganière et al. 2010, Leuschner et al. 2013). The comparison of paired pine and beech stands on similar substrate and on soils with long forest continuity can minimize these confounding factors. This approach has been adopted on a local scale (e.g. in the Veluwe/the Netherlands and Brandenburg/Germany, Heinsdorf 2002, Schulp et al. 2008, Leuschner et al. 2013), but not yet on a supra-regional level. Here, we present the results of a country-wide study on the soil C and nutrient stocks (organic layer plus mineral soil measured to 60 cm and extrapolated to 100 cm) in paired beech and pine stands along a climate gradient (temperate-oceanic to temperate sub-continental) in the Pleistocene lowlands of northern Germany, spanning from the North Sea coast to the Polish border. As many pine stands stock on soils that were arable land or heathland in the more distant past, we also address the importance of stand history on SOC stocks.

The goal of the study was to examine the influence of tree species (beech vs. pine), stand history (ancient vs. recent forest), and climate (560-820 mm yr^{-1} precipitation) on (i) the SOC pool and SOC distribution in the profile, and (ii) the soil pools of the macro-nutrients N, P, Ca, Mg and K. To reduce the influence of soil chemical factors, the stands were selected on fairly uniform geological substrate, i.e. base-poor unconsolidated glacial deposits which dominate in the region. The influence of forest continuity (‚ancient forest sites': > 230 years vs. ‚recent forest sites': c. 50–130 years) was addressed by comparing our results (mostly ancient forest sites) to data from 7 recent pine forest sites provided by the study of Leuschner et al. (2013) in the study region.

2.2 Materials and Methods

2.2.1 Study sites

The study was conducted in the lowlands of northern Germany in nine pairs of European beech and Scots pine stands on glacial unconsolidated sandy to loamy sediments from the last (Weichselian) or penultimate Ice Age (Saalian). The nine study sites were located between Bremen in the west with a cool-temperate oceanic climate to the river Oder in the east with a cool-temperate sub-continental climate (Fig. 1). Mean annual temperature varied between 9.0 and 9.6 °C, mean annual precipitation decreased from 712-823 mm yr^{-1} in the west to 564–657 mm yr^{-1} in the east (Table 1). The air temperature (2 m) and precipitation data for the nine sites were derived from the 1 km x 1 km grid data of temperature and precipitation interpolated by Deutscher Wetterdient (DWD) from its dense climate station net (DWD Climate Data Center, v1.0). The geological substrates comprise sandy to loamy moraine deposits, glacio-fluviatile sandy deposits and sandy substrates covered by aeolian sandy loess. All substrates led to the formation of acidic, nutrient-poor soils without groundwater influence. The soil types were spodo-dystric Cambisols and Podzols.

Information given in Glaser and Hauke (2004) and consultation of local sources (Meyer et al. 2006) indicated that most of the forest stands (all beech forests and 6 out of 9 pine stands) grew on sites with long forest continuity, i.e. uninterrupted forest cover during at least the last

200 years. It is likely that these 15 sites were also covered by forest during the Middle Ages and probably have never been cleared for agricultural use. The remaining three pine stands were either heathland or farmland 200 years ago and thus have a relatively short continuity. The paired beech and pine stands were selected in short distance to each other on similar geological substrate. In most pairs, the distance between the beech and pine stands was less than 1 km. Only in case of site 1 (Weichel), the distance was greater (20 km).

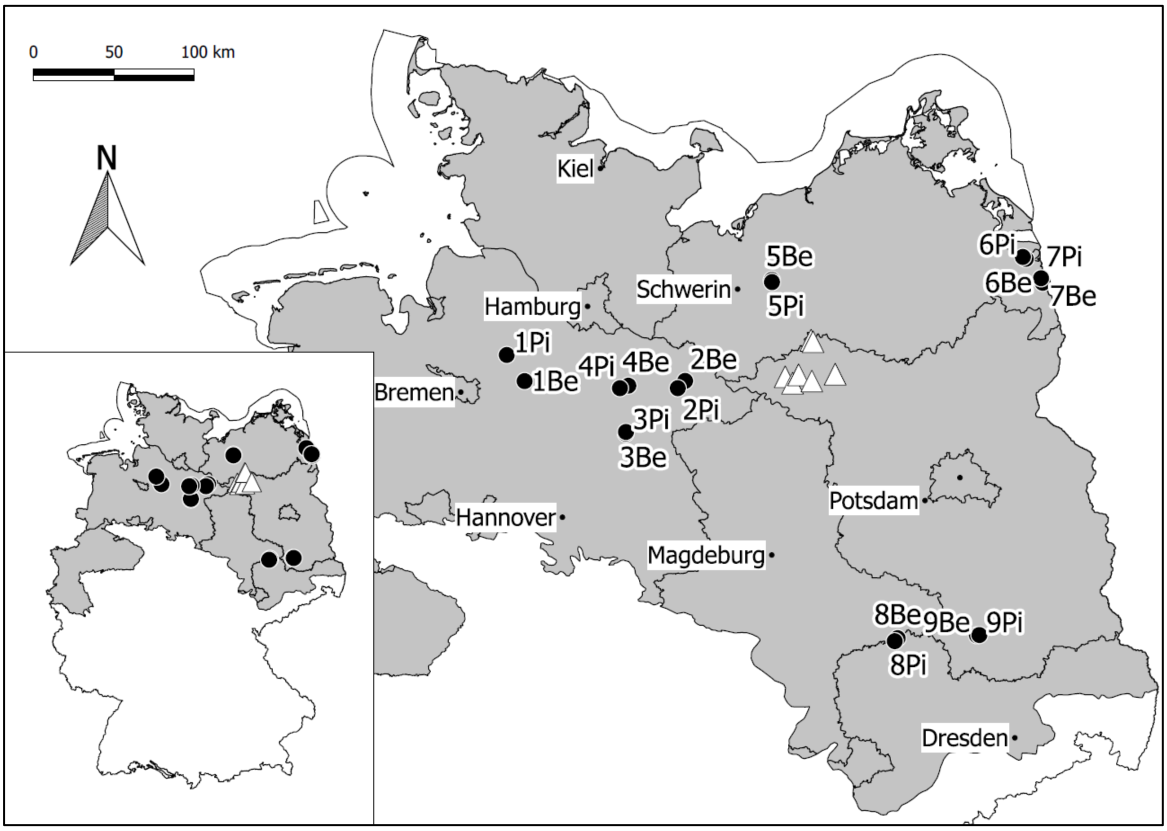

Figure 1. Location of the nine study sites in Germany (inlet) and location of the 18 stands in the North German Plain (grey-shaded, Be = near-natural beech forests, Pi = pine forests). The white triangles mark the location of the additionally analyzed seven recent pine stands in western Brandenburg adopted from Leuschner et al. (2013).

Table 1. Location and characteristics of the nine study sites.

Site	Location	Forest type	Latitude (°N)	Longitude (°E)	Age (yr)	Forest continuity	MAP (mm)	MAT (°C)	Basal area (m^2 ha^{-1})	Stem density (n ha^{-1})	Size of forest stand (ha)
1	Weichel	Be	53.13	9.39	144	ancient	779	9.7	35.5	159	32.4
		Pi	53.28	9.23	68	ancient	823	9.5	26.0	475	12.5
2	Ewige Route	Be	53.12	10.89	134	ancient	725	9.2	31.9	281	40.7
		Pi	53.08	10.82	66	ancient	712	9.2	23.6	288	13.3
3	Lüssberg	Be	52.83	10.33	195	ancient	805	9.0	23.6	139	29.2
		Pi	52.84	10.33	66-68	recent	801	9.1	26.7	375	14.2
4	Süsing	Be	53.10	10.36	139	ancient	771	9.3	37.9	299	66.6
		Pi	53.09	10.28	58-69	recent	794	9.2	27.2	552	22.5
5	Kaarzer Holz	Be	53.67	11.73	112	ancient	657	9.2	21.6	202	11.2
		Pi	53.66	11.73	60-74	recent	654	9.2	29.7	535	13.3
6	Eggesiner Forst	Be	53.71	14.13	95-115	ancient	578	9.2	22.1	266	18.3
		Pi	53.72	14.10	62	ancient	569	9.1	23.4	429	23.4
7	Ueckermünder Heide	Be	53.57	14.27	147-152	ancient	577	9.1	31.9	156	21.0
		Pi	53.59	14.26	62	ancient	564	9.2	31.0	731	25.8
8	Authausener Wald	Be	51.64	12.74	166	ancient	653	9.6	21.6	347	18.8
		Pi	51.62	12.71	55	ancient	644	9.7	26.2	572	18.7
9	Weißhaus	Be	51.63	13.45	146	ancient	617	9.6	31.3	127	15.4
		Pi	51.63	13.47	62	ancient	623	9.5	25.4	628	15.5

Each study site is presented by a pair of beech (Be) and pine stands (Pi). Given are stand age, forest continuity, mean annual precipitation (MAP), mean annual temperature (MAT), stand basal area, stem density, and stand area. Forest stands were classified as “ancient” for >200 years of forest continuity, and “recent” for <150 years of continuity.

2.2.2 Study design and soil sampling

In each stand, ten circular plots were established at random positions. The plots had a size of 0.1 ha (35.68 m in diameter), and the minimum distance between the plot centers was 66 m. Thus, at least 30 m separated the circle edges from each other. To exclude edge effects, the distance to forest paths and forest edges was at least 20 m. One soil profile each per plot was dug at a random location to 60 cm depth and soil samples were taken at four depths (0–10, 10–

20, 20–40 and 40–60 cm) and in the organic layer (L, Of and Oh horizon according to Forstliche Standortsaufnahme 2016). Three samples per depth were collected at the three walls of the pit and combined to one composite sample for each depth and profile. We chose a sampling depth to 60 cm according to fine root studies on sandy soils by Meier et al. (2018) in the North German Lowlands and investigations by Anders et al. (2004) in a forest area in the North-east German lowlands, which show that beech and pine have the largest amount of root mass in the uppermost 60 cm of the mineral soil. Thus, a very large proportion of the rooted soil volume was covered by our soil chemical sampling scheme. Soil was sampled with a metal cylinder of 100 cm^3 volume. The organic layer was sampled with a root corer (5.5 cm in diameter) at three locations close to the soil profile; the samples were combined to a single sample as well. Corresponding to the number of circular sampling plots, the number of analytical replicates was 10 at the stand level (one sample per depth per plot) and thus 900 in total (2 species x 9 stands x 5 depths x 10 stand-level replicate plots). The soil samples were stored in plastic bags and kept at 4 °C in the laboratory.

2.2.3 Soil analysis

Prior to analysis, the mineral soil was sieved through a 2-mm sieve and roots were picked out by hand from the mineral soil and organic layer. 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)). Total C and total N were measured in ground soil that was dried at 70 °C for 48 h. C and N 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 and after combustion at 640 °C. To obtain organic C content, inorganic C content (determined as the C content remaining after combustion) was subsequently subtracted from total C content (determined as the C content before combustion). The total content of K, Mg and Ca in the organic layer was determined by ICP-OES analysis (Perkin Elmer Optima 5300 DV). In the mineral soil, only the salt-exchangeable base cations were determined. 2.5 g of fresh soil was percolated with 0.2 M $BaCl_2$ solution and the concentration of K, Ca, Mg, Al, Fe and Mn determined in the solution with ICP-OES. Total phosphorus (P) concentration was measured in the organic layer samples with ICP-OES, while in the mineral soil, resin-extractable P was determined (resin-bag method). 1 g of fresh soil was suspended in 30 ml of water and P was extracted with the anion exchanger resin Dowex 1 x 8-50. P was then re-exchanged from the resin with NaCl and NaOH solutions, and the P concentration determined in a photometer at 712 nm against water using the colorimetric molybdate-ascorbic acid method. To obtain element pools for the mineral soil depth levels, the concentration data were converted to volumetric data using the bulk soil density of the depth levels, that were determined separately in all profiles and depths. The organic layer data were multiplied with organic layer mass per area to obtain element stocks per ground area.

2.2.4 Statistical analysis

Data analysis was conducted with R, version 3.6.3 (R Core Team 2020) in the framework of the tidyverse (Wickham et al. 2019). Stand-level averages were calculated from the 10 samples per stand. The means (and standard errors) per tree species used in the graphs are derived from the mean values calculated at the stand level for each of the nine pine and beech stands. In order to obtain element pools for a standard 1-m soil profile, we fitted a Michaelis-Menten curve to the element pools of the 0–10, 10–20, 20–40, and 40–60 cm soil depth levels and extrapolated the pools down to a depth of 1 m based on the resulting concentration-depth curve fitted for each soil plot. We applied ANOVA (F-test) over stand-level averages of all study sites and all soil depth levels to test for significant differences between stand types (beech vs. pine). Here, we also accounted for study site (stand) and soil depth level as additional model variables and considered different trends across soil depth levels (interaction forest type *x* soil depth). Significantly different means were identified post-hoc with Tukey´s HSD test. As recent pine stands, established on sites with former agricultural or heathland use, are more widespread in the study region than ancient pine stands with longer forest continuity, we extended our stand sample by including data from 7 recent pine forests on similar soil in western Brandenburg (study of Leuschner et al. 2013), and tested for the combined effect of stand type and forest continuity (ancient beech stands vs. recent pine stands or ancient pine stands) in a similar testing procedure (recent beech forests were not available). Significantly different means were identified post-hoc with Tukey´s HSD test. Further, the influence of important climatic and edaphic variables (temperature, precipitation, pH of the subsoil) on the soil C, N, P and base cation pools in the 0–100 cm profile (C and N: organic layer, mineral soil, and total profile; base cations: only mineral soil considered in the analysis) was tested in linear models, that of management factors (stand age, stand type and history) in multiple-regression analyses. In case of the climatic variables, we considered 30-year averages of annual and summer temperature means and precipitation sums. Before we built the maximal models, we tested the explanatory variables for autocorrelation using the R package cormorant v. 0.0.0.9007 (Link, 2020), which revealed a close correlation of summer temperature and precipitation to annual temperature and precipitation, respectively (Fig. A5 in the Appendix). Subsequently, we applied Spearman's rank correlation analysis (R package Hmisc v.4.4-1, Harrell, 2020) to investigate direct univariate relationships between mineral and organic layer C, N, P and base cation pools with stand age, temperature and precipitation variables, and pH of the subsoil (Tab. 2). Accordingly, annual temperatures explained the trends in SOC and nutrient pools across the study sites better than summer temperatures, while summer precipitation had a similar or slightly larger influence than annual precipitation. Consequently, we excluded summer temperature and annual precipitation from the following multiple-regression analyses, also in view of the high autocorrelation of the variables related to annual and summer climatic conditions (Fig. A5 in the Appendix). This variable selection matches the ecology of the tree species, as growth is most closely related to summer precipitation, while growing season length may depend more on spring and autumn temperature, which is better reflected in mean annual temperature. Thus, starting from maximal models that contained stand age, pH (subsoil), mean summer precipitation (MSP) and mean annual temperature in addition to stand type and forest continuity as possible explanatory variables of the SOC and nutrient pools, the variables in each model were backward-selected by iterative reduction of the least significant variable until only significant variables remained.

2.3 Results

2.3.1 Influence of tree species on the soil C and nutrient pools

The organic layers tended to be thicker under pine stands by about 6 mm and stored about 80 % more C than the organic layer under beech stands (52.0 vs. 28.6 Mg C ha^{-1}; difference significant; Fig. 2a). In particular, the slightly decomposed Of layer was markedly thicker under pine than beech, while the fresh litter layer (L) was thinner (Fig. A1 in the Appendix).

The SOC pool in the mineral soil to 100 cm was about 27 % higher in the pine stands (89.1 Mg C ha^{-1}) than in the beech stands (70.4 Mg C ha^{-1}). The total SOC pool (organic layer and mineral soil) was on average about 40 % greater under pine than beech (141.2 vs. 99.1 Mg C ha^{-1}; difference significant; Fig. 2a). Yet, variation between the nine investigated sites was considerable (Fig. 3) and in two of the 9 pairs, the SOC pool was larger in the beech than the pine stand (site 4 and 9).

The soil N content was closely related to the SOC content but the difference between beech and pine stands was smaller. The pine stands stored about 50 % more N in the organic layer than the beech stands (2007 vs. 1330 kg N ha^{-1}; Fig. 2b), but the difference was not significant. While the mineral topsoil under pine was slightly richer in N than the equivalent layers under beech, the subsoil tended to have slightly smaller N pools, resulting in similar mineral soil N pools (3897 vs. 3638 kg N ha^{-1}). The total soil profile stored about 20 % more N under pine than under beech (5903 vs. 4968 kg N ha^{-1}; difference significant; Fig. 2b). The C:N ratio was by about 3 g g^{-1} higher under pine in the entire soil profile (Fig. 4c).

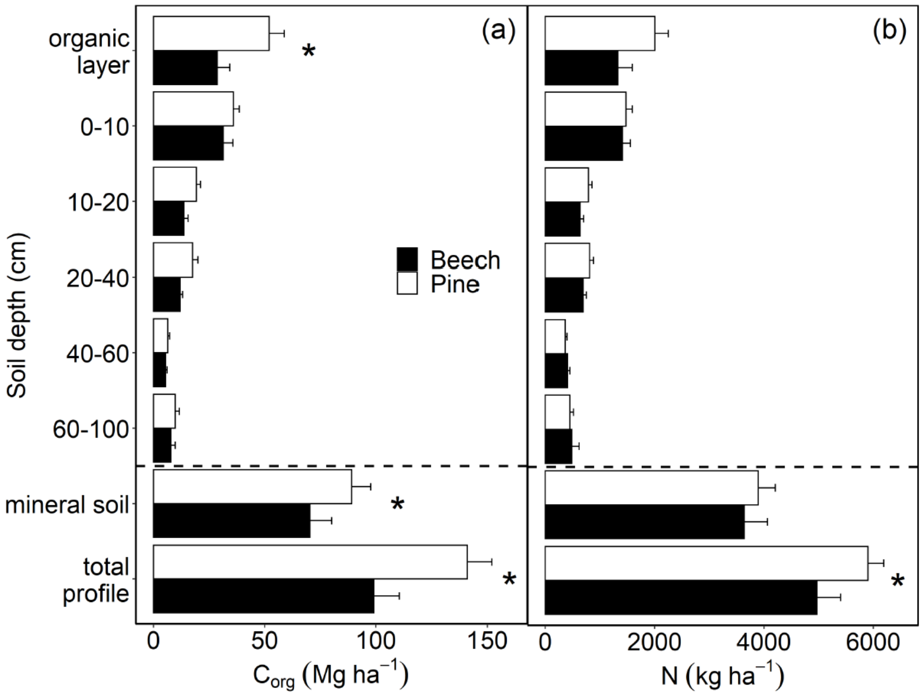

Figure 2. Pool of organic C (a) and total N (b) in soil profiles to 100 cm depth (data for 60–100 cm were computed by extrapolation) under beech (black bars) and pine stands (white bars). Total profile refers to mineral soil plus organic layer. Significantly different pool sizes between the stand types are marked with an asterisk (ANOVA). Given are means and standard error of each nine stands, in which each 10 profiles were investigated.

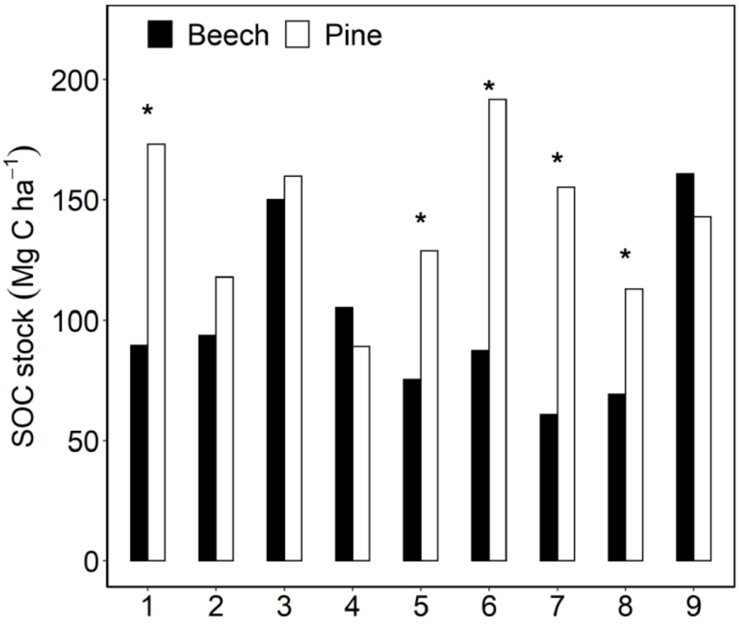

Figure 3. Mean SOC stocks in the mineral soil (0-100 cm, data for 60–100 cm were computed by extrapolation) and the organic layers of the each nine beech (black bars) and pine stands (white bars) at the sites 1 to 9 (given are the means of 10 profiles per stand). Significantly different pool sizes between the stand types are marked with an asterisk (paired t-test).

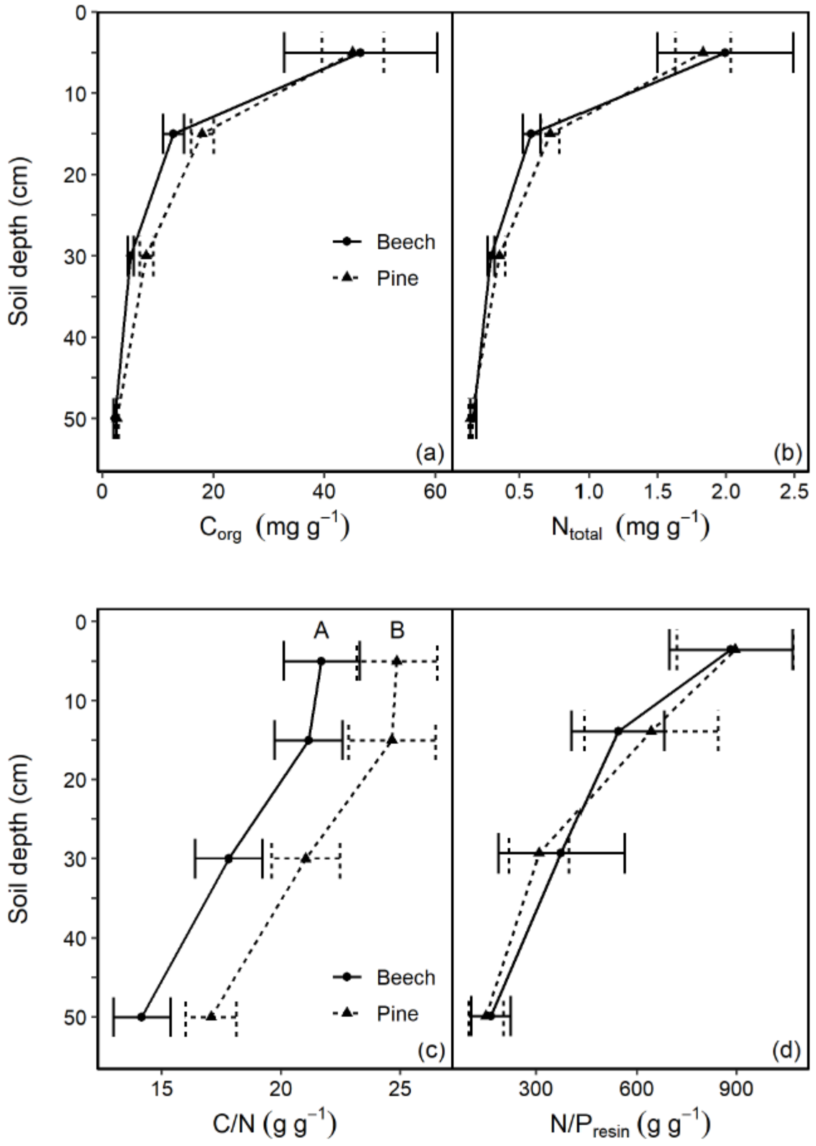

Fig 4. Mean concentration (and standard error) of (a) organic C, (b) total N, (c) C:N ratio and (d) $N:P_{resin}$ ratio in mineral soil profiles under beech (solid line) and pine stands (dotted line). Different capital letters mark significant differences between stand types for the whole profile (ANOVA). Given are means and standard error of each nine stands, in which each 10 profiles were investigated. Depth-wise differences were not significant.

With 87 kg P ha^{-1}, the pools of total phosphorus in the organic layer were about 25 % larger under pine than under beech (70 kg P ha^{-1}, Fig. 5a; difference not significant). In the mineral soil to 100 cm, the pool of plant-available P (resin-P) was slightly (but not significantly) higher under beech than pine (62 vs. 58 kg P_{resin} ha^{-1}; Fig. 5b). Due to the higher C_{org} content, the C:P ratio in the mineral topsoil (> 30 cm depth) was somewhat higher under pine than beech (Fig. A2b in the Appendix), while the N:P ratio was similar among the forest types (Fig. 4d).

In contrast to N, we found somewhat larger pools of basic cations (Ca, K, Mg) in the organic layer (total pool) and in the mineral soil ($BaCl_2$-exchangeable pools) under beech than pine (17.6 vs. 13.9 $kmol_c$ ha^{-1} to 100 cm, Fig. 6a and b), but the differences were not significant. Cation exchange capacity (CEC) and base saturation were generally low in the subsoil (< 20 μmol$_c$ g^{-1} and < 10 %), with a somewhat higher CEC at 50 cm and a slightly higher base saturation in the topsoil under beech (Fig. A3a and b in the Appendix). Acidity was very similar in the mineral soil of beech and pine stands (Fig. A4 in the Appendix). Only in the subsoil (50 cm depth), pH (KCl) was slightly (not significantly) lower under beech, while it was much lower (by 0.5 units) under pine in the organic layer (3.1 vs. 3.6; difference significant).

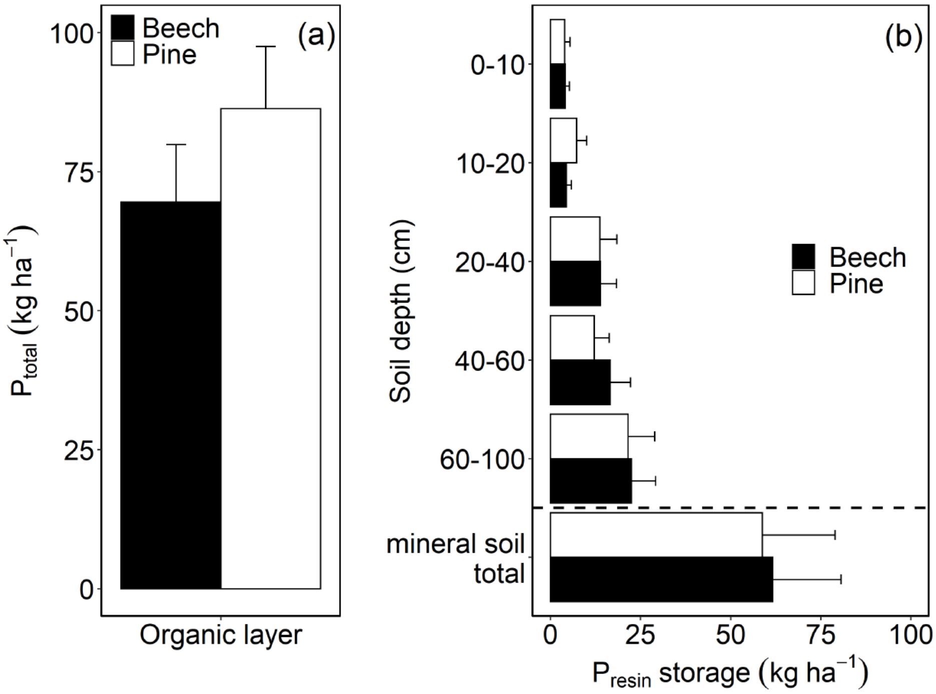

Figure 5. Total pool of phosphorus in the organic layer of beech (black bar) and pine stands (white bar) (a), and pools of plant-available P (resin-P) in mineral soil profiles to 100 cm depth (data for 60–100 cm were computed by extrapolation) under beech (black bars) and pine stands (white bars) (b). Significantly different pool sizes between the stand types are marked with an asterisk (ANOVA). Given are means and standard error of each nine stands, in which each 10 profiles were investigated.

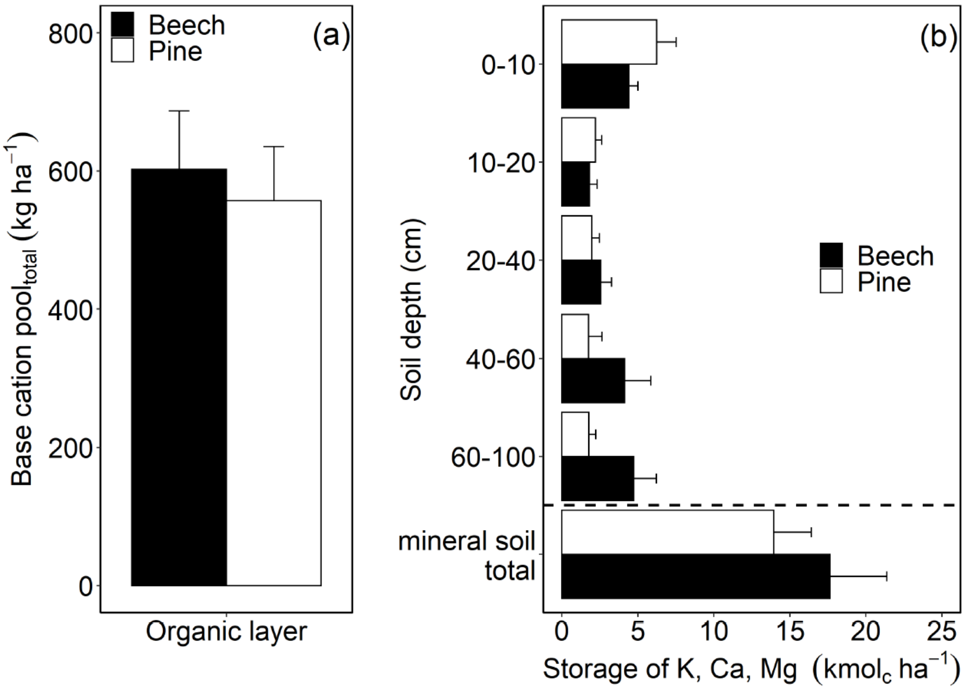

Figure 6. Total pool of base cations (Ca, K, Mg) in the organic layer of beech (black bar) and pine stands (white bar) (a), and pools of exchangeable base cations in mineral soil profiles to 100 cm depth (data for 60–100 cm were computed by extrapolation) under beech (black bars) and pine stands (white bars) (b). Significantly different pool sizes between the stand types are marked with an asterisk (ANOVA). Given are means and standard error of each nine stands, in which each 10 profiles were investigated.

2.3.2 Differences in SOC and soil nutrient pools between ancient and recent forest stands

The analysis of an extended forest stand sample completed with data from recent pine forests (Leuschner et al. 2013) showed that ancient pine stands had a total SOC stock (organic layer and mineral soil to 100 cm) of 148.9 Mg ha^{-1}, which is about 27 % higher than in recent pine stands (116.8 Mg ha^{-1}) and 50 % higher than in ancient beech stands (99.1 Mg ha^{-1}) (Fig. 7a). While the difference in the mineral soil was not significant, ancient pine stands stored almost twice as much C in the organic layer than recent pine stands (60.5 vs. 33.9 Mg C ha^{-1}, Fig. 7c). Total N pools were also higher in the organic layer of ancient than recent pine stands, while the mineral soil N pool tended to be larger in recent pine stands (Fig. 7e and f). Consequently, the profile total N pools differed not significantly among the stand types, but were in tendency larger in recent and ancient pine than beech stands. The resin-P pool in the mineral soil was significantly larger in recent than in ancient pine stands and higher than in ancient beech stands (Fig. 8a). For the mineral soil base cation pool ($BaCl_2$-exchangeable fraction), a tendency for lower stocks under ancient pine stands was found, but the difference to recent pine and beech stands was not significant (Fig. 8b).

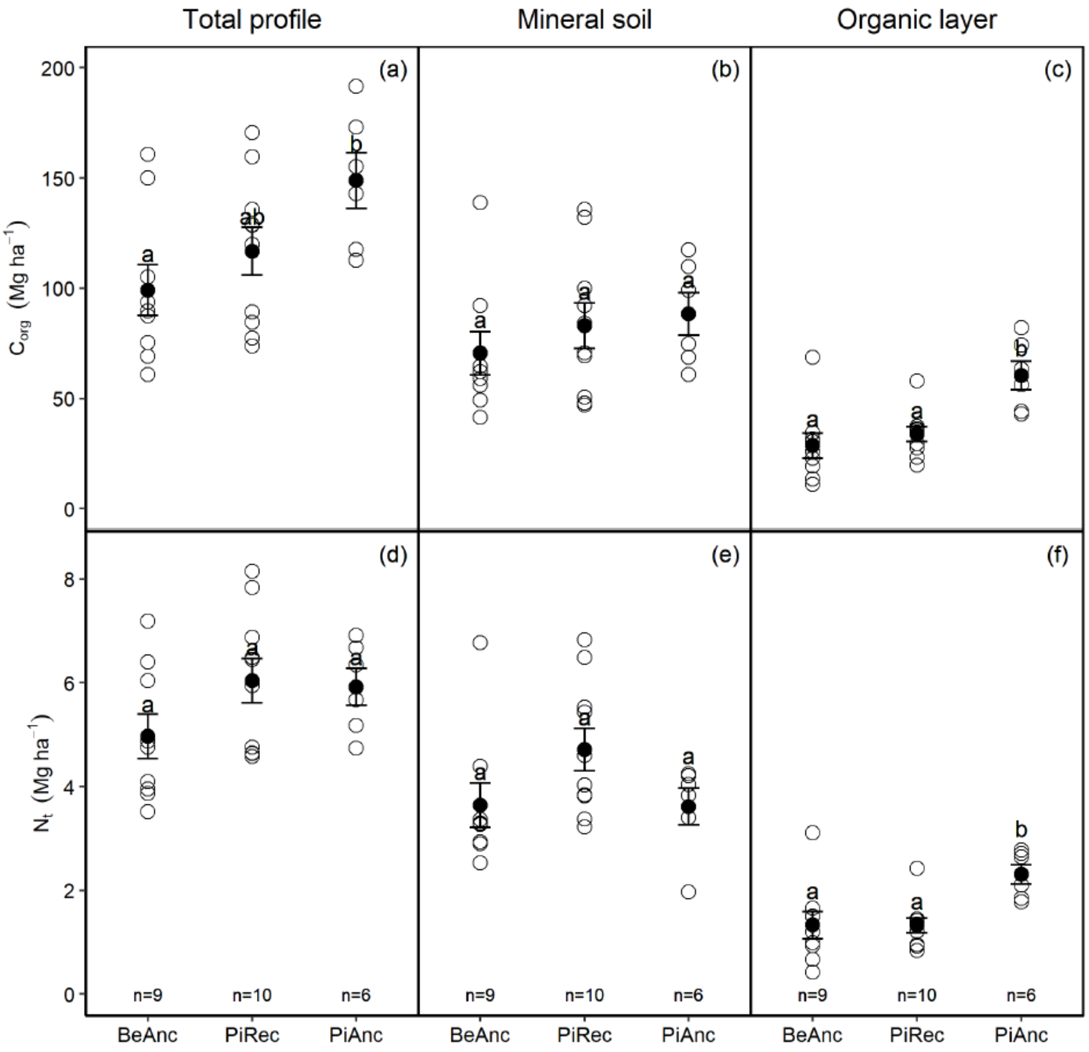

Figure 7. Mean pools of organic C in the soil under ancient beech (BeAnc), ancient pine (PiAnc) and recent pine stands (PiRec) for the total profile to 100cm (including organic layer, data for 60–100 cm were computed by extrapolation) (a), the mineral soil (0-100 cm) (b), and the organic layer (c), and mean pools of total N in the three forest categories for the total profile to 100 cm (including organic layer) (d), the mineral soil (0-100 cm) (e), and the organic layer (f). Given is the population mean (black dot) and the standard error, and the individual means of the stands (open circles). Significantly different population means between the stand types are marked with different small letters. The stands comprise those analyzed in this study and seven additional recent pine stands from western Brandenburg according to Leuschner et al. (2013).

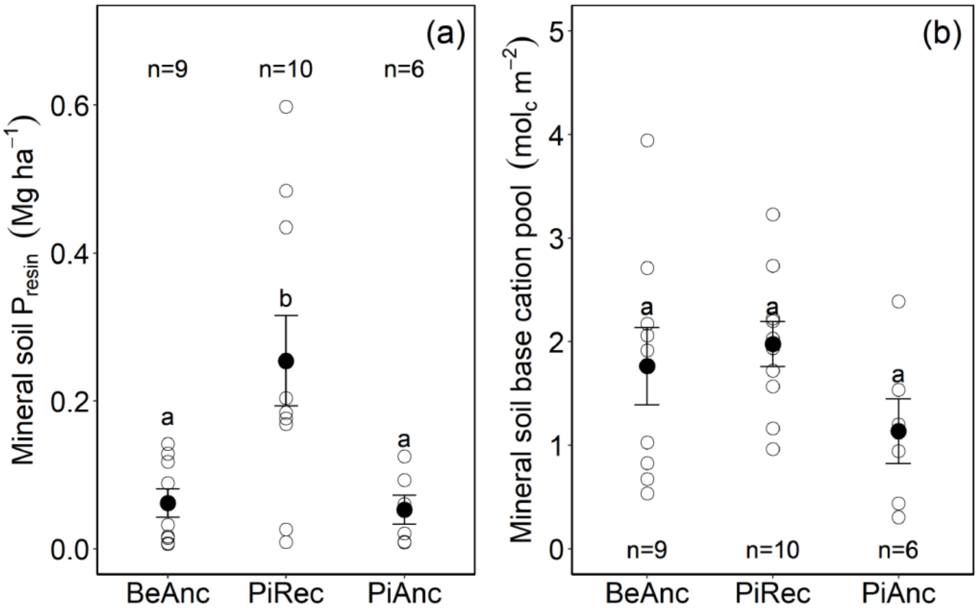

Figure 8. (a) Mean pools of available P (resin P) and (b) $BaCl_2$-exchangeable base cations in the mineral soil (0-100 cm, data for 60–100 cm were computed by extrapolation) under ancient beech (BeAnc), ancient pine (PiAnc) and recent pine stands (PiRec). Given is the population mean (block dot) and the standard error, and the individual means of the stands (open circles). Significantly different population means between the stand types are marked with different small letters. The stands comprise those analyzed in this study and seven additional recent pine stands from western Brandenburg according to Leuschner et al. (2013).

2.3.3 Influence of climatic and edaphic factors, and stand structure combined with stand history on SOC and soil nutrient pools

The univariate relationships of SOC with the covariates stand age, subsoil pH and temperature and precipitation differed between beech and pine stands (Table 2). The organic layer C pool in beech stands tended to increase with mean annual temperature (MAT) and to decrease with stand age, but both relationships were not significant (Table 2). In contrast, the organic layer C pool in pine forests significantly increased with a pH decrease, while the influence of climate and stand age was very weak (Table 2). The mineral soil SOC pool was not related to any of the tested climatic, edaphic or stand structural (species, forest history, age) variables, neither in beech nor in pine stands (Tables 2 and 3). Modeling pool size variation with a SOC model that accounts for both the environmental and stand structural (species) factors indicated in case of the total profile a significant effect only for stand type (beech vs. pine) and stand history, in case of the organic layer only for stand age, stand type and stand history, while climate and soil pH were insignificant factors (Table 3), despite a soil acidity increase with stand age (Fig. A5 in the Appendix).

The N_t pool in the organic layer significantly increased with a pH decrease in the pine stands; in the beech stands, only an insignificant trend toward a N pool increase with MAT was visible (Table 2). In the mineral soil, the N_t pool increased with mean annual precipitation in the beech, but not in the pine stands. However, in a similar manner as was observed for the C pools, these direct effects of climatic and edaphic factors disappeared, when the influence of stand type and history was included in linear models. Stand type and history remained as the only significant explanatory variable for the organic layer N pool (Table 3). None of the tested variables had a significant influence on the mineral soil C and N pools in the linear models. Our results thus suggest that due the close linkage of N accumulation to C sequestration in the soil, tree species and stand history effects are overriding effects of temperature, precipitation and also atmospheric N deposition patterns in our study region.

The resin-P pool of the mineral soil of both beech and pine stands decreased towards drier sites (significant only in pine), and significantly decreased with increasing soil acidity in pine (Table 2). In the linear models with all factors included, these effects where of minor importance, and only summer precipitation and stand type and history remained as the principal explanatory variables for the resin-P pool (Table 3).

The exchangeable pool of basic cations in the mineral soil in the beech stands showed a strong and significant relationship to mean annual temperature (MAT) and an insignificant influence of mean summer precipitation (MSP), with an increasing pool of basic cations towards warmer and moister sites (Table 2). However, MAT remained as the only significant explanatory variable, when exploring the combined effect of all explanatory variables in our model analysis (Table 3).

Table 2. Results of a Spearman rank correlation analysis.

			Age	MAT	MST	MAP	MSP	pH
OL	C	Be	-0.46	0.50	0.25	0.01	0.15	-0.11
		Pi	-0.09	0.12	0.08	-0.11	0.01	**-0.51**
	N	Be	-0.36	0.48	0.23	0.00	0.16	-0.13
		Pi	-0.08	0.13	0.06	-0.12	0.01	**-0.48**
MS	C	Be	0.13	-0.08	-0.11	0.43	0.25	-0.25
		Pi	-0.01	-0.08	-0.30	-0.12	-0.06	-0.01
	N	Be	0.31	0.06	-0.31	**0.68**	0.60	-0.18
		Pi	0.08	-0.05	-0.15	-0.26	-0.27	0.40
	P	Be	-0.60	-0.31	-0.10	-0.56	-0.48	0.16
		Pi	0.24	-0.03	0.36	**-0.52**	**-0.63**	**0.55**
	BC	Be	0.40	**0.68**	0.40	0.25	0.60	-0.16
		Pi	0.34	0.09	-0.01	0.25	0.06	0.07

Analysis of the dependence of C_{org} and N pools of the organic layers (OL), and C_{org}, N, P and base cation pools (BC) of the mineral soil (MS) (0–100 cm), on stand age (age), mean annual temperature (MAT), mean summer temperature (MST), mean annual precipitation (MAP), mean summer precipitation (MSP), and subsoil pH (KCl) (40-60 cm soil depth) in the beech and pine stands. Given are the ρ values of the relationships. Significant values are printed in bold. Climatological means refer to the last 30 years.

Table 3. Model results on the influence of climatic and edaphic variables on nutrient pools.

		MAT	MSP	Stand age	Stand type and history	Soil pH (40-60 cm)
C pool	total	-	-	-	x	-
	OL	-	-	x	x	-
	MS	-	-	-	-	-
N pool	total	-	-	-	-	-
	OL	-	-	-	x	-
	MS	-	-	-	-	-
P_{resin} pool	MS	-	x	-	x	-
BC pool	MS	x	-	-	-	-

Variables influencing the pools of C_{org} and N_t (total soil profile, mineral soil 0–100 cm (MS) and organic layer (OL)) and resin-P (mineral soil 0–100 cm) and exchangeable base cations (BC, mineral soil 0–100 cm) in the beech and pine stands according to linear models. The initial models included mean annual temperature (MAT, last 30 years), mean summer precipitation (MSP, last 30 years), stand age, soil pH at 40–60 cm and stand type in combination with forest history (ancient beech, ancient pine and recent pine stands); insignificant variables (-) were subsequently removed until only significant explanatory variables (x) remained.

2.4 Discussion

2.4.1 Tree species effects on the SOC pool

Our paired-plot study revealed under pine an on average about 40 % greater SOC pool than under beech (organic layer and mineral soil combined). Only two of the nine investigated plot pairs showed a higher C content under beech. Our results are generally in line with the conclusions of Boča et al. (2014) from a meta-analysis, who found conifers to have on average 26 % and 19 % more SOC in the forest floor and mineral soil, respectively, compared to beech-dominated stands. It has been discussed, whether there is a difference in the vertical allocation of SOC stocks between conifers and broadleaf trees rather than a difference in total SOC stocks. Various authors suggested that less C in the mineral soil offsets higher C stocks in the forest floor and vice versa (Vesterdal et al. 2008, 2013; Prescott and Vesterdal 2013). This is not the case in our study, where SOC stocks were higher under pine in both the organic layer and mineral soil. Other studies directly comparing pine and beech forests on similar soil in the Pleistocene lowlands of northern Central Europe came to partly contradicting results: Fischer et al. (2002) reported 30 % higher total SOC pools under pine compared to beech in eastern Brandenburg (north-eastern Germany), Heinsdorf (2002) and Schulp et al. (2008) found similar pools under pine and beech in Brandenburg and the Veluwe (eastern Netherlands), and Leuschner et al. (2013) measured 25 % higher pools under beech than pine in western Brandenburg. It appears that the effect of tree species on SOC pools varies from one region to another. This is underpinned by the great variation in SOC pools among the nine stand pairs of our study (beech: 60.8–160.9 Mg C ha^{-1}, pine 89.2–191.7 Mg C ha^{-1}, 0–100 cm). Nevertheless, stand characteristics, i.e. tree species and stand history, were the most important predictors of soil C, N and P pools, while climatic and edaphic factors had only a weak or no influence in the global models. Climate was an additional explanatory factor only for the mineral soil P-resin pool, and it was the only factor in case of the base cation pool.

Lower SOC pools under beech than pine match the observation of Prietzel (2004) that planting beech in pine stands reduced C storage in the organic layer over 16 to 83 years and resulted in a 5 % smaller total SOC pool. Beech and pine forests differ in many aspects, which are relevant for SOC accumulation. First, mature beech forests produce substantially more aboveground litter than pine plantations. Litter bucket measurements of leaf litter production in the stands of this study gave for the years 2015 and 2016 by 25 to 48 % higher annual litter amounts in the beech stands than the pine stands (Förster et al. 2021). Moreover, fine root biomass is much higher in beech than pine stands, indicating a higher C transfer from the beech root system to the SOC pool (A. Förster, pers. comm.). Anders et al. (2004) reported a total root biomass of 17.9 Mg ha^{-1} in beech stands compared to 10.0 Mg ha^{-1} in pine stands in north-eastern Germany, i.e. a difference by 80 %. Thus, the annual organic matter input with aboveground and belowground litter is considerably higher in beech than pine stands. In addition, the beech fine root system typically penetrates to greater depths than the often shallow fine root system of pine (Polomski & Kuhn 1998), which should lead to higher C inputs particularly in the subsoil under beech.

There is a striking mismatch between the larger SOC pool under pine and the relatively low annual C input with above- and belowground litter. This sheds some light on the relative importance of C input on the one side, and organic matter processing and C stabilization in the soil on the other side, for C sequestration in the soil (Angst et al. 2019). While the SOC accumulation of agricultural soils generally increases with the biomass input (Jenkinson 1988), this seems not to be the case in these forests on acidic, clay-poor soil. It has been found that the net accumulation of new tree-derived C can be greater under a low-productive stand on loamy soil than under a high-productive stand on fertile sandy soil (Hagedorn et al. 2004). According to biomass inventories in our stands, the pine forests stored only half of the aboveground biomass C that was recorded in the beech forests (Förster et al. 2021). Summing up the C pools in aboveground biomass and in the soil (without roots) gives on average an about 15 % higher ecosystem C storage in the beech than the pine forests (246 Mg C ha^{-1} vs. 213 Mg C ha^{-1}). This result may help to quantify the consequences for C sequestration of future changes in Scots pine plantation area in the lowlands of northern Central Europe. According to current forestry planning schemes, the area of pine plantations will shrink in northern Germany in future times to give way to more broad-leaved forests (predominantly beech) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantations (Anders et al. 2004), which would increase ecosystem C storage. In the German state of Lower Saxony, for example, the forest area planted with pine is expected to decrease from 21 % in 2015 to 15 % in 2055 (NW-FVA & NL 2019).

2.4.2 Litter quality effects on the SOC pool

Litter quality is probably much more decisive for explaining the elevated SOC pools under pine than the amount of C transferred from biomass. The chemistry of root tissues may play a key role (Angst et al. 2018, 2019). The C:N ratio of fresh foliage litter is typically by 15 to 40 g g^{-1} higher in pine than beech with N concentrations of 8–9 mg g^{-1} in beech and 5-7 mg g^{-1} in pine litter (Hertel 1995, Lorenz et al. 2004, Hobbie et al. 2006). Similar to needle litter, pine root litter has a low N content and high C:N ratio, and the lignin content is also high (Silver & Miya 2001). Correspondingly, the C:N ratio of soil organic matter was in our study by ~3 g g^{-1} higher under pine than beech throughout the profile. As the C:N ratio is a good predictor of decomposition rate across different litter types (Enriquez et al. 1993, Pérez-Harguindeguy et al. 2000), one would assume that litter decomposition should proceed faster under beech than pine, which would explain the smaller SOC stocks under beech. Moreover, pine needle litter has a much lower Ca content than beech litter, which may hamper forest floor C dynamics (Hobbie et al. 2006). However, litter bag experiments with pine and beech foliage in neighboring stands showed that pine needles decomposed significantly faster in the first and also the second year in stands on sandy soil than beech litter (Hertel 1995, Lorenz et al. 2004, Hobbie et al. 2006). The higher decomposition rate of pine litter is unexpected not only from the higher C:N ratio, but also from the often more pronounced drying of the organic layer in pine forests as compared to beech forests (Leuschner 2001, Anders et al. 2004). One explanation could be the lignin and tannin content of fresh beech litter, which is considerably higher in beech than in pine leaf litter (Lorenz et al. 2004, Hobbie et al. 2006). Whatsoever the reason, the turnover of the labile and intermediate SOC pools is thus unrelated to the flux of C into the stable soil C pool in these forests (Poeplau et al. 2018).

It is astonishing that soil N concentration, soil C:P and N:P ratios, and base saturation at the cation exchangers all were similar in soil profiles under beech and pine in our study, even though the foliage and leaf litter of beech contains significantly more N and other nutrients, which are returned to the soil. The ‚soil-ameliorating' effect of the more nutrient-rich beech litter (Anders et al. 2004, Prietzel 2004,) seems to be limited to the organic layer, affecting the mineral soil only marginally.

Our results suggest that the P-resin content may primarily depend on climatic factors, notably growing season precipitation. According to the meta-analysis of Hou et al. (2018), available P in forest soils generally decreases with increasing MAT and MAP, matching our results of a significant negative relationship between MSP and P-resin pools in the mineral soil of the pine stands. Possible drivers of this relationship are a higher P leaching when precipitation is high, and decreased P uptake in drier soil. Our data do not show a clear temperature effect on P-resin pools.

As beech leaves are typically richer in lignin than pine needles (Berg & McClaugherty 2003, Hobbie et al. 2006), it is probably not lignin that fosters the transfer of pine litter components to the stable SOC pool. It is also unlikely that differences in the stabilization of SOM (e.g. the abundance of reactive clay mineral surfaces) have caused the higher SOC pools under pine, given that the geological substrates and associated soil mineral contents were similar among the paired beech and pine sites. This is supported by the fact that the profiles under pine and beech had very similar cation exchange capacities. Other, probably local, factors must be responsible for the higher soil C accumulation under pine than beech. One factor could be stand history.

2.4.3 The combined influence of forest history, climate, and soil

Due to century- or millennia-long human impact on the forests, land use history is often a main determinant of the actual SOC pools in temperate forests (Verheyen et al. 1999, Compton & Boone 2000, Leuschner et al. 2013). Many pine plantations in northern Germany have been established on former heathland or arable land during the last 250 years, causing reaccumulation of C especially in the organic layer, but also in the mineral soil (Heinsdorf 2002, Vesterdal et al. 2002). The linear models developed to test for the combined effects of climate, soil pH, stand age, and tree species in conjunction with stand continuity (ancient beech, ancient pine, recent pine) revealed no consistent effects of soil (pH) and climate (temperature and precipitation) on SOC stores. Rather, the models showed a dominant influence of tree species together with stand continuity, which masked any significant relationship between SOC pool size and environmental factors that was visible in the beech and the pine data sets in correlation analyses. Our data set, completed by seven pine stands with less than 150 years of forest continuity (‚recent pine stands'), thus shows a large increase in organic layer C_{org} (by on average 30 Mg C ha^{-1}) from recent to ancient pine stands (> 230 years of continuity) and a smaller (non-significant) increase in the mineral soil (Fig. 7a-c). The C accumulation corresponds to a parallel accumulation of N mainly in the organic layers (Fig. 7).

The extended data set (16 pine and 9 beech stands) further indicates significantly higher plant-available P stocks (P_{resin}) in the mineral soil of the recent pine stands (Fig. 8a), which may point at agricultural use of the sites in the distant past. Thus, legacy effects seem to play an important role for P availability in the studied forests, besides the dependence of available P on precipitation. The significant positive relation between the pool of exchangeable base cations and MAT in the beech stands and the positive effect of MAT on the base cation pool in the model suggest that a warming climate might affect base cation availability in these forests, perhaps through altered weathering rates (Akselsson et al. 2016, Houle et al. 2020). Despite an assumed role for temperature and precipitation for the availability of P and base cations in our stands, the temperature and precipitation gradients covered in our study (8.4 °C–9.1 °C and 560–820 mm yr^{-1}) may be too short to significantly influence the soil stocks of C and N in our sample in relation to the influence of the other factors. On the national level, climate was also found to be only of secondary importance for soil C stocks in the soil survey of German forests (Grüneberg et al. 2019). Thus, attempts to explain SOC stocks by edaphic and climatic factors without considering forest history may in our study region be not comprehensive enough.

2.5 Conclusions

Our study suggests that the tree species effect on soil C and N accumulation can hardly be deduced from forest productivity and litter decomposition rate in the studied forest ecosystems. Regarding the climate warming mitigation potential of pine and beech forests in the study region, it is an important finding that the SOC stocks are on average larger under pine than beech. However, this must be put in relation to the C stock in the aboveground biomass, which is considerably lower in pine than beech. Although covering large parts of Northern Germany, it must be kept in mind that this study is a case study and the results should be interpreted under the constraints that local variation in geological substrate, forest management and forest history may have significantly affected current SOC stocks. In agreement with other studies, it is evident from this study that tree species effects on soil C relations often are closely linked to forest histories and management regimes, which makes it difficult to disentangle biological effects related to productivity, litter chemistry, and root system properties from management effects. This is even more so in large-scale forest soil inventories, where a strong interaction between tree species and substrate type likely is obscuring tree species effects on soil C storage.

Abbreviations

SOC: Soil organic carbon, MAP: Mean annual precipitation, MAT: Mean annual temperature, MSP: Mean summer precipitation (last 30 yrs), C: Carbon, N: Nitrogen, P: Phosphorus, K: Potassium, Ca: Calcium, BC: base cation, NFSI: National Forest Soil Inventory, Be: near-natural beech forests, Pi: pine forests, BeAnc: ancient beech stands, PiAnc: ancient pine stands, PiRec: recent pine stands

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Appendix

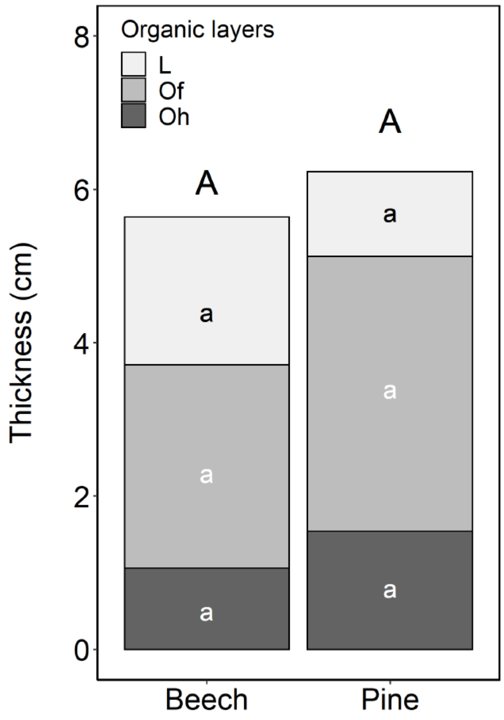

Figure A1. Mean thickness of organic layers on the forest floor of the beech and pine stands (L, Of and Oh layer according to Forstliche Standortsaufnahme 2016). The shared capital and small letters indicate that there were no significant differences between total organic layer depth and between individual layers.

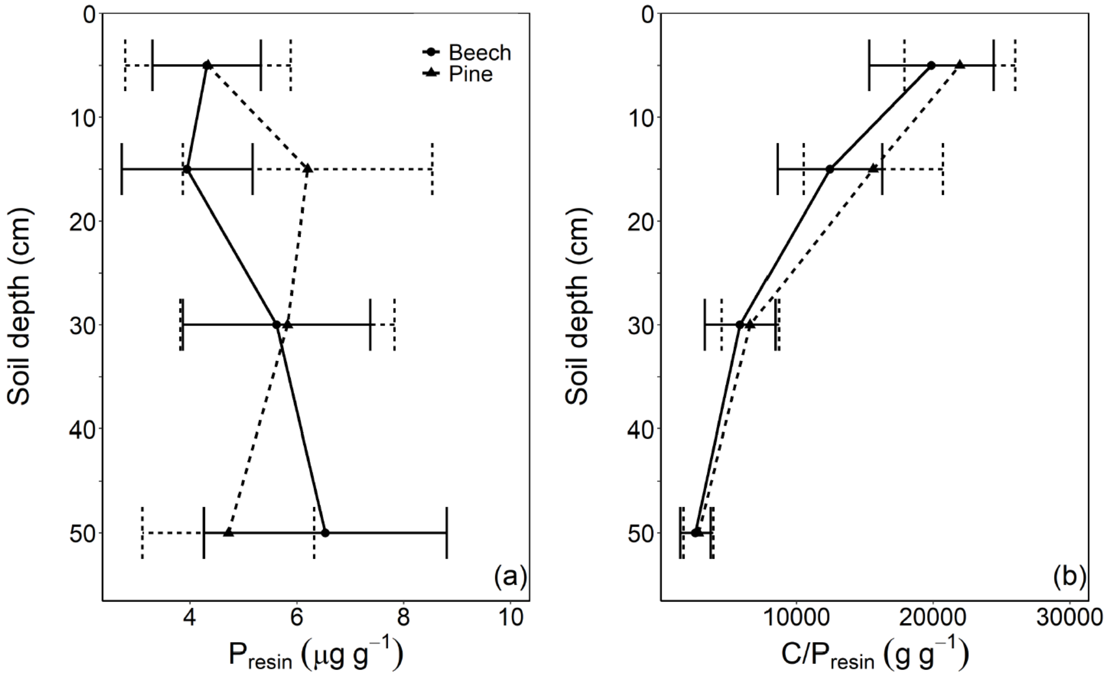

Figure A2. Mean concentration (and standard error) of plant-available phosphorus (resin-P) (a), C:P_{resin} ratio (b) in mineral soil profiles under beech (solid line) and pine stands (dotted line). No significant differences between stand types were found (ANOVA). Given are means and standard error of each nine stands, in which each 10 profiles were investigated.

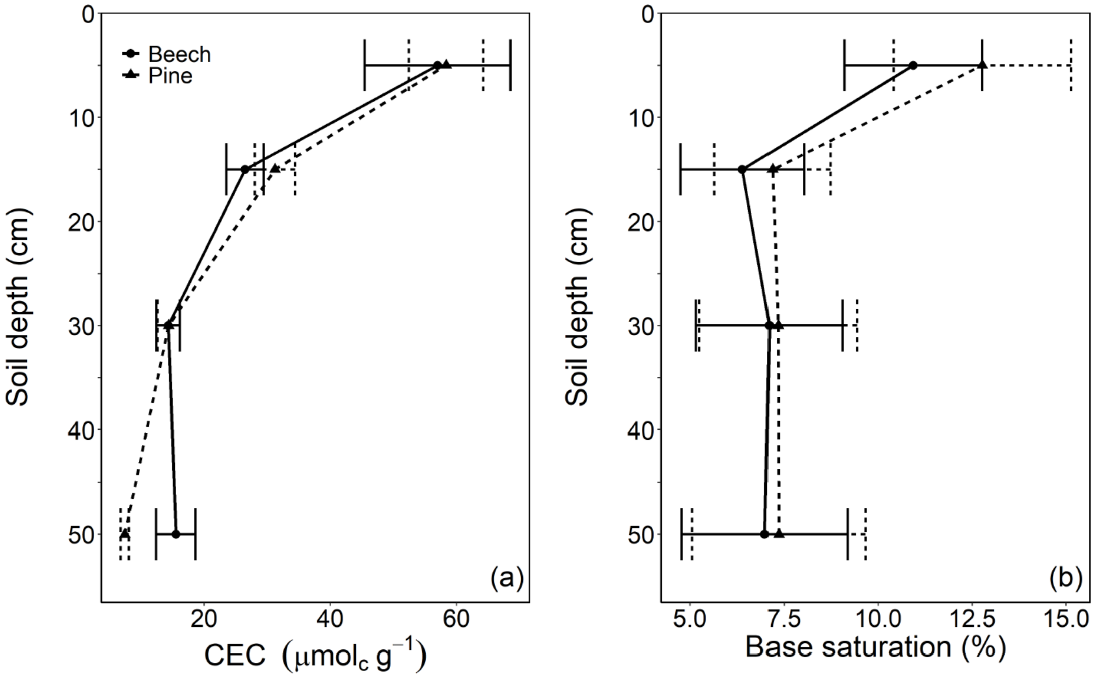

Figure A3. Cation exchange capacity (CEC, a) and base saturation (b) in soil profiles under beech (solid line) and pine stands (dotted line) (means and standard error). No significant differences between stand types were found (ANOVA). Given are means and standard error of each nine stands, in which each 10 profiles were investigated.

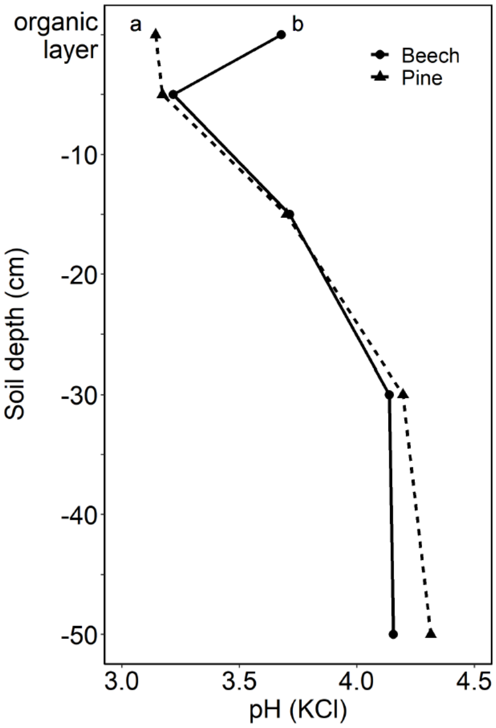

Figure A4. Soil depth dependence of pH measured in 1 M KCl in soil profiles under beech stands (solid line) and pine stands (dashed line). Given are means and standard error of each nine stands, in which each 10 profiles were investigated. Significantly different means between forest types in a given depth are marked with different small letters (ANOVA).

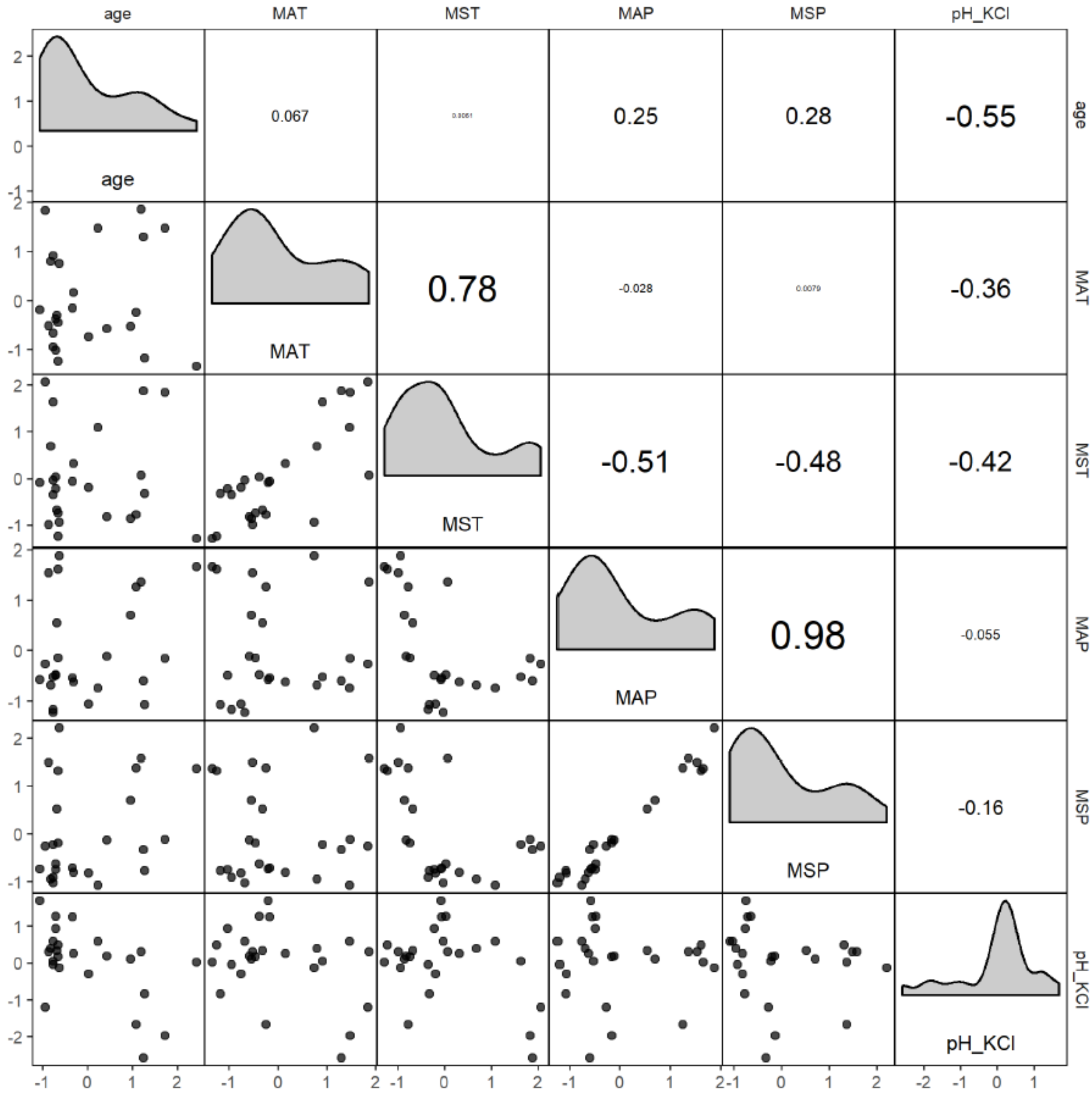

Figure A5. Test for autocorrelation between potential explanatory variables of the SOC pool in order to exclude highly correlated variables prior to further statistical modelling. Given are data from all 25 plots (beech and pine stands including the 7 pine stands from Leuschner et al. 2013), age: stand age, MAT: mean temperature of the last 30 years, MST: mean summer temperature of the last 30 years, MAP: mean precipitation of the last 30 years, MSP: mean summer precipitation of the last 30 years, pH_KCl: mean pH-value of 40–60 cm.

CHAPTER 3

Scots pine growth is sensitive to hot droughts along a north German precipitation gradient, but growth reductions are recently compensated by faster growth due to late-winter warming

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In Review by Ecosystems

Abstract

More than half of the forest area of the North German Lowlands is stocked with Scots pine-dominated forests. Climate change suggests a declining suitability of Europe's temperate zone for conifer plantations, but only few studies have examined the growth dynamics of Scots pine in this region. We studied the radial growth patterns of Scots pine over the last 60 years at ten sites along a precipitation gradient (823–564 mm mean annual precipitation) from an oceanic to a sub-continental climate, analyzing the spatial and temporal variability of the climate sensitivity of growth in order to identify limits of the drought and heat tolerance of the species by means of linear mixed models. Inter-annual growth variation is mainly driven by sensitivity to late-winter temperatures (February, March) and summer drought and heat (June–August), with sensitivity increasing from the oceanic to the drier continental sites. Warmer late-winter periods apparently have stimulated growth during the last decades, while the sensitivity to summer-drought rose until 1995 to decrease thereafter. Until recently, the negative impact of increasingly warm summers on growth has been compensated by the positive effect of late-winter warming, resulting in stable (or increasing) growth trends. Our site comparison suggests an increasing drought and heat sensitivity of Scots pine growth and reduced

productivity in the northern German lowlands in the future, demanding for more cautious planning of pine plantations in the face of climate warming.

3.1 Introduction

Forests play a key role for the global carbon and water cycles and they harbor a large part the earth's terrestrial biodiversity (Millennium Ecosystem Assessment (Program) 2005; Hill and others 2019). The last two decades have seen a rapid increase in the reporting of large-scale tree vitality loss and forest dieback in many regions of the world, which were attributed to the direct or indirect impact of drought and heat stress due to climate warming (van Mantgem and others 2009; Allen and others 2010; Carnicer and others 2011). In the temperate forests of Central Europe, widespread dieback occurred especially after the severe hot droughts of 2003 and 2018/2019, which primarily hit drought-sensitive Norway spruce (*Picea abies* Karst.), but also other main timbers such as European beech (*Fagus sylvatica* L.), and more locally Scots pine (*Pinus sylvestris* L.), sessile oak (*Quercus petraea* (Matt.) Liebl.), and Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) (Bigler and others 2006; Braun and others 2020; Schuldt and others 2020; Obladen and others 2021). This left foresters with the challenge of selecting drought-hardier timber species in order to achieve the declared goals of 'climate-smart forestry', i.e. maintaining (or increasing) timber yield in a warming climate, increasing forest resistance and resilience to drought and heat, and to increase the contribution of the forest sector to the climate change mitigation goals (Bowditch and others 2020; Verkerk and others 2020). In Central Europe's forests, the natural broadleaf forest cover has been largely replaced by conifer plantations. In Germany, for example, 54 % of the current forest area is stocked by fast-growing conifers, such as Scots pine in the northern lowlands (Thünen-Institut, Dritte Bundeswaldinventur - Ergebnisdatenbank 2021), where pine forests would naturally cover only about 2.3 % (Förster and others 2021a).

Due to its unproblematic establishment, tolerance of infertile soils and fast growth, pine has been planted on more than 9 Mio ha in Germany, Poland and the Netherlands since about 250 years to meet the high demand for conifer wood (Hille and den Ouden 2004; Milnik 2007), often making it the economically most important timber species. Scots pine tolerates nutrient-poor and dry sites relatively well, (Schütt and Stimm 2006; Roloff 2008) as is demonstrated by its natural occurrence on top of sand dunes at the Baltic coast (Dicrano-Pinion communities) and on shallow south-exposed slopes in limestone mountains (Erico-Pinion communities; (Leuschner and Ellenberg 2017). Scots pine thrives under very different thermal and water balance conditions from the Mediterranean to the northern boreal zone and from the Atlantic coast to the Pacific coast (Caudullo and others 2017) partly as a consequence of drought-adjustment in the hydraulic system and enhanced stomatal control during water deficits (Poyatos and others 2008; Martínez-Vilalta and others 2009).

Across its wide distribution range, the limiting climate factors of Scots pine growth differ largely. As expected, in cold regions, low temperature is limiting the establishment and growth (Rickebusch and others 2007; Mathisen and Hofgaard 2011; Matías and Jump 2014). In accordance, in a comparison of five pine populations across Europe, autumn, winter, and spring temperatures were more important in the studied Central and Northern European populations, while growth was strongly limited by summer heat and drought at the drier southern sites (Matías and others 2017). That warmer winter and spring periods are currently promoting Scots pine growth through an extension of growing season length, has also been reported by other studies (Lebourgeois and others 2010; Harvey and others 2020). At the species' southern distribution limit in the northern Mediterranean region, low spring and summer precipitation remain the main factors limiting pine growth (Andreu and others 2007; Matías and Jump 2012; Sánchez-Salguero and others 2012). With this large spatial variation in tree growth-climate relationships, studies on the long-term growth dynamics of Scots pine in a climate change context must lead to contrasting results across Europe. In Central Europe, no distinct changes in long-term growth trends have mostly been found (Kint and others 2012; Bauwe and others 2013, 2015), while positive growth trends were reported in the North, e.g. in Lapland (Mielikäinen and Sennov 1996). In contrast, in drought-affected regions of southern and Central Europe, decreasing growth trends have been observed, often in association with increasing mortality rates (Bigler and others 2006; Giuggiola and others 2010; Rigling and others 2013; Etzold and others 2019; Archambeau and others 2020).

In the lowlands of north-east Germany, Bauwe and others (2013, 2015) found no climate change-induced turning point in the growth trends of Scots pine. This may be explained by the intermediate position of these stands in the transition zone between declining southern "rear-edge" (Martínez-Vilalta and others 2008; Reich and Oleksyn 2008; Giuggiola and others 2010; Matías and Jump 2014) and northern "leading-edge" populations (Juntunen and others 2002; Reich and Oleksyn 2008; Kullman 2014; Matías and Jump 2014). Despite the wide distribution of Scots pine in the lowlands of northern Germany and Poland, only few dendrochronological studies have been conducted in these pine populations so far (Bauwe and others 2013, 2015; Liang and others 2013; Stolz and others 2021), and it remains unclear under which environmental conditions Scots pine growth in this region may shift from a growth-stimulating effect of the warming to growth impairment due to drought and heat impacts. From the simplistic perspective of the species' climate envelope, Germany's forested area with its pronounced oceanic-to-continental climate gradient is expected to become more unfavorable for Scots pine growth in large parts with the expected 21st century warming (Kölling 2007), leaving the species' future uncertain.

Against the background of a marked increase in mean annual temperature in Germany since 1881 by about 1.6 °C (DWD 2020) and the diversity of pine growth–climate relationships observed across Europe, predicting future growth dynamics of pine in Northern Germany and Central Europe requires a more comprehensive assessment of recent growth dynamics in their regional variation across the lowland region, taking soil hydrology and stand structure also into account. A better understanding of regional variation in climate-growth relationships and long-term growth trends is also needed to assist foresters in their efforts to establish more climate-stable forests and chose appropriate tree species (Bowditch and others 2020; Verkerk and others 2020).

In this study, we investigated the radial growth dynamics of Scots pine along a climate gradient from the more oceanic western to the more continental eastern part of the North German Lowlands, thereby covering a longer climate gradient than in previous studies. Study aim was to examine the sensitivity of Scots pine radial growth to climatic and edaphic factors and to study climate change effects on growth during the last 60 years across this climate gradient in order to identify drought- and heat-induced limits of the species in northern Central Europe.

The following questions guided our research: (i) Does the climate sensitivity of Scots pine growth increase towards drier regions? (ii) Which climatic, edaphic and stand structural factors are influencing growth most in the past and at present? (iii) How do long-term growth trends respond to climate change and how does this response vary along the studied climate gradient?

3.2 Material and Methods

3.2.1 Study sites

The study took place in 10 Scots pine (*P. sylvestris* L.) stands in the North German Lowlands on Pleistocene sandy soils at elevations of 17 to 157 m a.s.l. All stands were managed 55- to 74-yr-old even-aged cohorts that have been thinned regularly in the past. The stands are located along a climate gradient from a cool-temperate oceanic climate near the North Sea coast in the west to a cool-temperate sub-continental climate in the east close to the Polish border. Along this west–east gradient, mean annual temperature varied between 9.0 and 9.7 °C, while mean annual precipitation decreased from 823 mm yr^{-1} to 564 mm yr^{-1} (Figure 2b). During the observation period (1960–2017), winter and summer temperatures have increased by more than 2 °C, resulting in a higher evaporative demand, while summer precipitation changed only little (Figure A1, Appendix) (Schönwiese and Janoschitz 2008; DWD 2020).

3.2.2 Tree-ring data

At each of the 10 sites, 10 sample plots were established in homogenous sections of the stand (see Diers and others (2021)). Per plot, one wood core was extracted at breast height (1.3 m) from each two dominant, vital trees, resulting 20 cores per site. Coring was conducted with a 5mm-incremnt corer (Haglöf, Längsele, Sweden) between December 2017 and April 2018 from either the western tree side or parallel to plot inclination to avoid the influence of tension and compression wood. The wood cores were glued onto wooden mounts, and a plain surface was cut on the samples with a microtome. For better contrast, the samples were colored with safranin and then powdered with chalk.

Annual ring width was measured with a moveable measuring table (Lintab 5, Rinntech, Heidelberg) employing TSAP-Win software of Rinntech (Rinn 2012) for cross-dating. At all sites, the each 20 tree-ring series had a similarity to each other of at least 65 % (Gleichläufigkeit, Eckstein and Bauch (1969)) and a t-value of 3.5 (Baillie and Pilcher 1973). The tree-ring series were detrended to obtain the dimensionless ring-width index (RWI) (function "detrend" in the dplR-package, Bunn and others (2021); R version 4.0.4) applying a smoothing spline function with a 50 % frequency cut-off in a 20-years moving window (Cook and Peters 1981). Each of the 20 standardized RWI-series of a forest stand were then averaged (Tukey´s bi-weight robust mean, Bunn and Korpela (2021)) to obtain mean chronologies for the 10 study sites (Figure 2b). We further calculated annual basal area increment (BAI) from the raw tree-ring series and the diameter at breast height of each tree (function BAI.out in the dplR package, Bunn and others (2021)).

3.2.3 Environmental variables

We obtained climate data (monthly temperature and precipitation) from the Climate Data Center (DWD Climate Data Center (CDC) 2019a, 2019b) of the German Weather Service (Deutscher Wetterdienst, Offenbach) for the period from 1959 to 2017 (R package "rdwd" v.1.4.0, Boessenkool (2021)). The Standardized Precipitation Evapotranspiration Index (SPEI) as an indicator for climatic aridity and the occurrence of drought periods was calculated with the R package "SPEI" v.1.7 (Beguería and Vicente-Serrano 2017).

Forest structure data were available for every plot and used in the analysis as site means. Variable employed in the analysis were the stand density index after Reineke (1933), the mean number of living and standing trees per hectare [n ha^{-1}], the diameter of mean basal area at breast height [cm], the timber volume of living and standing trees per hectare [m^3 ha^{-1}], the cumulative basal area of living and standing trees per hectare [m^2 ha^{-1}], stand age [years], and the time since last thinning operation [years].

Soil chemical data were collected in a soil profile dug in each sample plot (Diers and others 2021), which were averaged to obtain site means (n = 10 per site). Soil chemical variables include profile totals (0-60 cm of mineral soil, "ms") of the salt-exchangeable base cations (BC_{ms} [mol$_c$ m^{-2}]) potassium (K), calcium (Ca) and magnesium (Mg), soil organic carbon content (C_{ms} [Mg ha^{-1}]), total nitrogen content (N_{ms} [kg ha^{-1}]), plant-available phosphorus content (resin-exchangeable P, P_{resin}, [g m^{-2}]), and profile averages of base saturation (BS_{ms}, [%]), C:N ratio (CN_{ms}, [g g^{-1}]), pH(KCl) (pH_{ms}), and clay content (cl_{ms}, [%]). In addition, the total amounts of base cations (BC_{ol}, kg ha^{-1}), organic carbon (C_{ol}, [Mg ha^{-1}]), total nitrogen (N_{ol}, [kg ha^{-1}]), and total phosphorus (P_{total}, [kg ha^{-1}]) were determined for the organic layer ("ol", O horizon), as well as the base saturation (BS_{ol}, [%]), C:N ratio (CN_{ol}, [g g^{-1}]), and pH(KCl) (pH_{ol}) of this layer.

3.2.4 Statistical analysis

In order to analyze tree growth–climate relationships separately for each site, we correlated the RWI data with the annual time series of monthly climate variables (monthly averages from previous year's June to current-year September) ("dcc" function in the "treeclim" package of R v.2.0.5.1, Zang and Biondi 2015) and used Pearson's *r* to express the strength of relationships. To account for non-stationarity of climate–growth relationships (Wilmking and others 2020) during the observation period, we split this analysis into an earlier (1960–1988) and a later period (1989–2017) of 29 years each. According to this initial correlation analysis, we selected the major growth-limiting climate factors and investigated their temporally variable importance in a moving-window analysis over the entire 58-year observation period for each site ("dcc" function with a window size of 30 years and 1-year offset).

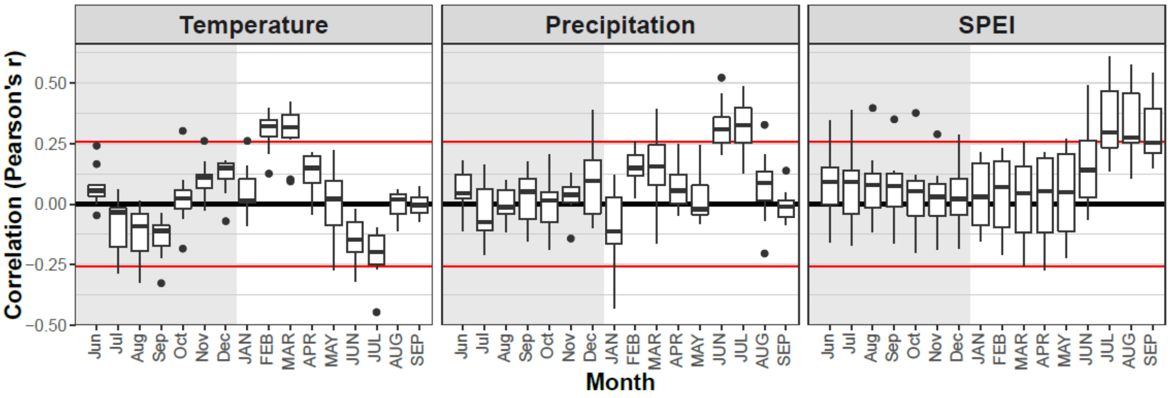
We applied linear regression analyses and linear mixed models to examine how climate, forest structure and local edaphic factors influence tree growth trends using the BAI series. We first set up a climate-only model in order to explain site-average (1960–2017) BAI by site averages (1960–2017) of the major growth-limiting climate factors as detected in the climate-sensitivity analysis. Then, we attempted to increase the performance of this initial model by iteratively adding and dropping factors related to forest structure and soil chemistry. We used Akaike's Information Criterion (AIC) to select the best model (Akaike 1974) and took care to exclude autocorrelation between the explanatory variables in the model (Figures A3 and A4, appendix). In order to account for temporal growth variability in addition to exploring average differences between sites, we further built stepwise a linear mixed model with "site" as a random intercept, as described above for the linear model, but included the 1960–2017 BAI and climate time series instead of averages of BAI and climate variables in the model. We calculated the explained variance of each environmental factor in the final models using the R-package "variancePartition" (v.1.20.0, Hoffman and Schadt (2016); Hoffmann (2020)), and assessed the quality of the linear mixed model by the conditional pseudo r^2 following (Nakagawa and Schielzeth 2013) using the R-package "MuMIn" (v.1.43.17, Bartoń (2020)). To account for tree-specific age trends in the mixed model, we standardized the BAI series to the typical age trend of Scots pine in the study region by dividing the measured value by the expected value from a regression of BAI on tree-ring age.

3.3 Results

3.3.1 Climate sensitivity of Scots pine growth

The climate sensitivity analysis showed that late-winter and early-spring temperatures were in the study region the most important climatic drivers of pine radial growth, when considering the whole 58-year observation period. Most sites revealed a significant positive relation of growth with March or February temperature (Figure 1a). The other most influential climatic factor was a water deficit in summer (Figure 1a). High temperatures in current-year June (and to a lesser degree in May) tended to affect growth negatively (not significant). We detected no consistent effects of previous-year weather conditions on growth. When comparing the earlier (1960-1988) and the later period (1989-2017), the largest differences in sensitivity were found for the temperature of the winter months, as the share of significant winter temperature correlations increased from the earlier (no significant correlation with February temperature at any site) to the later period (nine sites with a significant February temperature signal) (Figure 1b). In contrast, the growth sensitivity to mid-summer drought (negative correlation with July/August precipitation and SPEI) persisted across both observation periods; yet, the sensitivity to low early-summer (June) precipitation weakened from the earlier to the later period (Figure 1b and Figure A2 in the Appendix). Analyzing growth responses to aggregate measures of summer drought intensity (MSP, mean June–August precipitation total) reveals that summer drought has a strong negative effect on pine growth at nearly all studied sites, especially at the drier sites (Figure 2). An aggregate measure of late-winter/early-spring temperature (February–March temperature average) correlated positively with growth at all sites except for one (Figure 2b right panel), but without differences along the rainfall gradient in the study area (correlation of winter temperature sensitivity with MAP: $r^2 = 0.08$; data not shown).

a) 1960 – 2017



b) Earlier vs. later period

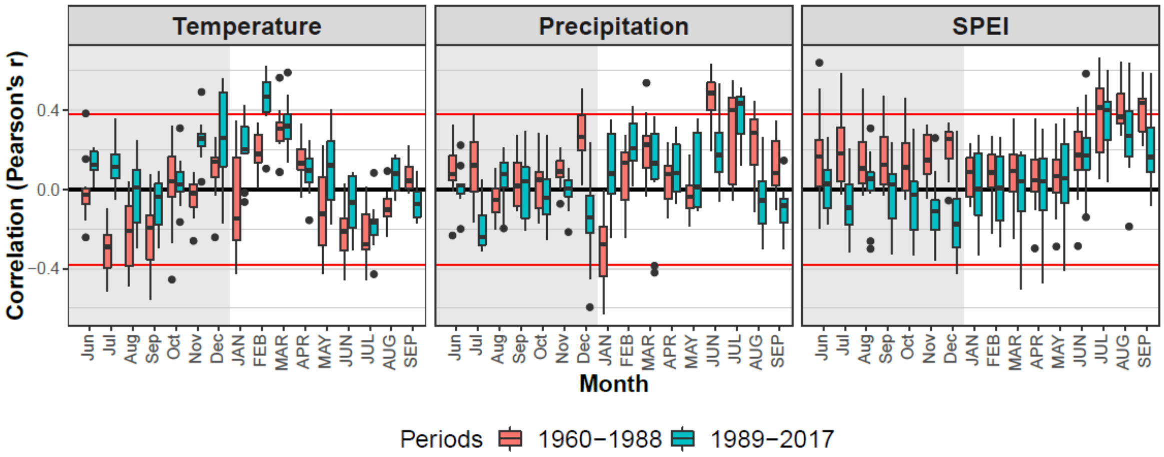


Figure 1. Correlation coefficients for the relationship of ring width (RWI) with monthly temperature, precipitation and standardized precipitation evapotranspiration index (SPEI) calculated separately for each of the 10 pine stands (each whisker-box represents 10 sites = 10 individual correlations) for January to September of the current year (in capitals) and June to December of the previous year (grey background) based on the data of the whole observation period (1960–2017) (a) and split into the periods 1960–1988 (red boxes) and 1989–2017 (blue boxes) for demonstrating temporal shifts in climate sensitivity of growth (b). The threshold for significant correlations is indicated by the red lines. For the full period (n = 58 years), $p < 0.05$ corresponds to $|r| > 0.26$ and for the split periods (n = 29 years), $p < 0.05$ corresponds to $|r| > 0.38$. The black dots mark outlying correlation coefficients of individual stands.

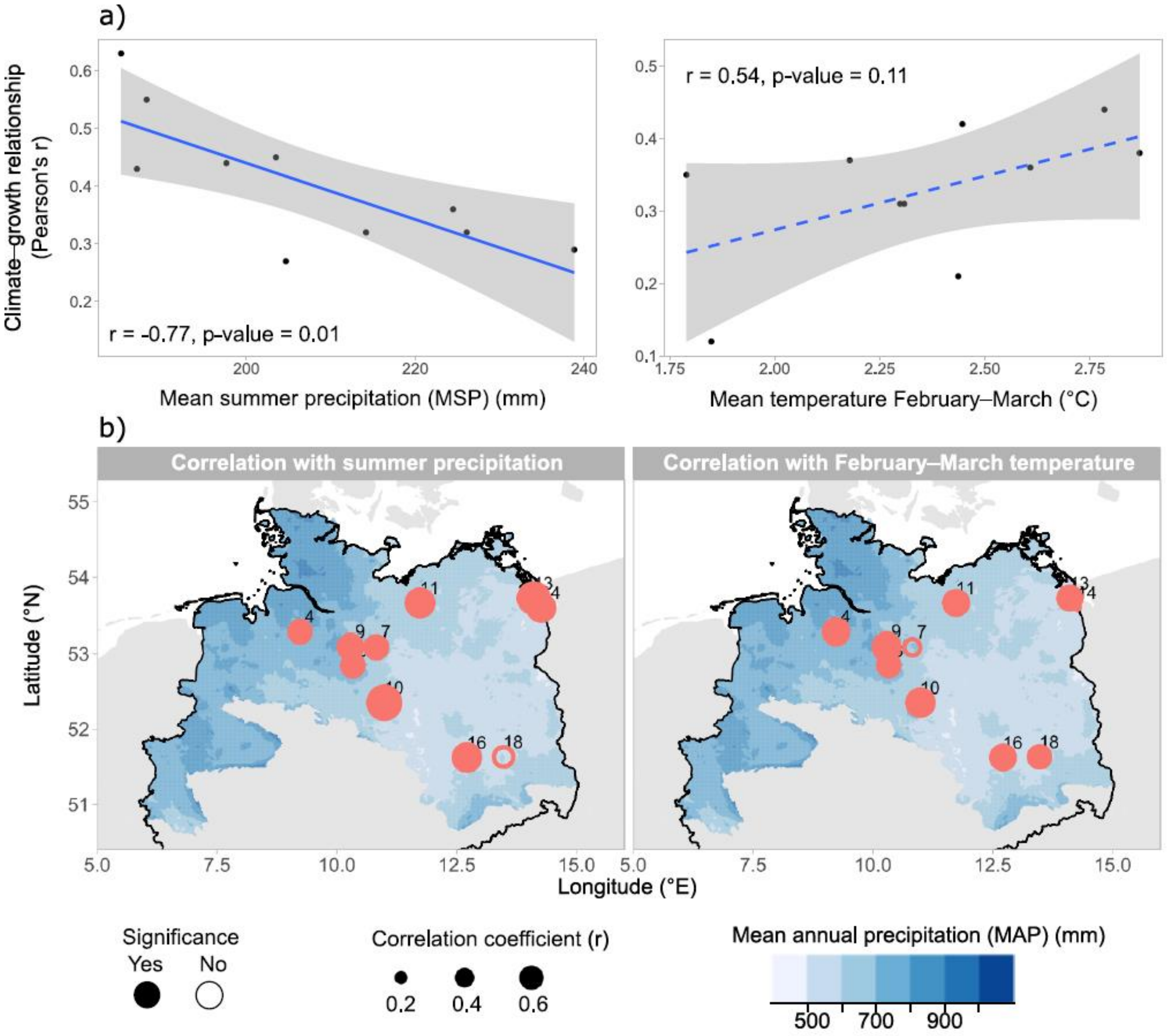


Figure 2. (a) Correlation strength of summer precipitation (June–August total) and growth and winter temperature (February–March) and growth, respectively, in the 10 pine stands in northern Germany regressed against the average climate of the sites. Numbers indicate the different forest sites. (b) Summer precipitation and winter temperature signals (tree growth–climate correlations) at the 10 pine forest sites across the climatic landscape of the North German Lowlands.

The moving window analysis shows that the growth-promoting influence of warm periods late in winter (especially February and the average of February–March) increased continuously during the last six decades at most of the ten sites (Figure 3). At one of the wetter sites, tree growth seemed to profit more from a warmer February than at the other sites, while one of the driest stands seemed not to profit at all over the 58-yar period. Further, the correlation strength of June precipitation decreased in the last two decades at most sites, while that of July precipitation increased (Figure 3). This shift is more pronounced at the wetter sites. On the other hand, the sites with lowest mean annual precipitation maintained their high precipitation sensitivity in June during the observation period (Figure 3). The growth sensitivity to SPEI of July, August or the summer months (June–August) was particularly high in the driest stands throughout the observation period with a slight decline in the last 20 years.

At the moistest sites, the SPEI of July and the summer period tended to increase over the observation period, but not the August SPEI (Figure 3).

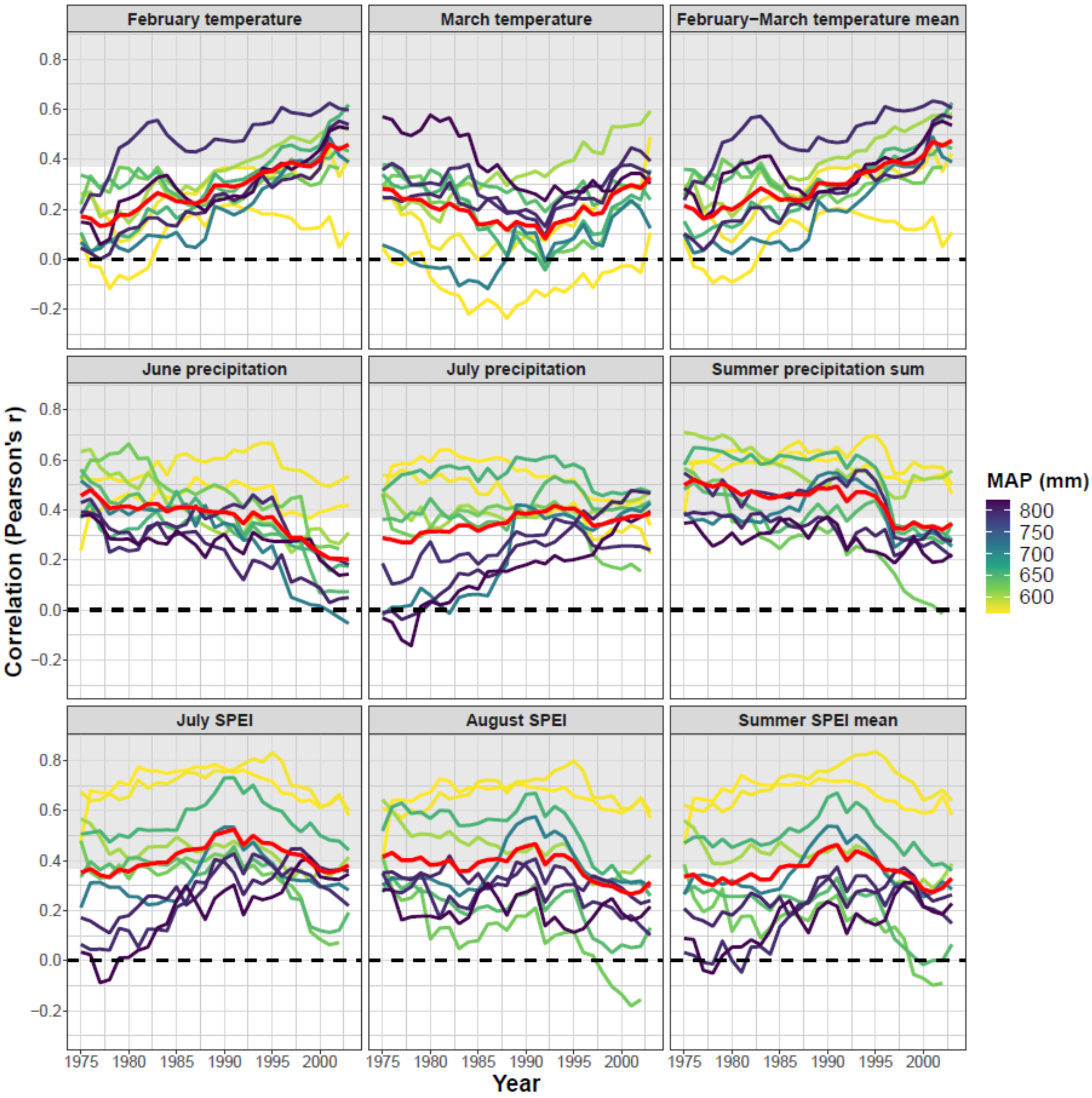


Figure 3. Mowing-window correlation analysis of climate variables with ring width (RWI) for the months with greatest influence and aggregated precipitation, Standardized Precipitation Evapotranspiration Index (SPEI) and temperature means/totals of the summer period (June–August). The x-axis shows the central year of the 30-year moving window. Each line represents one forest site (colored according to the mean annual precipitation (MAP)) and the mean correlation of all 10 sites (red). The grey background corresponds to $|r| > 0.37$ at $p < 0.05$ for $n = 30$ years.

3.3.2 Long-term growth trends

The annual BAI of all 10 forest sites reveals a strong increase over the 58 observation years (Figure 4a). The increase at sites with low mean annual precipitation (MAP) tended to be somewhat smaller than at sites with high MAP, but one dry site also showed a marked basal area growth increase over time (Figure 4a+b). Average annual BAI significantly increased from the earlier to the later period (Figure 4c).

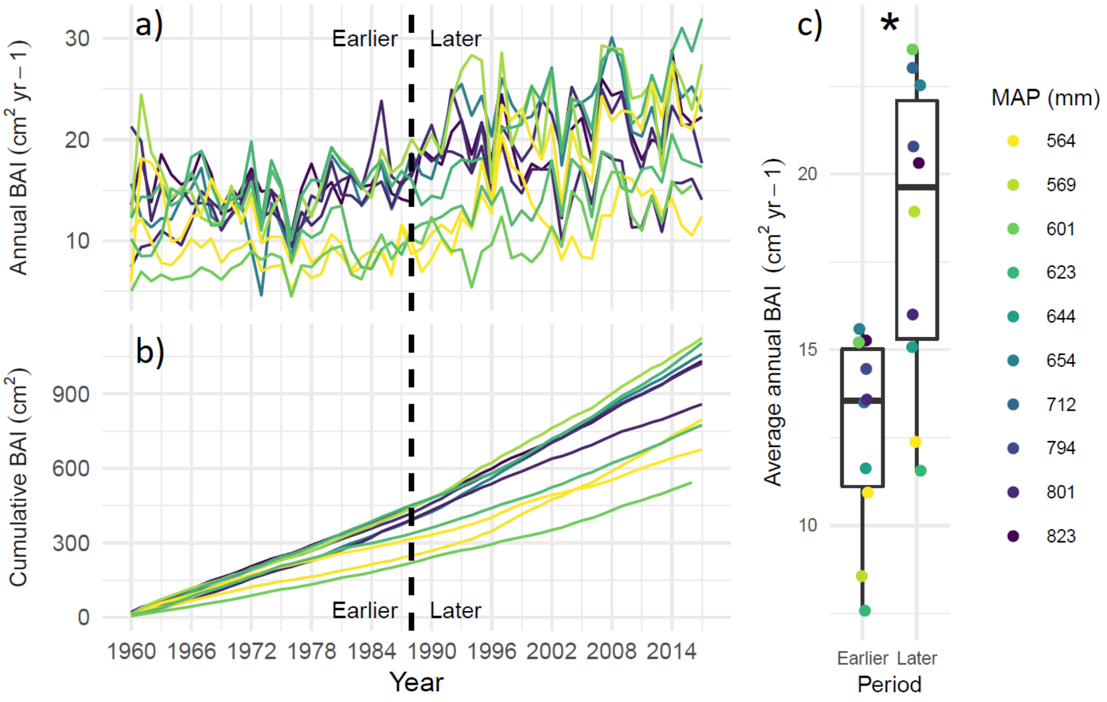


Figure 4. Mean basal area increment (BAI; average of 20 trees per stand) per year (a) and cumulative mean BAI over the 58-year period (b) for each forest site, and average BAI (c) of the earlier and later period summarized as boxplot with each forest site being represented as a dot. Lines and dots are colored according to the mean annual precipitation (MAP, 30-year mean) of each site. The difference between earlier and later period in (c) was tested for significance in a linear mixed effects model with site as random factor.

3.3.3 Environmental factors explaining basal area increment

The average summer temperature (MST, 1960–2017) of a site and thus thermal site differences were the most important factor explaining BAI differences among sites, with MST and BAI being negatively related to each other (Table 1, Table A1). As the second-most important variable, the average summer precipitation at a site influenced mean BAI also negatively, i.e. a higher precipitation level reduced average BAI. The third-most important variable, average February/March temperature, on the contrary, had a strong positive effect on growth. Unlike variable importance in the models, however, the comparison of slope coefficients shows that the positive effect of a 1 K warmer winter is larger than the negative effect of 1 K warmer summer across the sites (Table 1). In comparison to the large growth differences attributable to the different average climatic conditions at the sites, the influence of interannual climate fluctuation on annual growth variability was small. Interestingly, summer precipitation influences BAI positively (positive slope coefficients), when different summers are compared, but negatively (negative slope coefficients), when sites with different MAP are contrasted

(Table 1). Of the soil factors, only the mineral soil C/N ratio remained as a significant factor in the model (negative effect of C/N ratio and positive effect of soil N content). Forest structure did not have any influence on mean BAI at the different sites. In sum, most of the explained growth variance is due to differences in average climate conditions between sites, compared to the significant but small influence of the actual weather conditions in a given year.

Table 1. Model results of the influence of environmental variables on BAI.

	Variable	Slope coefficient (unit BAI/unit explanatory variable)	Degrees of freedom	Explained variance (%)	Marginal/ conditional r^2
	Site (Random Intercept)	-		4.8	0.50/0.54
Long-term average climate	Average summer precipitation	-16.5mm^2/mm	5	15.3	
	Average summer temperature	-661.4mm^2/K	5	16.5	
	Average temperature of Feb. and Mar.	797.3mm^2/K	5	13.3	
Climate fluctuation (weather)	Summer precipitation (June–August)	1.5mm^2/mm	567	1.5	
	Temperature (February–March)	39.1mm^2/K	567	1.3	
Soil	C/N-ratio of mineral soil (0–60 cm)	-26.4mm^2/(g/g)	5	2.2	
Residuals		-		45.1	

The marginal r^2 refers to the explained model variance of the fixed effects, the conditional r^2 to fixed and random effects.

3.4 Discussion

3.4.1 Higher drought sensitivity at the drier sites, but recently decreasing sensitivity

Our results show that the radial growth of Scots pine in northern Germany is more drought-sensitive at drier sites with a less humid sub-continental climate (Figure 2, Figure A2), which is in line with the findings of Stolz and others (2021) from a shorter rainfall gradient in the northeast German lowlands and with pan–European patterns that revealed greater drought sensitivity in southern dry regions than in wetter and cooler northern parts of Europe (Matías and Jump 2012; Henttonen and others 2014; Camarero and others 2021) Our results indicate that Scots pine growth in this northern Central European region is impacted by both winter warming and summer drying, and the trees thus seem to operate in the transition zone from temperature limitation in the north (Harvey and others 2020; Janecka and others 2020) to drought limitation more in the south (Bogino and others 2009; Matías and Jump 2012; Camarero and others 2021).

The observed shifts in climate sensitivity over time might be caused by both climatic changes and age-related effects. The pronounced warming since the 1980s was accompanied by a decrease in summer SPEI by about 0.4 units (DWD 2020). Thus, the evaporative demand and the climatic water deficit has increased especially in early summer at most sites, irrespective of summer rainfall change, with decreases in part of the region but increases in others (Banzragch et al., Unpublished Manuscript). These climate trends seem to contrast with the observed decreasing growth sensitivity to drought-related variables in the last two decades, proving non-stationarity of climate-growth relationships in *P. sylvestris*. Similar patterns have been observed for other temperate tree species as well (*Acer platantoides, Fraxinus excelsior, Tilia cordata*: Fuchs and others (2021), *Quercus petraea*: Dobrovolný and others (2016)) and could result from successful drought acclimation, but other explanations such as deeper root penetration with increasing age or growth release after larger thinning operations are also possible. In any case, the long-term BAI increase despite a summer SPEI decline may suggest that the pines in the study region have indeed successfully acclimated during the past decades. One biological reason for the recently stable or increasing BAI trends even in drier eastern Germany could be the response of the Scots pine fine root system to reduced precipitation levels. A fine root study in our pine stands suggests that pine is capable of acclimatization to drier summers by increasing the fine root biomass and surface area, while decreasing fine root tip numbers, to meet the higher evaporative demand, while the fine roots themselves seem to be more robust upon climate warming and soil drying (Förster and others 2021b). Hydraulic adjustment, such as reduced branch-level leaf area-to-sapwood area ratio to increase the hydraulic capacity per unit leaf area, could be another reason why drought-affected pine trees can maintain their growth for quite long time, as far as hydraulic safety margins are not crossed (Mencuccini and Bonosi 2001; Martínez-Vilalta and others 2009).

3.4.2 Increasing growth stimulation by late-winter/early-spring warming

Low winter temperatures have been identified as a growth-limiting factor in various studies on Scots pine in central and northern Europe, and the positive influence of climate warming on growth seems to increase towards colder environments (Reich and Oleksyn 2008; Lebourgeois and others 2010; Matías and others 2017; Harvey and others 2020). In general, winter-cold sensitivity is found in both evergreen conifers and broadleaf deciduous trees, which may relate to fine root damage by strong soil frost events in mid-winter (Pederson and others 2004; Weigel and others 2018 a, 2021), among other negative effects of cold. However, we found a greater influence of temperatures on the brink of winter to spring than during the mid-winter months with lowest temperatures. This likely rules out mid-winter frost damage as an explanation for smaller annual growth rings with lower winter temperatures. In our study region, temperature-induced ring width variation is more likely caused by the positive effect of a warmer spring. The onset of xylogenesis is thought to be a threshold response to critical spring temperatures (Liang and Camarero 2018), which now likely have been crossed in most studied pine forest sites in the course of climate warming since the 1980s. Hence, a positive relationship between late-winter temperature and growth has emerged and growing season length is extending, which seems to act as a major driver of stable or increasing annual growth rates in Scots pine in our region (Henttonen and others 2017; Babst and others 2019).

3.4.3 Growth trends and the role of regional climate

Long-term trends in basal area increment may provide valuable information on climate-driven vitality decreases (Jump and others 2006). One explanation of the continued rise in BAI of our pine stands is certainly the regular thinning of the stands, which has promoted the growth of the remaining trees in the stand. This indicates that the climatic changes experienced especially since the 1980s have in total not reduced productivity. In correspondence, Scots pine forests in neighboring Poland have increased their height growth by 29 % in the period 1900-2000, independent of age effects, suggesting more favorable climatic (and perhaps edaphic) conditions in recent time (Socha and others 2021). Even in several southern-marginal pine populations in Spain, growth rates have increased at least at the wetter sites in recent time (Martínez-Vilalta and others 2008). Our findings fit well into this picture that growth increases persist even at the driest sites in northern Germany despite recently increasing climatic aridity. Since stand structural variables do not explain the differences in average growth rates between sites in our BAI models across the precipitation gradient, it is likely that the observed growth increases are at least partly attributable to climatic drivers. Martínez-Vilalta and others (2008) suggested increased atmospheric CO_2 concentration as an explanation, but other factors, notably increasing drought exposure, are expected to cancel out this CO_2 fertilization effect in the long run (Peñuelas and others 2011). Atmospheric nitrogen deposition is a more likely factor that should have influenced Scots pine growth in northern Germany in the past decades, as foliar N concentrations have markedly increased (Sardans and others 2016; Wellbrock and Bolte 2019; Prietzel and others 2020), suggesting decades of growth stimulation. In correspondence, our models showed that smaller topsoil C:N ratios (indicating a faster soil N mineralization) enhance average radial growth at the different sites, albeit weakly compared to the influence of climate.

By addressing both inter-annual and spatial variation in growth rate, the chosen BAI modelling approach indicates that the largest portion of the explained BAI variance in the dataset is attributable to average climatic differences between the 10 sites, while annual climate fluctuations explain much less. The results indicate that it is primarily the gradient in precipitation and atmospheric evaporative demand, and to a lesser extent differences in edaphic conditions and the thermal regime, to which the trees are more or less adapted, that are determining the growth potential of Scots pine at a given site. Importantly, this finding urges considering the spatial differences in life history and the legacy of past influences of climate on tree growth, when predicting absolute tree growth rates (as approximated by BAI, Bauwe and others (2015)) in climate change scenarios (Kellomäki and others 2018).

It comes as a surprise that the climatic influence on tree growth is different when considering interannual variability in growth as compared to spatial (regional) growth variation. On the one hand, we found that Scots pine is summer drought-sensitive, because unusually dry years led to growth reductions compared to the norm (RWI data). On the other hand, our BAI models nevertheless predict relatively high absolute (BAI) growth rates at the drier sites, though at higher sensitivity to summer SPEI. Although our northeastern sites are relatively dry with <600 mm MAP, they seem to remain in all years except for extraordinary dry summers still above the threshold pine can tolerate (Kölling 2007). In the 2018/2019 drought, however, which probably was the severest drought in Central Europe since 2000 years (Büntgen and others 2021), various pine stands in the eastern German state of Brandenburg and elsewhere suffered dieback (Obladen and others 2021), and widespread infection of weakened pines by the fungal endophyte *Sphaeropsis sapinea* occurred (Rohde and others 2021). It is too early to draw conclusions on the resulting growth trends of the surviving pine trees in response to this millennial drought. Scots pine populations in Southern Europe and also in the Central Alps also have been found to suffer from decreasing growth trends (Giuggiola and others 2010; Matías and Jump 2014), and widespread dieback in response to severe droughts is recorded (Giuggiola and others 2010; Rigling and others 2013; Etzold and others 2019; Archambeau and others 2020), confirming the species' sensitivity to extreme water deficits.

Although the temperature differences across our study region are small (MAT varies from 9.0 to 9.6 °C), they appear to be large enough to have an impact on BAI. In fact, pine stands tended to be more productive at sites with a lower mean summer temperature. This finding may suggest that the potential of Scots pine to maintain its growth rates and to adapt to further summer warming and heat exposition may be limited. It is possible that summer heat is harming the Scots pine foliage directly (Way and Sage 2008; Gette and others 2020), but this has to be proven in physiological experiments. On the other hand, pine stands also tended to grow better under reduced precipitation levels, which seems to contradict the finding of growth stimulation by summer rainfall on the interannual scale. We assume that the generally higher cloudiness (and the slightly lower temperatures) of the sites with higher precipitation are responsible for this effect.

Compared to the negative influence of hot summer periods, the late winter/early spring warming was similarly important according to the explained variance in our model and it exerts an even stronger impact on radial growth as evidenced by the large model slope coefficients. This suggests that pine tree growth is today in many cases still all in all benefiting from recent climate warming (Harvey and others 2020; Stolz and others 2021). In accordance, the climate-driven growth models of Bauwe and others (2013, 2015) predict for north-east German Scots pine stands neither a strong increase nor a strong decrease in productivity with ongoing climate warming, as the positive effects of an extended growing season might be balanced by the negative effects of increased drought exposure. However, we call into question that the stimulating effect of late-winter warming will be large enough and persist in future to balance the negative effects of increasingly hot and dry summers on pine growth in northern Central Europe, given the higher growth sensitivity of the drier stands to summer precipitation and SPEI.

3.5 Conclusions

While foresters in Central Europe have valued Scots pine as an undemanding timber species, our growth records based on basal area increment evidence the species' sensitivity to hot and dry summers, especially in the more continental regions. Even though climate warming still has a positive effect on pine productivity in the region, the greater drought sensitivity of the drier stands of our sample together with the frequent dieback that happened after the extreme 2018/19 drought in this area indicate that pine vitality likely will decrease in future at sites with a negative climatic water balance in summer and low soil water storage capacity. Even though Scots pine is an economically important timber species in northern Germany and in Poland, the Netherlands and other Central European regions, silvicultural decision making, which is driven by the high demand for conifer wood of local and international markets, has to be more careful in future when planning large-scale pine plantations in this region. Moreover, the evapotranspiration of pine stands is relatively high in comparison to the locally native beech forests (Müller and Bolte 2009), and pine stands are thus usually exacerbating site water deficits and soil drying (Leuschner and others, Unpublished Manuscript). Possible alternatives are more drought-resistant native broadleaf trees such as *Acer platanoides, Quercus petraea* and *Tilia cordata*, which however requires adaptation of wood markets to more hardwood supply. Our results demonstrate large temporal and also spatial variation in climate-growth relationships of the same species, which has to be considered in tree vitality and growth projections in a warming and drying climate.

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Appendix

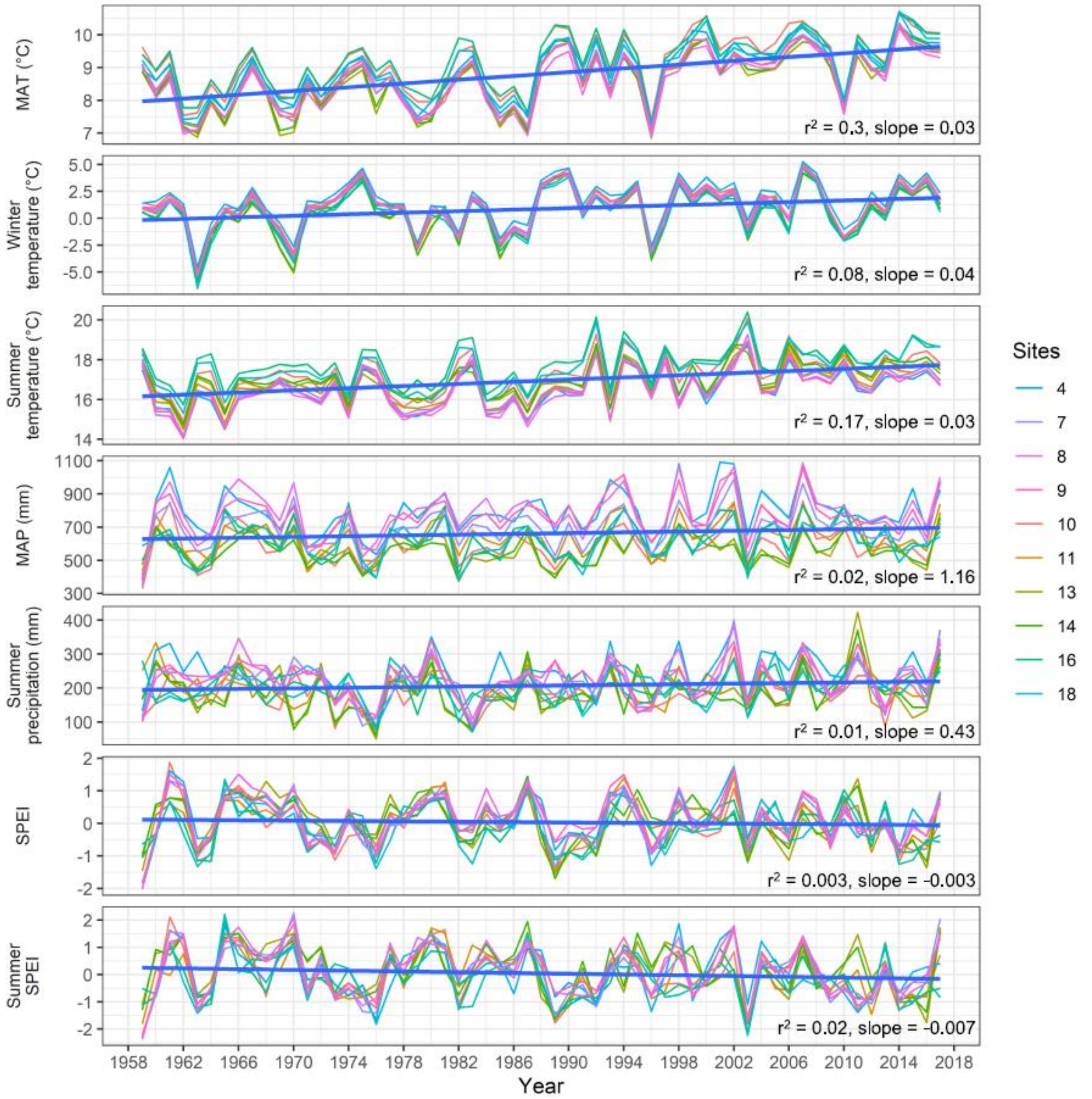

Figure A1. Temporal pattern of mean annual Temperature (MAT), mean winter and summer temperature, mean annual precipitation (MAP), mean summer precipitation and the 3-month Standardized Precipitation Evapotranspiration Index (SPEI) averaged for the whole year and for the summer at each site. Blue lines show the linear regression trend over time. The slope of the linear trend is in the units of °C/year (temperature), mm/year (precipitation), 1/year (SPEI). Data source (DWD Climate Data Center (CDC) 2019a, 2019b).

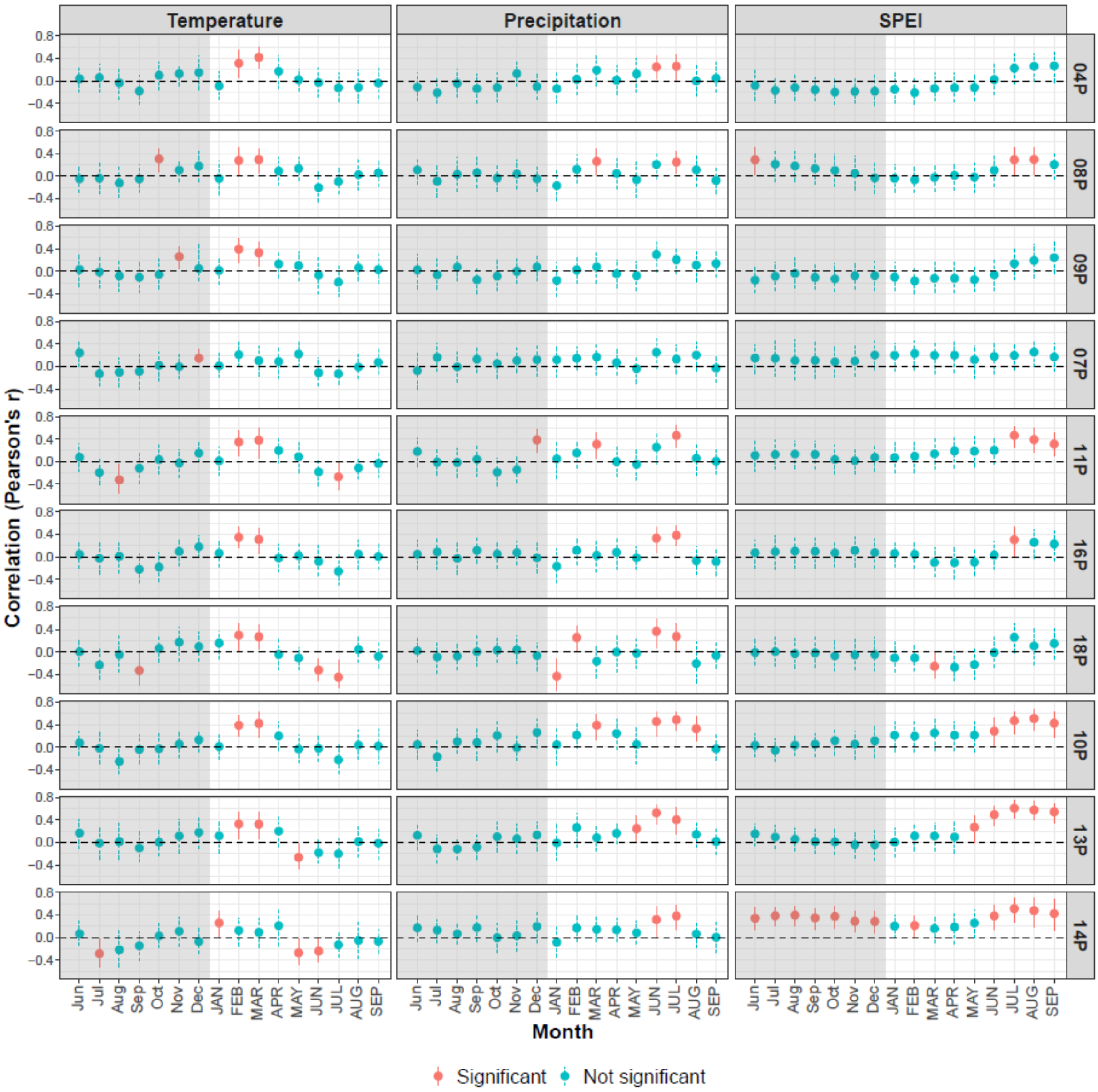

Figure A2. Correlation coefficients (Pearson´s r) per site and month for the relation between BAI and the climate factors temperature, precipitation and SPEI. Red dots indicate significant correlations ($p < 0.05$), which was assessed in a regular 1000-fold bootstrapping procedure according to (Efron and Tibshirani 1986) (“dcc” function, R package treeclim).

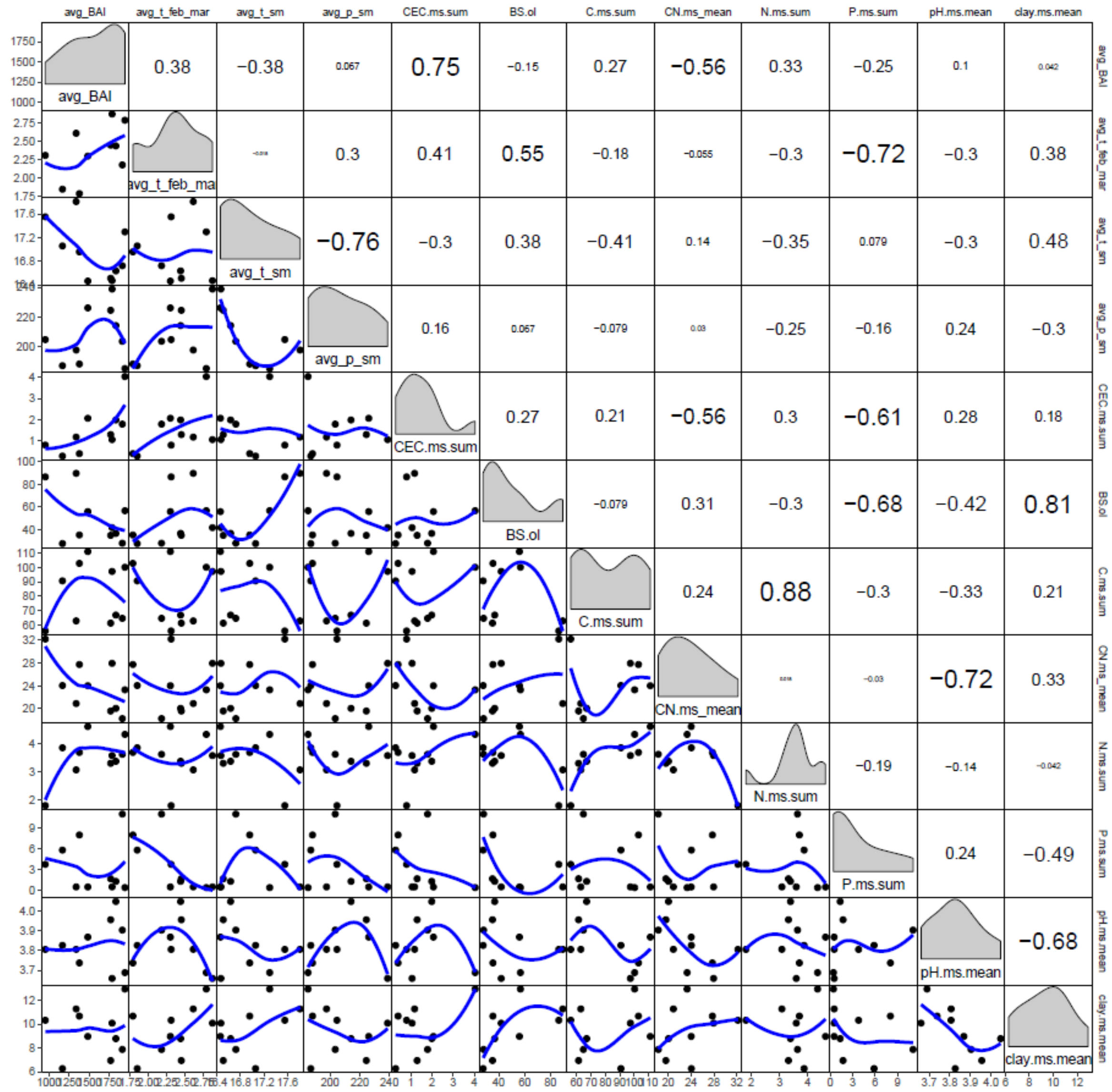

Figure A3. Spearman correlation matrix of average BAI (**avg_BAI**) with climate (**avg_t_feb_mar**: average temperature of February and March, **avg_t_sm**: average temperature of summer (June to August), **avg_p_sm**: average precipitation sum in summer (June to August)), and soil variables (**CEC.ms.sum**: exchangeable cation pool in the mineral soil up to 60 cm soil depth, **BS.ol**: base saturation of the organic layer, **C.ms.sum**: total organic carbon pool in the mineral soil up to 60 cm soil depth, **CN.ms_mean**: average CN-ratio of mineral soil, **N.ms.sum**: total nitrogen pool in the mineral soil up to 60 cm soil depth, **P.ms.sum**: exchangeable phosphorus pool in the mineral soil up to 60 cm soil depth, **pH.ms.mean**: average pH-value of the mineral soil, **clay.ms.mean**: average clay content of the mineral soil). The spline curve is calculated by using local polynomial regression fitting (loess) with a smoothing parameter (span) of 1.5.

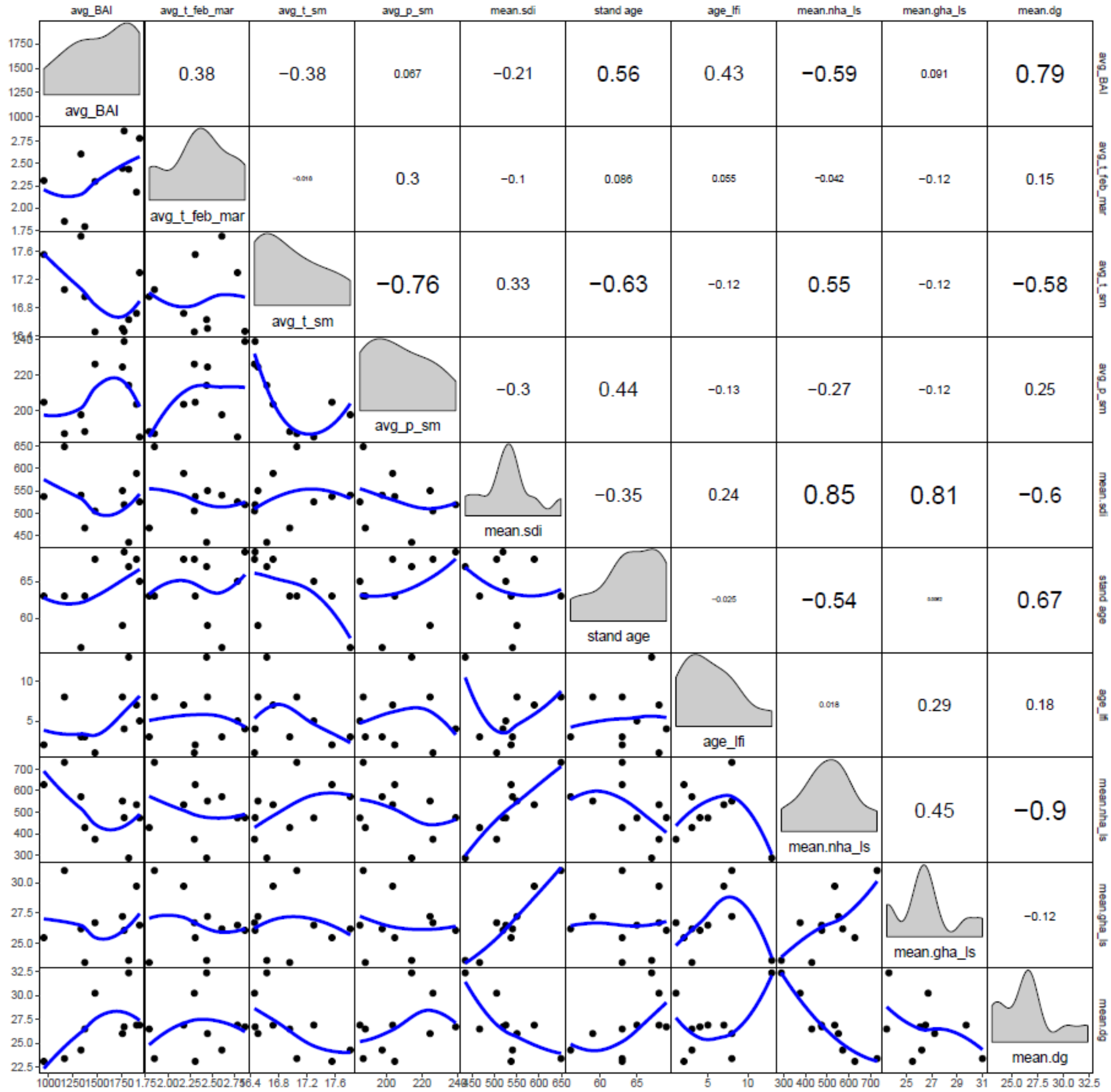

Figure A4. Spearman correlation matrix of average BAI (**avg_BAI**) with climate (**avg_t_feb_mar**: average temperature of February and March, **avg_t_sm**: average temperature of summer (June to August), **avg_p_sm**: average precipitation sum in summer (June to August)) and forest structure (**mean.sdi**: average stand density index after (Reineke 1933), **stand age**: forest age, **age_lfi**: years since last forest management intervention, **mean.nha_ls**: average number of living and standing trees per hectare, **mean.gha_ls**: average basal area of living and standing trees per hectare, **mean.dg**: average basal area of all trees per site) variables. The spline curve is calculated by using local polynomial regression fitting (loess) with a smoothing parameter (span) of 1.5.

Table A1. Model results on the influence of environmental variables on BAI in a comparison of sites

Variable	Effect (Coef)	F-value	p-value	Expl.Var.p.Var (%)
Avg_t_feb_mar	1005.87	32.3393	0.0047	24.18
Avg_t_sm	-674.07	40.8889	0.0030	30.58
Avg_p_sm	-12.70	40.1959	0.0031	30.06
CN.ms._mean	-21.35	9.8171	0.0350	7.37
Sum				92.19

Avg_t_feb_mar: average temperature of February and March, A**vg_t_sm**: average temperature of summer (June to August), A**vg_p_sm**: average precipitation sum in summer (June to August), **CN.ms_mean**: average CN-ratio of mineral soil

CHAPTER 4

Both climate sensitivity and growth trend of European beech decrease in the North German Lowlands, while Scots pine still thrives, despite growing sensitivity

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Published in Trees (2022)

Abstract

Climate warming exposes forests to increasing abiotic stress, demanding for difficult silvicultural decisions about the right choice of future timber species. Scots pine (*Pinus sylvestris*) and European beech (*Fagus sylvatica*) are major timber species in the north German lowlands which have suffered from recent hot droughts, thus raising concern about their suitability for future production forests in the region. We investigated the climate sensitivity of tree growth and long-term growth trends of 10 paired beech and pine forests along a precipitation gradient in the north German lowlands with the aim to compare the species' climate sensitivity and to search for species-specific climatic thresholds. In the majority of beech stands, basal area increment (BAI) has lost its positive trend since the 1980s or growth declined since then, while the BAI of pine has continually increased. Long-term change in June precipitation is in the study region a more important determinant of beech growth trends than the amount of MAP, while pine growth is largely dependent on the warmth of February/March. Yet, pine growth is also sensitive to dry mid summers, with sensitivity increasing toward low MAP. Climate sensitivity of growth has significantly declined since the 1980s in beech, while the dominant drought signal of June persisted in pine. We conclude that recent climate change is affecting radial growth of beech and pine differently with both species revealing signs of vulnerability to hot droughts, suggesting for the drier part of the study region the preference of more drought-tolerant hardwood timber species over beech and pine.

4.1 Introduction

Forests play a key role for climate regulation, the water cycle, and as habitats of a rich biodiversity (FAO and UNEP 2020). Moreover, global forests provide humans with an annual harvest of c. 4 billion m^3 roundwood, a highly valued resource (FAO 2021). The last four decades have seen rapid climate warming with an increase in the frequency and severity of extreme weather events (IPCC 2021). In parallel, the length of summer heat waves has doubled between 1880 and 2006 in western Europe (Della-Marta et al. 2007; Barriopedro et al. 2011). In many regions on earth, widespread reduction in tree vitality and increased mortality have been reported, which has been linked to the increasing aridification of climate in recent time (van Mantgem et al. 2009; Allen et al. 2010; Carnicer et al. 2011; Braun et al. 2020). Long-term decreases in summer precipitation have locally further increased the drought exposure of forests (Bat-Enerel et al. 2022).

Hot droughts like those of 2003 or 2018/2019 led in Central Europe to widespread dieback of many tree species, notably Norway spruce (*Picea abies*, Karst.), but also European beech (*Fagus sylvatica* L.), Scots pine (*Pinus sylvestris* L.), sessile oak (*Quercus petraea* (Mat.) Liebl.) and Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) (Bigler et al. 2006; Schuldt et al. 2020; Braun et al. 2020; Obladen et al. 2021). This confronts foresters with the difficult task to establish forest stands with higher drought and heat tolerance, while maintaining timber production to meet a growing wood demand. These efforts have led to the definition of "climate-smart forestry" as a prime goal of future forest policy (Bowditch et al. 2020; Verkerk et al. 2020).

In central Europe, much of the former natural broadleaf forest cover has been replaced by conifer plantations during the last centuries, mostly of Norway spruce and Scots pine (Leuschner and Ellenberg 2017). In Germany, fast-growing conifers stock nowadays on 54 % of the current forest area (Thünen-Institut 2022), whereas the natural cover of conifer forests would be less than 1 % (Suck et al. 2014). In the north German lowlands on Pleistocene substrates, where beech forests would naturally cover about 50 % of the forested area, planted Scots pine stands represent 53.2 % of the current forest area, while contributing with only about 2.3 % to the former natural forest cover. Pine plantations occupy between 6 and 75 % of the forest cover in the lowlands between the Dutch border in the west and river Oder in the east, while actual beech forest area was reduced to 2–22 % of forest cover (Bohn and Neuhäusl 2003; Förster et al. 2021a; Thünen-Institut 2022; Leuschner et al. 2022).

Both beech and pine are important timber species in Central Europe (Müller 2007; Leuschner 2020). Pine is a light-demanding pioneer tree species with marked tolerance of nutrient-poor and dry soils (Schütt and Stimm 2006; Roloff 2008). Distributed through Eurasia from the Atlantic in the West to north-eastern Russia, the species is predominantly a boreal taxon with some of its range extending till the northern Mediterranean region (Carlisle and Brown 1968).

Due to its broad range of tolerated climatic and edaphic conditions, Scots pine is the second-most widespread conifer and most widespread pine species of the world (Eckenwalder 2009). Its natural occurrence in Central Europe is on sand dunes (Dicrano-Pinion communities), shallow south-exposed limestone slopes (Erico-Pinion communities) and in swamp forests (e.g. Ledo-Pinetum community) (Leuschner and Ellenberg 2017).

European beech is the most widely distributed species of the genus *Fagus* (Fang and Lechowicz 2006). Its natural distribution is centered in the temperate zone of Europe and ranges from southern Italy to southern Norway and from northern Spain to eastern Romania (Bohn and Gollub 2007). Beech is a shade-tolerant late-successional species that is susceptible to drought and thus requires sufficient moisture in summer and mild temperatures in winter (Packham et al. 2012; Leuschner 2020).

In order to meet the challenges of climate change and weather extremes and to reach the declared goal of increasing the conservation status of forest biota (BMUB 2007; EU 2011), the forestry sector of various Central European countries including Germany has undertaken efforts to increase the cover of natural hardwoods at the expense of existing conifer plantations (Bauhus et al. 2021; Bundesministerium für Ernährung und Landwirtschaft (BMEL) 2021). The National Biodiversity Strategy (NBS) of Germany aims at expanding the cover of the natural forest vegetation, which would in large areas be *Fagus sylvatica* (Bohn and Neuhäusl 2003; Bauhus et al. 2021). Such a shift may also be necessary in the face of climate warming, as the main conifers planted in Central Europe are predominantly boreal species with an assumed adaptation to cooler climates (Hanewinkel et al. 2013; Schueler et al. 2014; Dyderski et al. 2018). Climate projections predict that Scots pine will lose 60% of its present range in Europe in future, depending on the climate scenario (Hanewinkel et al. 2013; van der Maaten et al. 2017; Thurm et al. 2018). However, beech likely will also meet its drought and heat limits in part of its Central European distribution range (Mellert et al. 2016; van der Maaten et al. 2017; Fischer 2019).

In fact, increasing evidence shows that beech is more drought sensitive than many other temperate broadleaf tree species, including the oaks, common ash, common hornbeam and small-leaved linden (Köcher et al. 2009; Rasztovits et al. 2014; Brinkmann et al. 2019; Leuschner 2020). Dendrochronological analyses demonstrate that the radial growth of beech responds negatively to low precipitation and high temperatures in previous year's or current summer (Scharnweber et al. 2011; Knutzen et al. 2017; Harvey et al. 2020). Long-term growth decline, elevated mortality and even replacement of beech by more drought-tolerant tree species in the course of climate warming were first observed at the species' southern distribution limit in south-western and south-eastern Europe (Jump et al. 2006; Piovesan et al. 2008; Lakatos and Molnár 2009). However, beech has also been found sensitive to drought and heat in its more northern and north-eastern distribution regions, where it also became increasingly sensitive to winter cold (Farahat and Linderholm 2018; Weigel et al. 2018). In Central Europe, various studies have recently reported negative growth trends from about the 1980s onwards, e.g. in northeastern France (Charru et al. 2010), Switzerland (Braun et al. 2017), Belgium (Aertsen et al. 2012) and south-western, central and northern Germany (Scharnweber et al. 2011; Zimmermann et al. 2015; Dulamsuren et al. 2017; Knutzen et al. 2017). Hacket-Pain et al. (2016) suggested that geographical variation in the climate sensitivity of beech may not be strong. However, recent studies indicate higher climate sensitivity and lower resistance to drought at sites in the center and north of the distribution range than in southern-edge populations (Cavin and Jump 2017; Muffler et al. 2020). It is assumed that this is related to local drought adaptation in the southern populations with their higher inter-population genetic diversity (Magri et al. 2006; Cavin and Jump 2017; Muffler et al. 2020). The severe drought episode of 2018/19 has resulted in canopy dieback and tree death in various Central European beech populations, which hints at the vulnerability of the species in the face of climate change (Braun et al. 2020; Schuldt et al. 2020; Obladen et al. 2021).

In contrast to beech, pine shows distinct differences in its climatic sensitivity within its large range. At the southern range edge, summer heat and drought are the principal growth-limiting factors, which are causing increased mortality with advancing warming in certain regions (Giuggiola et al. 2010; Matías et al. 2017; Archambeau et al. 2020). In the north, in contrast, the establishment and growth of pine is primarily limited by low temperatures (Rickebusch et al. 2007; Mathisen and Hofgaard 2011; Matías and Jump 2014). With the recent warming trend, increasing growth has been observed in these northern populations and is predicted to continue in future (Mielikäinen and Sennov 1996; Reich and Oleksyn 2008; Hickler et al. 2012; Socha et al. 2021). Central Europe can be considered as a transition zone (Bauwe et al. 2013, 2015) between the increasing growth trends in the north (Juntunen et al. 2002; Reich and Oleksyn 2008; Kullman 2014; Matías and Jump 2014) and prevailing negative growth trends in the south, where dieback is more frequent (Martínez-Vilalta et al. 2008; Reich and Oleksyn 2008; Giuggiola et al. 2010; Matías and Jump 2014). Evergreen Scots pine is further influenced by the temperature increase in winter, spring and autumn, which is hypothesized to lead to a marked extension of the growing season and growth stimulation (Lebourgeois et al. 2010; Harvey et al. 2020). In the north German lowlands, Diers et al. (submitted) and (Stolz et al. 2021) suggested that the positive effect of warmer winters currently may offset the negative effect of dry summers, resulting in an overall positive growth trend.

It is obvious that the climate sensitivity of growth of beech and pine differs not only between the species but also across the distribution ranges. Forestry needs more information on climate change effects on the growth and vitality of these species in order to define hydrometeorological and thermal thresholds to which beech and pine can be cultivated under the perspective of a warming and drying climate. A few dendrochronological analyses of beech and pine growth exist for the north German lowlands that address the species' climate sensitivity (Scharnweber et al. 2011; Bauwe et al. 2013; Knutzen et al. 2017), some of which include a direct species comparison. Mostly, these studied do not explicitly address the pronounced gradient in climate continentality that characterizes the north German lowlands, but rather focus on north-eastern Germany (Bauwe et al. 2015; Stolz et al. 2021) or the south Baltic coast in the transition between temperate and hemi-boreal climates (Harvey et al. 2020). We conducted a dendrochronological paired-plot study in nearby beech and Scots pine stands at ten sites that covered the climate continentality gradient from the oceanic North Sea coast to sub-continental eastern Germany near the Polish border (830 to 560 mm mean annual precipitation, MAP) in full length. The stands also include assumed dry-edge populations in the study region (Kölling 2007). By selecting beech and pine stands on similar soil, we attempted to minimize the influence of specific edaphic conditions on growth patterns and climate sensitivity. Our research was guided by the following three questions:

i) How do beech and pine differ in their climate sensitivity of growth on similar soil?

ii) How has climate sensitivity changed during the last decades in the two species?

iii) How do climate sensitivity and growth trends vary regionally and along the climate continentality gradient?

4.2 Material and Methods

4.2.1 Study sites

The study took place in ten pairs of European beech and Scots pine forests in the lowlands of northern Germany. The forest stands are located along a climate gradient from a cool-temperate oceanic climate close to Bremen in the west to a cool-temperate sub-continental climate in the east near river Oder at the Polish border (Figure 1). Temperature varied between 9.0 °C and 9.7 °C and mean annual precipitation (MAP) decreased from 823 mm yr^{-1} to 564 mm yr^{-1} along the west–east gradient (Figure 1, Table 1). Temperatures have increased in the 1960-2017 observation period in both winter and summer, while precipitation increased only in winter (DWD, 2020). All stands stock on acid, relatively nutrient-poor soils developed in glacial sandy to sandy-loamy deposits (except for beech stand no 10 on Triassic sandstone) (Diers et al., 2021). The selected 20 forests are mature stands with closed canopy (canopy closure >80 %) which had been managed in the past by regular thinning. The beech stands had an age of 95 to 195 years, the pine stands of 55 to 74 years, i.e. about 10-20 years before final harvest. In the beech stands, the last thinning operations took place 6 to 43 years ago, while the pine stands were last thinned roughly 2-14 years ago.

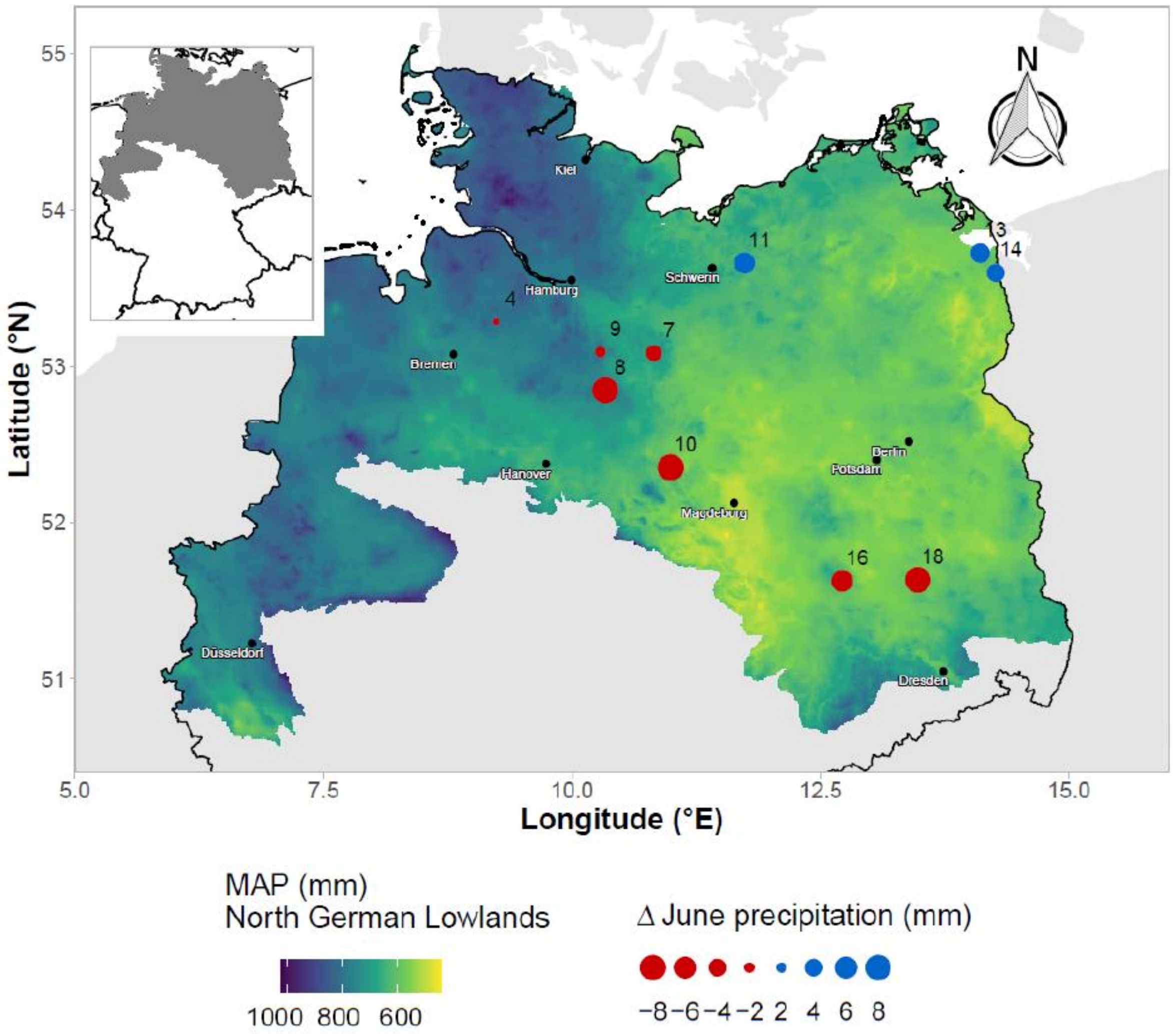

Figure 1. Location of the study sites in the North German Lowlands (inlet shows location of the lowlands within Germany). Area colored by mean annual precipitation (MAP, 1991-2020, (DWD Climate Data Center (CDC) 2022). Size and color of dots indicate change in June precipitation (ΔJune precipitation) between the earlier (1960-1988) and later (1989-2017) observation period.

4.2.2 Study design and wood core sampling

In each of the ten forest pairs, ten circular plots were established at random positions in the stands (100 circular plots for pine and 100 for beech in total). The plots were 35.68 m in diameter (size: 0.1 ha) and their edges were at least 30 m distant from each other. Edge effects were minimized by maintaining a distance of at least 20 m from forest paths and the forest edge.

Each two dominant trees with their crown in the upper canopy layer were selected in every plot and one wood core per tree was extracted at breast high (1.3 m) between December 2017 and April 2018 (i.e. two cores per plot, 20 cores per forest site, and in sum 200 trees sampled per species). Using an increment corer of 5 mm in diameter (Haglöf, Längsele, Sweden), the wood cores were extracted from the western side of a tree except for trees on slopes, which were sampled parallel to the slope inclination in order to avoid the influence of tension and compression wood. The wood cores were glued on wooden mounts; in case of pine cores, a plain surface was cut on the samples with a microtome, while the beech cores were sanded with sanding paper. Pine samples were colored with safranin, and both beech and pine samples were powdered with chalk in order to increase color contrasts.

Table 1. Study site characteristics. MAP = mean annual precipitation (30-year average, 1988–2017), MAT = mean annual temperature (30-year average, 1988–2017), Age = Stand age, BAI = average basal area increment of the 10 circular plots per site.

Site No.	Location	Species	Latitude (°N)	Longitude (°E)	Altitude (m)	MAP (mm)	MAT (°C)	Age (yr)	Stem density (n ha^{-1})	BAI (mm^2 yr^{-1})
4	Weichel	Beech	53.13	9.39	62	779	9.7	144	162	2203
		Pine	53.28	9.23	62	823	9.5	68	475	1778
7	Ewige Route	Beech	53.12	10.89	118	725	9.2	134	270	1624
		Pine	53.08	10.82	93	712	9.2	66	288	1848
8	Lüssberg	Beech	52.83	10.33	129	805	9.0	195	138	1864
		Pine	52.84	10.33	126	801	9.1	66-68	373	1494
9	Süsing	Beech	53.10	10.36	123	771	9.3	139	291	1761
		Pine	53.09	10.28	113	794	9.2	58-69	544	1791
10	Nievoldhagen	Beech	52.29	11.13	162	613	9.5	124	366	1961
		Pine	52.35	10.99	118	601	9.7	64	476	2071
11	Kaarzer Holz	Beech	53.67	11.73	75	657	9.2	112	192	2639
		Pine	53.66	11.73	71	654	9.2	60-74	525	1951
13	Eggesiner Forst	Beech	53.71	14.13	28	578	9.2	95-115	253	1540
		Pine	53.72	14.10	30	569	9.1	62	419	1373
14	Ueckermünder Heide	Beech	53.57	14.27	58	577	9.1	147-152	155	2453
		Pine	53.59	14.26	19	564	9.2	62	729	1202
16	Authausener Wald	Beech	51.64	12.74	146	653	9.6	166	423	3630
		Pine	51.62	12.71	140	644	9.7	55	574	1390
18	Weißhaus	Beech	51.63	13.45	140	617	9.6	146	125	2110
		Pine	51.63	13.47	145	623	9.5	62	614	971

4.2.3 Tree ring data

We used a moveable measuring table (Lintab 5, Rinntech, Heidelberg) to measure tree-ring widths of the cores. The samples from each forest were then cross-dated based on the coefficient of agreement ('Gleichläufigkeit', GLK; Eckstein and Bauch (1969)), the cross-dating index (CDI; Dobbertin and Grissino-Mayer (2004)), and Student's t-value (TVBP; Baillie and Pilcher (1973)), using TSAP-Win software (Rinntech, Heidelberg, Germany; Rinn 2012)). In most cases, the 20 tree-ring series per forest site had a GLK > 65%, a CDI > 2.0, and a TVBP > 3.5. In a few cases, we excluded 1–2 tree ring series due to low GLK. We used R software version 4.0.4 (R Core Team 2021) for the further analysis of the tree ring data using the packages "dplR" (v.1.7.2, Bunn et al. (2021)) and "treeclim" (v.2.0.5.1, Zang and Biondi (2015)).

The tree-ring series were detrended to the dimensionless ring-width index (RWI) using the function "detrend" (dplR, Bunn et al. (2021)), which applies a smoothing spline function with 20-year (pine) or 30-year (beech) moving windows with frequency cut-off at 50 % (Cook and Peters 1981) for eliminating the age trend or long-term effects of forest management. We built stand chronologies from the each (18–) 20 standardized RWI-series per forest stand for all ten forest sites (10 chronologies per species) with Tukey´s bi-weight robust mean (Bunn and Korpela 2021) using the function "chron" (dplR). Chronologies were considered reliable, when the expressed population signal (EPS) exceeded 0.85 (Wigley et al. 1984).

Long-term growth trends were analyzed based on time series of annual basal area increment (BAI) which was obtained from the raw tree-ring data with the equation

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

where r is the measured stem radius, t the given year and BAI_t the corresponding basal area increment. The BAI.out function (dplR, Bunn et al. (2021)) was used to analyze BAI trends for each tree calculated from the DBH data measured in the field and the ring-width series from younger to older rings. From the individual BAI series, we built a BAI chronology separately for each site.

4.2.4 Climate data

Monthly temperature and precipitation data for the period from 1960 to 2017 were extracted from the German Climate Data Center (CDC) of the German Weather Service (DWD, Deutscher Wetterdienst, Offenbach, (DWD Climate Data Center (CDC) 2019a, b)) using the R package "rdwd" v.1.4.0 (Boessenkool 2021). We computed the monthly values of the Standardized Precipitation Evaporation Index (SPEI across a 6-month period) for each site as an indicator of climatic drought intensity using the R package "SPEI" v.1.7 (Beguería and Vicente-Serrano 2017).

4.2.5 Climate–growth analysis and growth trend assessment

To explore the importance of selected climate variables for radial growth, we correlated the annual RWI data with the monthly climate data, considering monthly averages from previous year's June to current-year September, using the routine "dcc" (treeclim", v.2.0.5.1, Zang and Biondi (2015)). Pearson's r was used as a measure of the strength of the climate–growth relationship. We performed this analysis for each site and species separately. Furthermore, we split the analysis in two periods of equal length of 29 years (earlier period 1960-1988 with only slight temperature increase, later period 1989-2017 with more pronounced warming) to account for assumed non-stationarity of climate–growth relationships (Wilmking et al. 2020) during the observation period. Significance ($p < 0.05$) of the climate–growth relationships was assessed through a 1000-fold bootstrapping procedure (function dcc in treeclim) which allowed calculating confidence intervals of Pearson's r for significance testing (Efron and Tibshirani 1986).

Based on the BAI chronologies, we calculated growth trends by correlating BAI and calendar year for each species, forest site and observation period separately. The significance of trends was assessed with the Mann-Kendall trend test (R-package Kendall, McLeod (2015)). Subsequently, we analyzed correlations between the growth trend and long-term averages and changes of climate factors of the periods 1960–2017, 1960–1988 and 1989–2017 that were identified as important limiting factors in the climate–growth analysis (Fig. 2–5), notably summer precipitation, June precipitation, the difference in June precipitation between the two periods, summer SPEI, and the climatic water balance (CWB) of the summer.

4.3 Results

4.3.1 Climate sensitivity of growth in beech and pine

Radial growth of beech showed in the observation period 1960–2017 a significant positive impact of June precipitation in the current year at the four sites with lowest MAP, while this effect was visible only at two of the moister sites (no. 4 and 7; Fig. 2). A similar picture emerged also for pine, but this species' growth was also significantly stimulated by July precipitation especially at the drier sites. In contrast to pine, beech growth also profited from higher precipitation in previous year's July and June especially at the moister sites (and also at the two driest sites no. 13 and 14). Moreover, it appears that stands with a greater influence of previous year's precipitation are characterized by a smaller influence of current-year precipitation, as is observed at the moister sites. Carry-over effects of previous' summer precipitation on growth are lacking in pine.

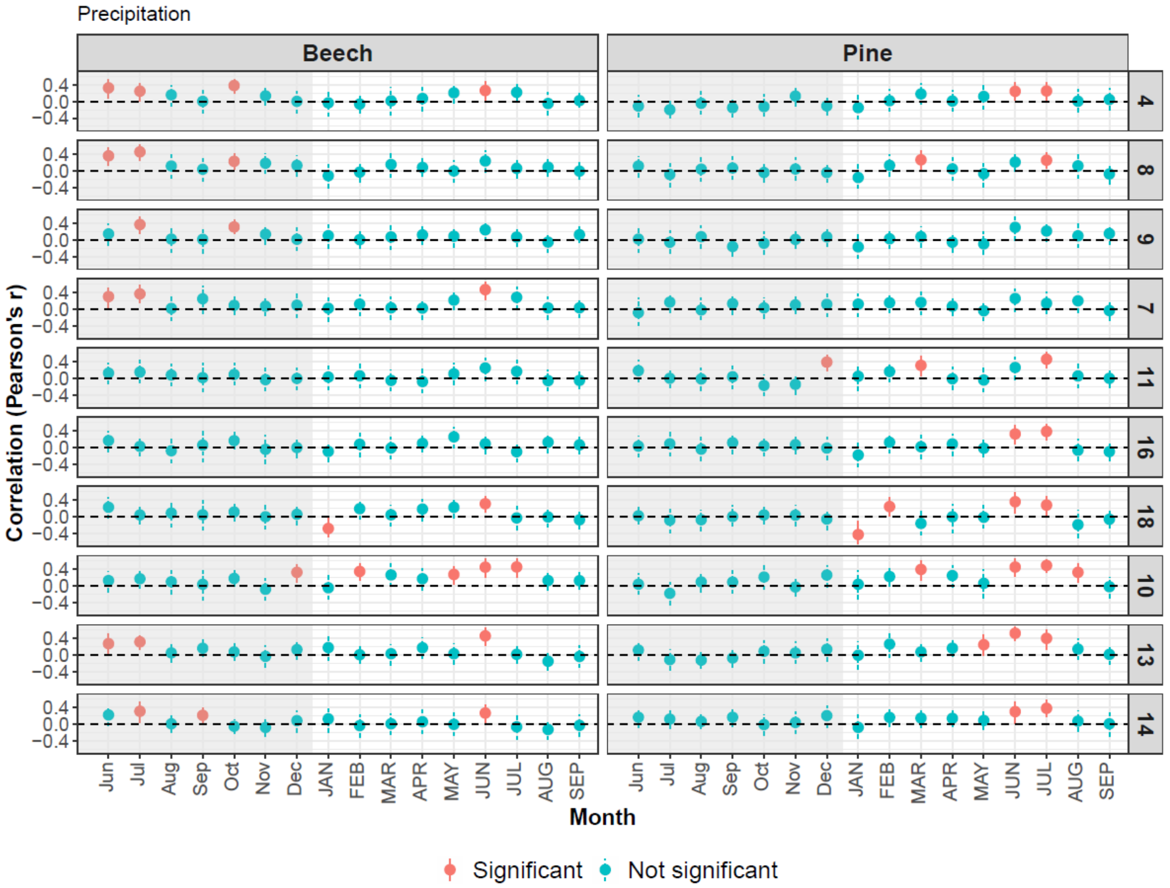

Figure 2. Correlation coefficients (Pearson´s r) for the 10 forest sites (ordered by decreasing MAP) and different months for the relation between RWI and precipitation in different months for the two species in the observation period 1960–2017. Significant ($p < 0.05$) r values according to a 1000-fold bootstrapping procedure are printed in red. Months of the previous year in small letters, months of the current year in capitals.

The temperature influence on growth differs markedly between the two species (Fig. 3). In beech, growth was negatively influenced by higher temperatures in previous year's July (and partly also August and September), or alternatively by a warmer current-year June. Winter temperature was of no relevance in our beech stands (except for a positive effect of December temperature in stand 11). Pine shows a very distinct growth stimulation by higher temperatures in February and March of the current year at most sites. Higher temperatures in current-year May and June (and July) had a negative effect on pine growth at some of the drier sites, while three pine stands were also negatively affected by higher temperatures in previous year's July, August and September (Fig. 3).

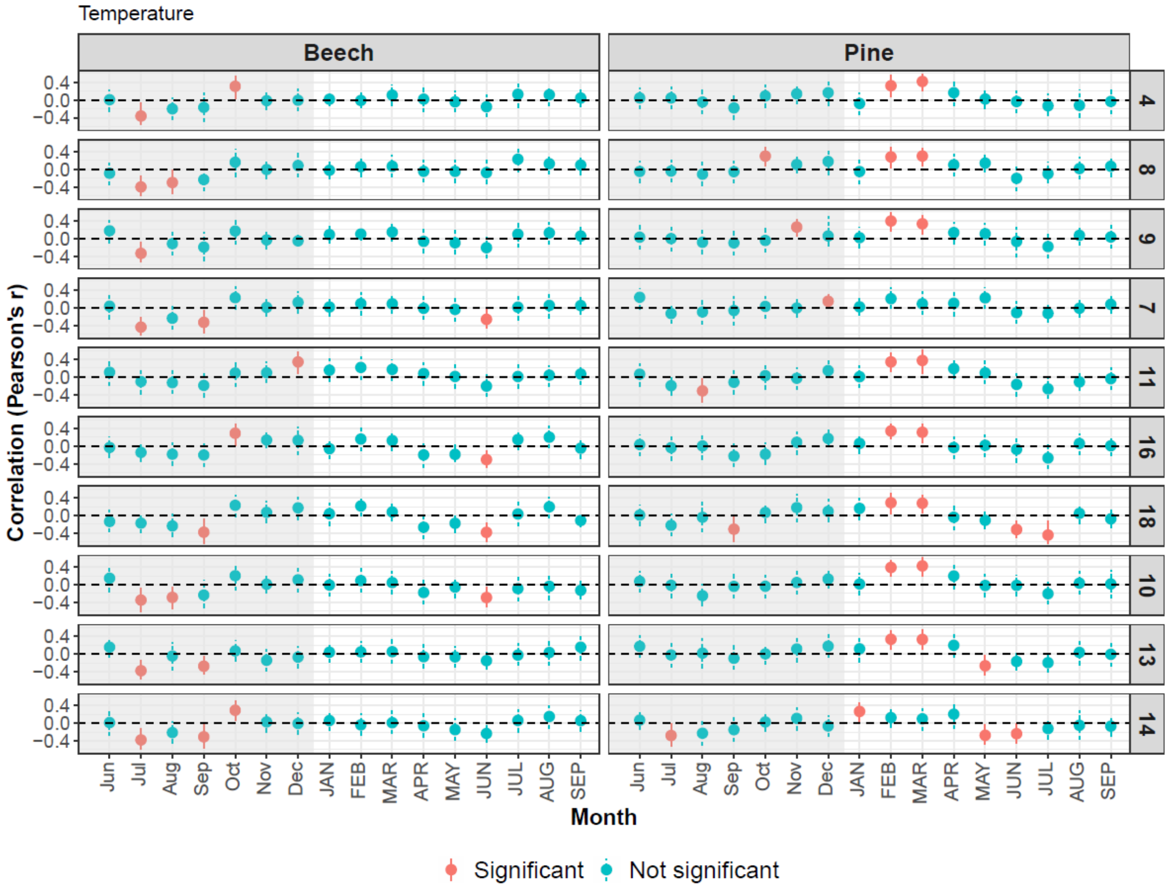

Figure 3. Correlation coefficients (Pearson´s r) for the 10 forest sites (ordered by decreasing MAP) and different months for the relation between RWI and temperature in different months for the two species in the observation period 1960–2017. Significant ($p < 0.05$) r values according to a 1000-fold bootstrapping procedure are printed in red. Months of the previous year in small letters, months of the current year in capitals.

A lower climatic drought exposition (higher SPEI) in previous year's late summer and autumn (July–December) had a significant positive influence on beech growth at the four moistest and two driest sites (Fig. 4). Elevated current-year SPEI values in spring and summer stimulated beech growth in five of the sites, mostly with lower MAP. Two sites (no. 11 and 16) showed no significant SPEI influence on beech growth at all. Most pine stands showed a positive influence of reduced drought exposition in current-year June to September on growth. The driest stand (no. 14) was also stimulated by a higher SPEI in previous year's June-December. Only one of the pine stands (no. 8) was also stimulated by a lower drought exposition of previous year's June. Pine stand no. 9 revealed no significant SPEI effect on growth in any month.

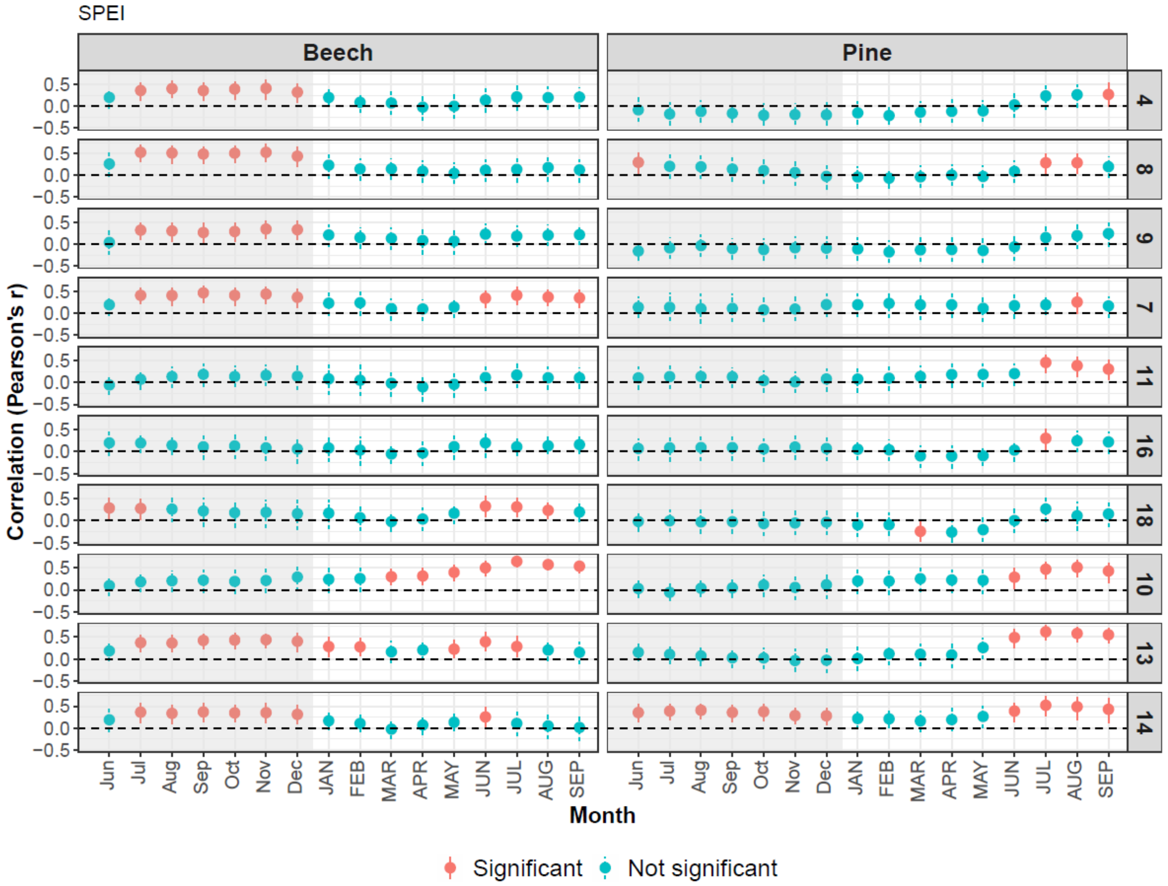

Figure 4. Correlation coefficients (Pearson´s r) for the 10 forest sites (ordered by decreasing MAP) and different months for the relation between RWI and the SPEI of different months for the two species in the observation period 1960–2017. Significant ($p < 0.05$) r values according to a 1000-fold bootstrapping procedure are printed in red. Months of the previous year in small letters, months of the current year in capitals.

4.3.2 Temporal change in the climate sensitivity of growth

Beech shows a distinct shift in climate sensitivity between the 1960-1988 and the 1989-2017 period. The significant climate–growth relationships depicted in Fig. 2 – 4 for the 1960-2017 period are in case of SPEI, temperature and precipitation more pronounced in the earlier period and diminish toward the second period (Fig. 5). The significant negative correlations of beech growth with June temperature (current year), and July and August temperature (previous year) as well as positive correlations with current-year June precipitation in the 1960-1988 period, have disappeared in the 1989-2017 period. The same is true for the significant positive correlation with previous year's SPEI from June-December, which has disappeared in the second period. In fact, beech growth shows no significant sensitivity to any of the three climate variables in the recent observation period any more (Fig. 5). The overall climate sensitivity of beech clearly has decreased compared to the earlier period. A moving-window analysis shows that especially at the sites, where June precipitation has increased (or remained stable) since the 1960-1988 period, growth sensitivity has decreased (decreasing r value), while it remained constant at sites with stable or increasing June precipitation (Fig. 8, Appendix). In pine, no general long-term trend toward decreasing climate sensitivity is visible. Yet, the positive effect of June precipitation and of lower drought exposition (SPEI) in August and September on growth has disappeared from 1960-1988 to 1989-2017, while the sensitivity to July precipitation and SPEI has remained (Fig. 5). The stimulating effect of higher February temperature has become significant only after 1988.

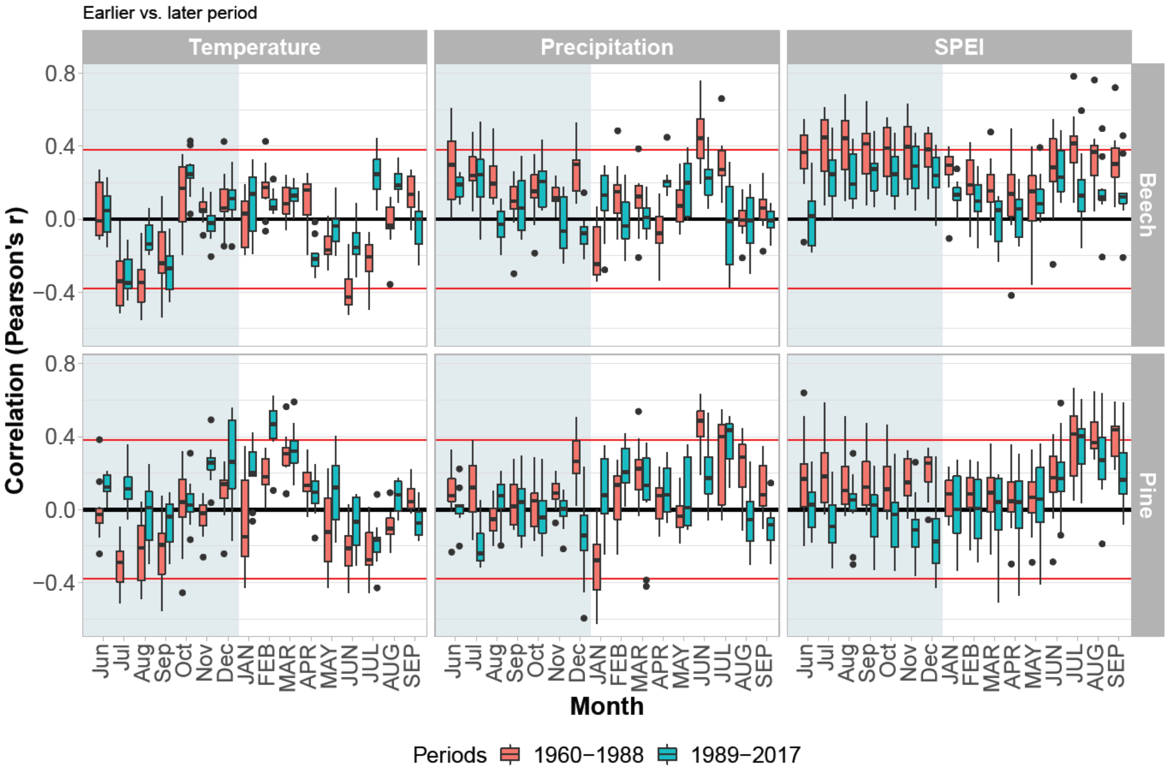

Figure 5. Spatio-temporal variation in correlation coefficients (Pearson's r) for the relationship of ring width (RWI) of beech and pine with monthly temperature, precipitation or the standardized precipitation evapotranspiration index (SPEI) for the periods 1960–1988 (red boxes) and 1989–2017 (blue boxes), demonstrating non-stationarity of climate–growth relationships since the 1960s. Each monthly box with whiskers represents the spatial variability of climate sensitivity, as it depicts the distribution of the 10 climate–growth correlations calculated separately for the 10 stands. The threshold for significant correlations is indicated by the red lines ($n = 29$ years), $p < 0.05$ corresponds to $|r| > 0.38$. The black dots mark outlying correlation coefficients of individual stands.

4.3.3 Long-term growth trends

The ten studied sites differ in their long-term trend of June precipitation, which has increased at three sites (no. 11, 13 and 14), but decreased at seven sites from the 1960-1988 to the 1989-2017 period (Fig. 6b). The long-term trend in June precipitation was not related to the long-term MAP of the sites (Fig. 6a). Interestingly, the two driest sites (13, 14) are characterized by an increase in June precipitation. The long-term BAI trend of beech was positive at the three sites with a June precipitation increase, but was negative at all sites with a June precipitation decrease (except for stand no. 7 with a slight growth increase despite decreasing June precipitation; Fig. 6c and Fig. 7 in the Appendix). A correlation analysis between the slope of the growth trend (Pearson's r) and the size of the difference in June precipitation between earlier and later period shows a significantly positive relation for beech (Tab. 2). Since the extent of June precipitation decline is unrelated to MAP (r = -0.44, p >0.05, Fig. 6 a & b), no relationship between site MAP and the extent of beech growth decline does exist (r = -0.46, n.s.).

For pine, this relation is not significant, as positive long-term growth trends appeared not only with increasing June precipitation, but also at several sites with a decreasing June precipitation (Fig. 6c). In fact, a negative growth trend was only recorded at pine site no. 8.

As the time since management had been abandoned varied in the beech stands between 6 and 43 years, we additionally examined the influence of this factor on growth trends. Accordingly, beech BAI was not influenced by the time since management abandonment (Tab. 3, Appendix).

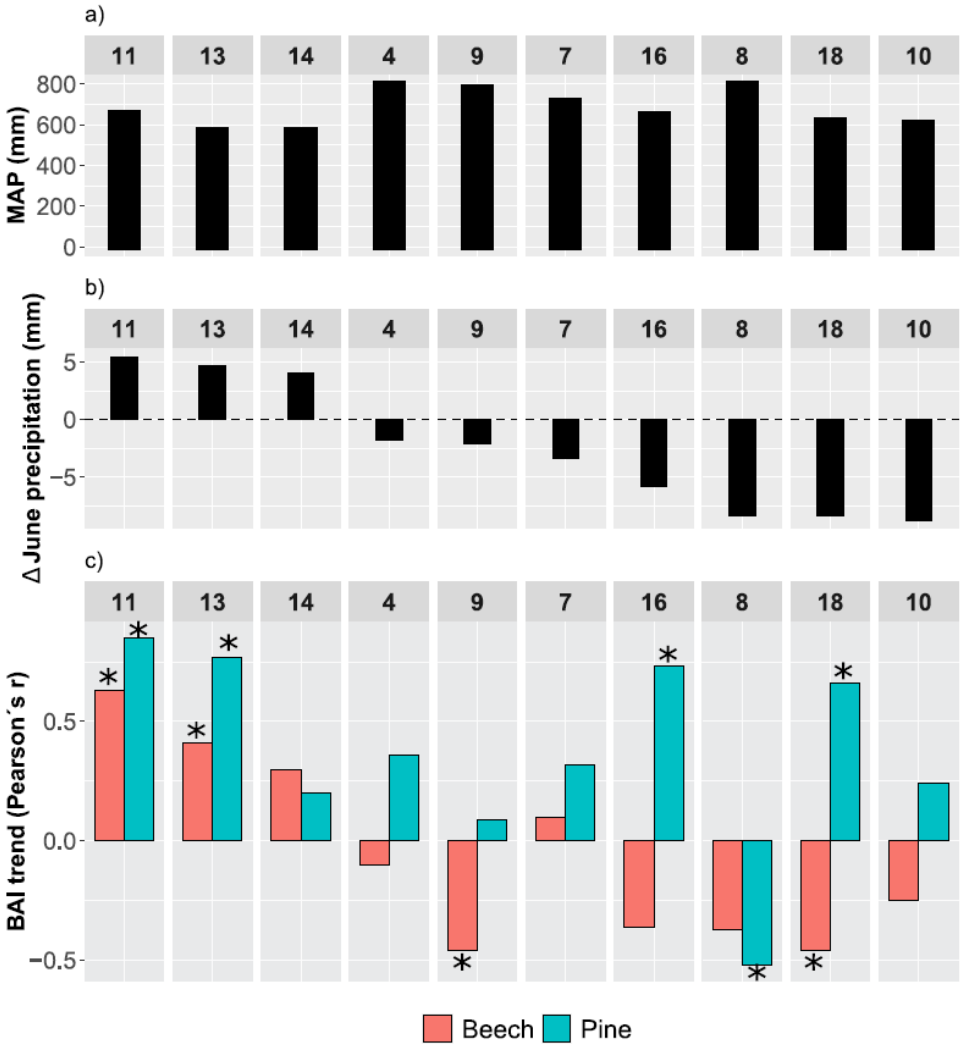

Figure 6. (a) Mean annual precipitation (1989-2017), (b) difference in June-precipitation (Δ-precipitation June) between the 1960-1988 and 1989-2017 period (negative values: decrease), and (c) growth trends in the period 1989-2017 of beech and pine in the 10 forests obtained by regressing the BAI chronology against year. Forest sites are ordered according to the Δ-precipitation June value (decreasing from left to right). Asterisks show significant BAI trends.

Table 2. Correlation coefficients (Pearson´s r) and p-values for the relation between the slope of the growth trends of pine and beech in the period 1989-2017 (‘change_BAI’) and the difference in June precipitation between the 1960-1988 and 1989-2017 periods.

Change_BAI~deltaPJune	Pearson´s r	p-value
Pine	0.39	0.259
Beech	0.86	0.001

4.4 Discussion

4.4.1 Differential climate sensitivity of beech and pine growth

Our comparison of beech and pine growth patterns at nearby sites in the north German lowlands reveals marked differences in the climate sensitivity of the two species, which are partly explained by the different tree functional types (deciduous broadleaf vs. evergreen conifer). Pine growth is in the studied ten stands primarily influenced by the weather conditions of the current year, both in late winter/early spring and in summer, while beech growth is to a larger degree dependent on the weather of the previous summer. This reflects the different carbohydrate allocation patterns of the two life strategies. According to Čufar et al. (2008), xylem growth in deciduous beech starts in Central Europe at the same time as leaf unfolding and usually peaks in June with about 35% of the current ring width being formed. Beech uses a large part of the stored starch reserves of previous year’s carbon gain to enfold its foliage in April/May and advance cambial growth in early summer. After cessation of ring formation, the beech foliage continues to photosynthesize for about 2–3 months, with the carbohydrates mainly transferred to storage organs, which explains the carry-over effect in terms of past weather influences on beech growth (Čufar et al. 2008). If the summer is hot and dry, the reserves cannot be built up sufficiently and less growth is possible in the following year. The development of cumulative soil water deficits in consecutive dry years as in 2018/19 may amplify the depletion of carbohydrate stores, thereby increasing the precipitation and SPEI effects on beech growth (Scharnweber et al. 2020). In addition, high temperatures and radiation intensities during summer droughts trigger masting in beech in the following year (Müller-Haubold et al. 2015; van der Maaten-Theunissen et al. 2016; Hacket-Pain et al. 2018), causing reduced radial growth and thus amplifying the effect of previous summer precipitation and SPEI on beech growth.

In contrast, evergreen pine produces new needles only from mid-summer onwards and thus is able to invest the C assimilated from late winter to early summer primarily into radial growth. This also explains the strong February/March temperature signal visible in pine radial growth. Higher fruit production in pine in certain years usually does not lead to reduced radial growth, and no change in the frequency of Scots pine fructification has been observed with climate warming in Europe so far (Martínez-Alonso et al. 2007; Nussbaumer et al. 2016). While low summer precipitation in the current year reduces the growth of both species, beech is sensitive mainly to low June precipitation, while pine is negatively impacted by low June and especially July rainfall. We speculate that cambial activity is impaired by water deficits in early/mid summer in both species, but pine frequently responds to dry spells later in summer by pre-senescent shedding of the oldest (2-year) needle generation, which may reduce C assimilation, while pre-senescent leaf browning and shedding occurs in beech only during exceptional droughts (Braun et al. 2020; Leuschner 2020). Pine showed a distinct influence of previous year's drought exposition on growth only at the driest study site (no. 14) with a MAP of only around 560 mm yr^{-1}. We speculate that, at this site, needle loss or fine root dieback in dry summers might have weakened the vitality of the trees with the consequence of reduced growth in the following year.

In addition to differing weather effects, pine and beech reveal contrasting recent growth trends in the study region. In pine, four of the stands showed a significant positive growth trend in the 1989-2017 period, and another five an insignificant growth increase or no change, while only one stand (site no. 8) revealed a significant recent growth decline. This indicates that increasing climatic aridity (and locally decreasing summer precipitation) in the course of climate warming has not yet negatively affected radial growth of pine at most of the studied sites. In beech, in contrast, decreasing growth trends were clearly related to climate aridification in summer at the sites, indicating a higher drought vulnerability than in pine.

Whether trees withstand drought at drier sites may partly depend on the species' capacity to acclimate to low site water availability. A fine root study at our sites found along the precipitation gradient increases in fine root biomass and total root surface area toward the drier pine stands, which points at a plastic root system response to water deficits in *Pinus* (Förster et al. 2021b). A similar response lacked in the beech stands (Förster et al. 2021b). Yet, an earlier study has reported increases in fine root biomass and productivity with decreasing MAP in other North German beech forests (Hertel et al. 2013). Contrary to expectation, evidence for deeper rooting at drier sites is scarce for mature beech stands (Meier et al. 2018). Moreover, beech has been found to increase average leaf size and stand leaf area from moister to drier sites along precipitation transects in northern and central Germany (Meier and Leuschner 2008; Weithmann et al. 2021), which we interpret as an additional weak point in the drought response strategy of beech that could explain the apparently higher drought sensitivity.

The marked positive effect of higher February/March temperatures on pine radial growth suggests that the growth-depressing effect of summer drought is still compensated by the positive effect of late-winter and early-spring warming (Stolz et al. 2021). In addition, Scots pine has been found to clearly profit from the extended growing season, which may cancel out assumed carbon gain losses due to water deficits and high temperatures in summer (Martinez del Castillo et al. 2018). Beech, in contrast, has profited from the recent warming through growing season extension less than other broadleaf species including the oaks (Menzel et al. 2003; Vitasse et al. 2009). Despite a so far less consistent drought signal in pine growth in comparison to beech, the significant current-year precipitation and SPEI sensitivity of pine growth and its increase toward dry sites indicate that advancing climate warming and aridification will have an increasingly negative influence on this species in the future as well.

4.4.2 Recent decline in the climate sensitivity of growth in beech

We found a marked change in the climate sensitivity of growth between the 1960-1988 and the 1989-2017 observation periods in both species. While pine exhibited an increase in the winter temperature-sensitivity of growth, as it was also observed by Stolz et al. (2021) in our study region, the growth sensitivity of beech to summer precipitation, temperature and drought (SPEI) declined over the last three decades with the consequence that none of the tested climate variables exerted a significant influence on beech growth in the recent observation period anymore. The latter finding was unexpected, as it contrasts with results reported from dendrochronological studies on beech and other tree species in central to northern Europe (Scharnweber et al. 2011; Kint et al. 2012; Harvey et al. 2020; Stolz et al. 2021), even though declining sensitivity of beech growth to summer drought has been noticed previously at some sites in Europe (Hacket-Pain and Friend 2017; Muffler et al. 2020; Weigel et al. 2022).

Our results also do not fit to the findings of van der Maaten-Theunissen et al. (2016) who reported for beech a shift in drought sensitivity from current-year to previous-year weather influences, as climate sensitivity of beech growth decreased in our data in the recent year as well. These authors explained the observed shift in drought sensitivity toward the previous year by the marked temperature increase in the second half of the 20th century, which increases the atmospheric evaporative demand and would render the water status of the previous year and soil water recharge in winter more important (van der Maaten-Theunissen et al. 2016; Scharnweber et al. 2020).

A decrease in climate sensitivity of beech growth since about 1990 was also observed by Hacket-Pain and Friend (2017) at the southern distribution range of the species, where growth rate is increasing despite a relatively warm and dry climate and a warming trend. The authors explain the unexpected drought resistance of beech with successful adaptation to the local climatic conditions. Comparable observations were made by Fuchs et al. (2021) who report a decreasing growth sensitivity in recent decades in several temperate broadleaf tree species in a dry region in Central Germany, which was accompanied by a constant or positive growth trend. The authors also assume successful acclimation or adaption to increasing drought in these species in recent time (Fuchs et al. 2021).

Our results deviate from these findings in that the sensitivity decrease was accompanied by stable or declining growth rates in beech. A possible explanation may be provided by the “sensitivity loss” phenomenon, i.e. non-stationarity in the climate–growth relationship, which was first observed in northern forests since the mid 20th century and has now been reported from various regions around the globe (Wilmking et al. 2020). We speculate that the beech trees of our study coped fairly well with the drought regime prevailing in the 1960s, 70s and 80s, even though being sensitive to summer drought and heat, which resulted in positive growth trends in that time. With increasing warming and climate aridification especially since the 1980s, the BAI of beech has ceased to increase or even declined since then in part of the study region, resulting in smaller tree rings which weakens the climate signal. Particularly influential is a decrease in June precipitation due to its large influence on radial growth in beech (Weigel et al. 2022). In fact, regions with a decadal decrease in June precipitation show the greatest decrease in beech radial growth and also in growth sensitivity to climate since the 1960-1988 observation period. This result differs from the findings of Stolz et al. (2021) who report an increasing growth sensitivity to drought in beech in the last decades in part of the north German lowlands. We assume that this discrepancy to our results is partly explained by the considerable regional variability in climate and also climate trends in the lowlands (Bat-Enerel et al. 2022), with the north-western coastal region experiencing a recent humidification of climate and positive growth trends in beech, while the climate became more arid further inland. Moreover, June precipitation has decreased in parts of the central and south-eastern lowlands with negative effects on beech growth (see Fig. 1), while precipitation increased elsewhere. This could explain increases and decreases in climate sensitivity of growth in neighboring regions.

4.4.3 Possible influences of tree age and size, and forest management

An alternative explanation of the apparently greater summer drought sensitivity of beech than pine growth and the weakening of the drought signal in beech growth over time could be the ageing of trees between the earlier and later observation period. Since the studied pine trees were on average about 78 years younger than the beech trees, tree size and age differences between beech and pine might have enhanced the species differences in climate-sensitivity of growth. As regular thinning is usually promoting the radial growth of the remaining trees, the more recent occurrence of stand thinning in the pine forests as compared to the beech forests could be one explanation for the prevalence of positive recent growth trends in this species, compared to beech. Moreover, the beeches were on average also larger than the pines in our study. Taller trees have frequently been found to be more sensitive to climatic signals than smaller ones due to greater canopy exposure to the atmosphere (Mérian and Lebourgeois 2011; Zang et al. 2014; Hacket-Pain et al. 2016). Yet, a recent leveling-off or decline in radial growth has been observed in parts of the study region also in beech stands with more recent thinning (Knutzen et al. 2017). In addition, canopy exposure was not different between the cored beeches and pines, as all trees were dominant in the upper canopy layer. This makes it likely that the growth trends revealed in our study are caused by a greater climate change impact on beech than on pine growth.

While tree ontogeny can indeed modulate climate sensitivity (Carrer and Urbinati 2004; Gallardo et al. 2022), the tree age effect on climate sensitivity seems to vary with species and environment, being greater either in older or younger trees (Pompa-García and Hadad 2016; Jiao et al. 2017; Peng et al. 2018; Sanchez-Salguero et al. 2018). Instead of age, Trouillier et al. (2019) suggested that climate sensitivity is rather affected by the tree size change throughout a tree's lifespan, which is increasingly acknowledged in tree-ring studies that address the effects of tree ontogeny (Bernal-Escobar et al. 2022; Martinez del Castillo et al. 2022). As xylem vessels usually widen in the stem xylem with increasing stem diameter in order to compensate for increasing flow resistances in the xylem path with height growth, higher drought sensitivity in older, taller trees could result from larger vessels and increased xylem vulnerability to cavitation (Anfodillo et al. 2013). An increase in climate sensitivity with age was indeed demonstrated for beech growth by Latte et al. (2015). Mérian and Lebourgeois (2011) thus concluded that shade-tolerant tree species, such as beech, are more sensitive to summer drought at larger than smaller size when age is similar, likely due to larger vessel diameters in young annual rings and the exposure of a larger crown to the atmosphere. This seems not to be valid for Scots pine as a shade-intolerant tree species, where no clear differences in drought sensitivity were found between size (diameter) classes (Mérian and Lebourgeois 2011). Yet, the temperature sensitivity of pine radial growth has been found to decrease with cambial age (Konter et al. 2016). These species-specific patterns offer no explanation for the observed sensitivity decline over time in beech, but it would suggest that the higher climate sensitivity of beech growth compared to pine is not caused by the higher age of the studied beeches.

Recent changes in forest management might also be considered as explanation for the recently decreasing sensitivity of beech growth, as growth often decreases when thinning is abandoned in managed stands. Indeed, Mausolf et al. (2018) observed a concomitant decrease in growth sensitivity to climate fluctuation in beech forests with management cessation. In correspondence, Bosela et al. (2016) found only managed beech stands in Slovakia to be negatively affected by increasing drought frequency in recent time, but not unmanaged stands. In fact, heavy thinning in beech forests may contribute to increased tree mortality even 60 years later, probably due to an increase in drought sensitivity after stand opening (Dulamsuren et al. 2022). This contrasts with the results of van der Maaten (2013), who found a decrease in drought vulnerability in German beech forests upon thinning. In our study, in only three of six beech stands with decreasing growth sensitivity, management had been abandoned since the earlier observation period, in the others it continued. In correspondence, the time since management abandonment had no influence in our model built to explain recent growth trends. Thus, it is not yet clear how forest management has affected the climate sensitivity of beech growth in our study. Further research is needed to convincingly explain the observed decline in beech growth sensitivity in our stands.

4.4.4 Regional variation in growth trends and their drivers

While the recent growth trend of the pines is positive at nearly all studied sites despite increasing climatic aridity, irrespective of MAP or recent trends in June precipitation, beech growth trends vary across the study region. We identified the direction of June precipitation change between the 1960-1988 and 1989-2017 period as the most important influential factor for this variation in beech. Regions with largest declines in June precipitation as southern Lower Saxony, Saxony-Anhalt and the south of Brandenburg with reductions by up to 10 mm and significant negative growth trends contrast with coastal regions where June precipitation has increased, and beech growth trends were mostly positive. However, negative growth trends can also be detected in regions with June precipitation increase due to the influence of other, non-climate drivers (Weigel et al. 2022). While the negative correlation between June precipitation trend and beech growth trend was highly significant ($r = 0.86$, $p < 0.001$), our results do not allow defining a MAP threshold, which separates positive and negative growth trends in beech. Possible reasons are the relatively low number of study sites in our study ($N = 10$) or too short environmental gradients. For example, Stolz et al. (2021) did not find any relationship between radial increment and MAP across a short precipitation gradient in northern Germany. In contrast, a more comprehensive study with 30 beech stands in northern Germany detected a tipping point at about 360 mm growing-season precipitation (MGSP, April – September), which separated positive and negative growth trends (Weigel et al. 2022). This matches the dendrochronological results of Knutzen et al. (2017) in the western part of our study region which suggest a similar threshold of about 350 mm MGSP or of ca. 660 mm MAP for the beech growth trend to turn negative.

The high importance of June precipitation for beech growth in Central Europe is supported by other studies (Scharnweber et al. 2011; Harvey et al. 2020; Stolz et al. 2021), while MAP seems to be of secondary importance. In fact, beech thrives in the driest region of Central Europe (near Halle/S. in central Germany) at <500 mm MAP on deep loess soils and shows a positive recent growth trend (Weigel et al. 2022). Similarly, beech growth reveals a strong positive trend in low MAP regions in northern Mecklenburg-Western Pomerania (sites no. 13 and 14), where June precipitation has recently increased (see Fig. 6). In regions where June precipitation has decreased, in contrast, beech shows a negative growth trend (except for site no. 7), even when MAP exceeds 770 mm. We explain the fact that the June precipitation trend is more important for the direction of recent growth trends than absolute amounts of GSP or MAP, with local acclimation or adaptation to the prevailing drought regime. Long-term change in water availability, especially in physiologically important June, has the potential to reduce beech vitality, probably because foliage, hydraulic architecture and fine root system are not well adjusted to the altered conditions. This might trigger further acclimation or, if not possible, lead to vitality decline and eventually death (Obladen et al. 2021; Walthert et al. 2021).

Our comparison of sites revealed that beech growth is favored by higher summer precipitation and reduced drought exposure in the previous year at both the driest and the moistest sites, but the former stands were additionally dependent on rainfall and drought in the current summer, a factor not relevant at the moister sites. This suggests a higher sensitivity to low precipitation and climatic drought at the sites with low MAP and may hint at limited adaptation in drier climates. The published work on regional differences in the drought adaptation of beech is partly controversial. (Martinez del Castillo et al. 2018) compared beech trees at dry sites and of marginal populations with beeches at wetter sites in the distribution center and found no better adaption of the former, which is in line with the findings of Scharnweber et al. (2011) and Stolz et al. (2021) observed in northern Germany. In contrast, Hacket-Pain et al. (2016), Cavin and Jump (2017) and Muffler et al. (2020) found in continent-wide studies a reduced drought sensitivity at drier sites and for dry-edge populations, which point at successful adaptation.

We cannot explain the performance of beech trees in stand no. 7, which show a positive growth trend despite decreasing June precipitation. Forest management can be largely excluded as a driver, as the last thinning took place in this stand in 1996 and no sudden increase in the growth curves can be detected thereafter (Fig. 7, Appendix). It is possible that natural disturbance events have altered the competitive balance between dominant and subdominant trees in this stand in the recent past.

Pine has in common with beech, that signs of its sensitivity to low summer precipitation and drought (and less pronounced to high summer temperatures) increased with decreasing MAP and MGSP; nevertheless, positive growth trends prevailed at most sites (except for site no. 8). Stolz et al. (2021) similarly found increasing drought sensitivity with decreasing MAP for the two species in northeastern Germany, but for pine only during the 1964-1993 interval, and not thereafter. In our comparison, pine, in contrast to beech, shows stable sensitivity to measures of summer water deficits of the current year, and this sensitivity apparently has shifted from June to July from the 1960-1988 to the 1989-2017 period (Diers et al., submitted). The negative effect of increasingly dry summers is currently offset by a positive influence of warm winters, so that pine continues to show a positive growth trend along the entire studied climate gradient, in contrast to beech. Certainly, we cannot fully exclude an effect of stand age on this difference, because the different rotation time for the two species caused different stand ages of the sampled trees. Nevertheless, even old beech trees >300 to 400 years have the potential to sustain high growth rates (Piovesan et al. 2003, 2008), which suggests that climate change, and not natural senescence, is the main driver of the observed growth decline in beech in our stands, where age varied between 95 and 195 years.

Precipitation and water deficits are modulated by soil physical factors in their effect on tree water status and growth. While all 20 stands were selected on sandy to sandy-loamy soils on glacial deposits, it is likely that the capacity for plant-available water (AWC) differs between the stands and thus may explain part of the variation in growth trends and climate sensitivity of growth (Fuchs et al. 2020; Scharnweber et al. 2020). Since soil physical data are lacking for our sites, the soil influence remains elusive. However, another study in 30 beech forests in the north German lowlands on similar soil revealed a significantly higher xylem embolism resistance of beech sun-canopy branches with a decrease in AWC from 300 mm to <100 mm on sandy soil, indicating successful acclimation of the hydraulic system of beech to reduced soil water storage capacity (Weithmann et al. 2021). Variation in soil properties could also influence the drought tolerance of trees through altered nutrient availability (Lévesque et al. 2016; Braun et al. 2021). Future research on tree growth patterns has to consider regional variation in both climatic and edaphic water availability to reach at a more complete picture.

4.5 Conclusions

The necessary shift to climate-smart forests requires comprehensive understanding of the drought and heat tolerance of tree species as well as of their effects on the biogeochemical cycles of forest landscapes. Comparative dendroecological studies of several co-occurring tree species across climate gradients, such as our study on paired pine and beech stands on similar soil along a steep precipitation gradient, can provide valuable information to achieve this goal. A higher carbon sequestration potential and positive effects on the water cycle, soil fertility and biodiversity suggest to replace pine plantations by beech forests in parts of the north German lowlands. However, the sensitivity of beech to increasing drought exposure and declining growth rates, as demonstrated here, suggest selecting more drought-tolerant broadleaf species in all regions with declining June precipitation, notably in Saxony-Anhalt (and adjacent regions of western Brandenburg and eastern Lower Saxony). Promising silvicultural alternatives can be *Quercus* species (notably *Q. petraea* and *robur*, but also *Q. frainetto*; (Kasper et al. 2022), *Acer platanoides*, *Carpinus betulus*, *Sorbus torminalis* and *Tilia cordata* (Fuchs et al. 2021), among others.

Beech will be a relatively safe option close to the North Sea (Schleswig-Holstein, north-western Lower Saxony) and Baltic Sea coasts (parts of northern Mecklenburg-Western Pomerania) and in northern Brandenburg, where the summer climatic water balance has turned more favorable in the recent past. Although our pine stands revealed until recently mostly positive growth trends, it is likely that the next pine generation will also suffer vitality and growth declines, should the current thermal and hydrometeorological trends continue in future.

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Appendix

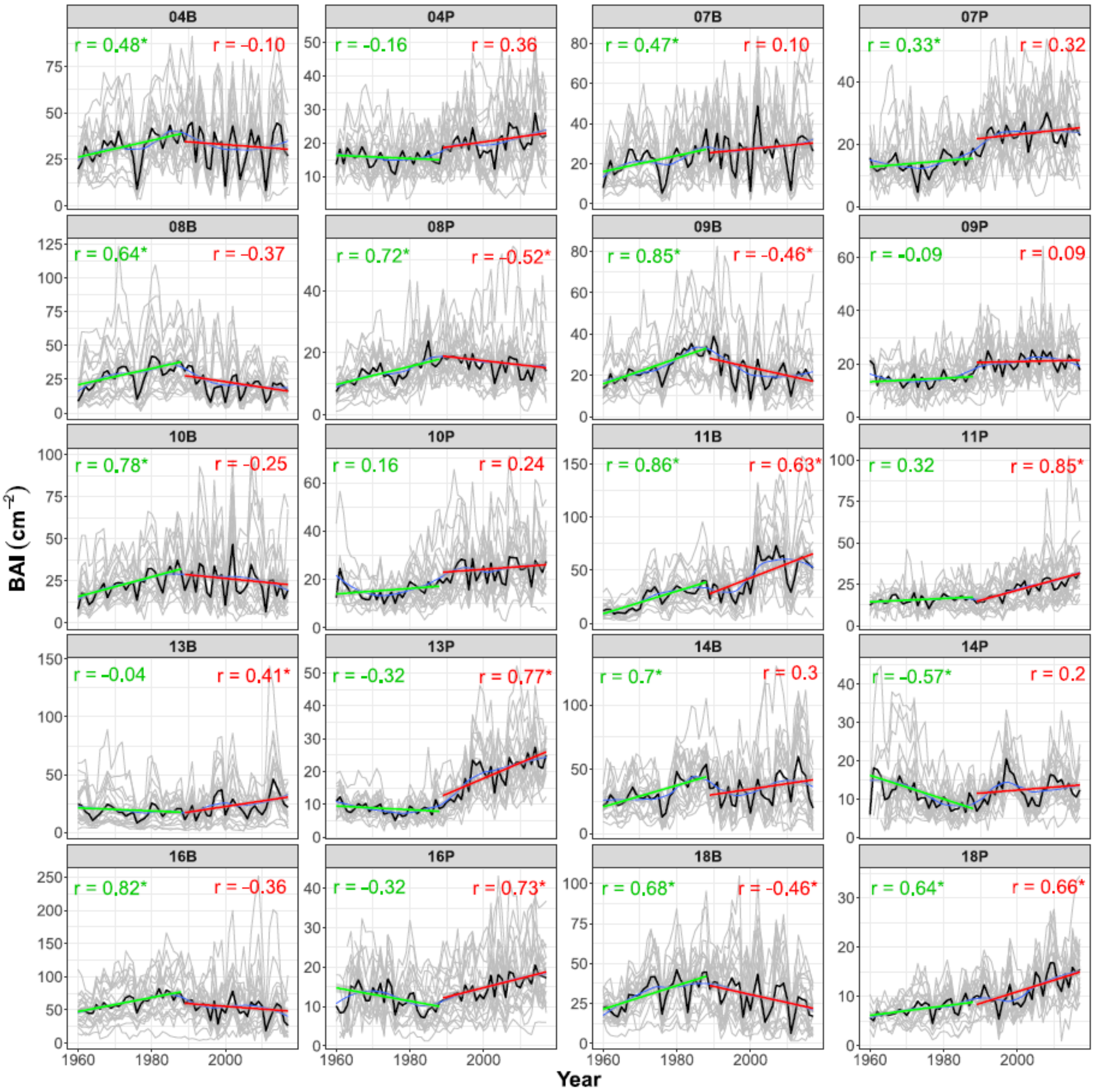

Figure 7. Temporal course of basal area increment (BAI) of the individual trees (grey lines) and of the stand chronologies (bold black line) in the period 1960-2017 in the each 10 beech (B) and pine (P) stands. Linear trends for the earlier period are depicted in green, for the later period in red. Given are Pearson's r values for the trend lines. Significance was calculated with a Mann-Kendall trend test. The spline curve (thin blue line) is calculated by using local polynomial regression fitting (loess) with a smoothing parameter (span) of 0.5.

Figure 8. Moving-window analysis of the correlation (Pearson's r) between ring width (RWI) with long-term June precipitation change since the 1960-1988 interval in the 10 beech stands. The sites are ordered by the amount of change in June precipitation between the 1960-1988 and the 1989-2017 period (sites no. 11-14: increase in June precipitation, no. 4 to 10: increasingly large decrease in June precipitation). The x-axis shows the central year of the 30-year moving window. The grey background marks the range with $|r| > 0.37$ at $p < 0.05$ for $n = 30$ years.

Table 3. Model output showing relationships between the factors long-term June precipitation decline (ΔJune precipitation) in (mm) and time since forest management abandonment and the interaction of the two factors on the growth trends of beech in our stand sample (model: change_BAI ~ ΔJune precipitation (mm)*Forest management abandonment). Significant relations are printed in bold.

Variable	Estimate	p-value
ΔJune precipitation (mm)	**0.078**	0.03
Forest management abandonment (yrs)	-0.011	0.46
ΔJune precipitation (mm)*Forest management abandonment (yrs)	-0.001	0.45

CHAPTER 5

Synopsis

Scots pine is one of the most important timber species in the North German Lowlands and covers more than 50 % of the forest area in this region (Leuschner et al., 2022). Since the beginning of the industrialization in the 18th century, forestry has largely replaced the naturally occurring beech and beech-oak forests with pine plantations, thus preserving beech forests on only 6.6 % of the recent forest area (Leuschner et al., 2022; Milnik, 2007). Regarding climate change and its potential mitigation by forests (Pan et al., 2011), it has been recommended to enrich pine stands with beech, to create more diverse and thus more stable forest ecosystems in the future (Metz et al., 2020). However, the applicability of beech to achieve this goal is controversially discussed due to its susceptibility to drought (Geßler et al., 2006; Leuschner, 2020; Metz et al., 2020).

In the context of large-scale, climate change-induced forest conversion, and the importance of pine and beech in this region, this dissertation thesis aimed to investigate the differences in soil chemical variables, especially C pools as well as the growth dynamics of neighboring pine and beech stands along a climate gradient in the North German Lowlands.

5.1 Future of Scots pine forestry in the North German Lowlands

Scots pine forestry has a long history and high economic relevance in the forestry of the North and especially Northeast German Lowlands (Bilke and Noack, 2007; Milnik, 2007; Thünen-Institut, 2022). However, it is evident that, in view of the climate change mitigation potential of forests, pure pine plantations do not provide sufficient ecosystem services, like carbon sequestration in biomass.

Regarding the climate warming mitigation potential of pine forests in the study region, it is an important finding that the SOC stocks are on average larger under pine compared to beech (Chapter 2). However, this must be related to the C stock in the aboveground biomass, which is considerably lower in pine than beech and thus, under suitable growing conditions, more C can be stored in a beech forest (Förster et al., 2021; Leuschner et al., 2022).

Results showed that temperature and precipitation in relation to stand age and the combination of stand type and history have no significant influence on carbon or nitrogen accumulation in the soil (Chapter 2). It is possible that the climate gradient is too short to detect an effect. Even in the context of the national soil survey, climate factors play a minor role (Grüneberg et al., 2019). In contrast, Kasper et al. (2021) showed that higher temperature has a reducing effect on the SOC pool. Warming of climate and thus soil can lead to an increase in microbial activity, which leads to an increase in decomposition rates and thus release of CO_2 from the soil to the atmosphere (Jansson and Hofmockel, 2020; Leuschner and Ellenberg, 2017; Melillo et al., 2017). The extent to which global temperature rise will result in an increase in the flux of CO_2 from forest soil, due to increased decomposition rates, is a matter of debate (Smith and Fang, 2010). Comparison of NIR radiations over pine and beech forests has shown that pine forests have lower albedo and thus warm up more than beech stands (Leuschner et al., 2022). A large-scale study shows that an increased occurrence of deciduous forests can reduce high temperature extremes in Europe (Schwaab et al., 2020). This indicates that pine stands can negatively affect both micro- and macroclimate through lower albedo, as well as through increased sensible heat flux during water shortages (Lansu et al., 2020; Leuschner et al., 2022; Teuling et al., 2017).

The amplifying characteristics of pine stands with respect to temperature and the associated reduction of the SOC pool, additionally lead to a reduction of groundwater recharge under pine stands (Leuschner et al., 2022). Higher temperatures in the canopy and stand result in increased evapotranspiration compared to natural beech forests, resulting in less water remaining in the stand and potentially in the soil (Müller and Bolte, 2009). In addition, a particularly hydrophobic organic layer in pine stands under dry conditions makes it difficult for the soil to become saturated with water (Leuschner et al., 2022). This may have a positive effect on the SOC content, because without sufficient moisture microbial activity is also inhibited, so that C pools on dry sites may increase (Davidson and Janssens, 2006; Fekete et al., 2021). On the other hand, in a warmer and drier climate, groundwater recharge is an important ecosystem function and drought stress leads to growth decline and inhibited C sequestration in biomass (Leuschner et al., 2022; Zhao and Running, 2010).

Even though pine is considered as a species with low habitat requirements and thus has the optimal characteristics for the nutrient-poor and dry sandy soils of the lowlands, it still demonstrates large temporal and spatial variations in climate-growth relationships (Chapter 3). Despite the ongoing positive effect of climate warming on pine productivity in the region, the greater drought sensitivity of the drier stands in our sample, as well as the increase in climate sensitivity between periods 1960–1988 and 1989–2017, along with frequent dieback following the extreme 2018/19 drought in the area (Behrens, 2020; Staatsbetrieb Sachsenforst, 2020), suggest that pine vitality is likely to decline in the future at sites with negative climatic water balance in summer and low soil water holding capacity (Chapter 3, Chapter 4, Stolz et al., 2021). Studies from southern Europe show that pine trees experience growth declines and dieback processes in excessively dry climates (Etzold et al., 2019; Matías et al., 2017). The increasing frequency of drought events appears to have led to a heightened vulnerability of pine to extreme drought (Bose et al., 2020). Consequently, water availability plays a central role for pine growth as well, despite its low site requirements.

In addition, soils under pine tend to become podzolized due to the soil acidifying property of the litter, which has a negative effect on soil biological activity (Leuschner et al., 2013; Riek et al., 2007). Furthermore, pine forests are more susceptible to abiotic forest damage caused by extreme weather events such as storms (windthrow), heat waves (forest fires), and biotic forest damage caused by insect outbreaks and pathogen attacks, which have increased markedly in recent times (DWD, 2020; Forzieri et al., 2021; Knoke et al., 2008; Möller et al., 2007). Drought and alternating warm and cold winter periods might weaken pine, predisposing it to pathogen and pest attack (Rohde et al., 2021).

Despite the larger C pool and the currently still positive growth trends, the negative characteristics outweigh the positive ones, regarding the increasing importance of ecosystem functions such as long-term carbon sequestration and groundwater recharge. Therefore, the pursuit of pure pine plantations is not recommended in future forestry and alternative timber species need to be found (Bauhus et al., 2021; Leuschner et al., 2022).

5.2 Native beech forests as an alternative to pine plantations

Besides pine, beech is an important hardwood tree species for forestry in northern Germany. Beech forests dominate the potential natural vegetation in large parts of Germany. (Bohn and Neuhäusl, 2003; Leuschner and Ellenberg, 2017). In the North German Lowlands, beech forests would naturally occur on 48.6 % of the forest area (Leuschner et al., 2022). Due to historical forest practices, there are even-aged pine plantations on more than 50% of the forest area of the North German Lowlands and beech stands on only 6.6% (Leuschner et al., 2022, see Chapter 1).

The finding in forestry science that mixed stands are more resilient and productive than pure stands, led to a change in forest management (Ammer, 2019; Spathelf et al., 2015). Thus, an increasing portion of deciduous and mixed forest – with tree species appropriate for the site conditions – is desired (Bauhus et al., 2021).

To adjust forests to the changing climate in terms of large-scale forest conversion, it appears initially logical to convert the widespread pine plantations into mixed pine-beech stands or beech stands. Near-natural forests, and in most cases deciduous forests, are expected to simultaneously form a stable ecosystem that can withstand the predicted climate and provide ecosystem services and functions, such as carbon sequestration and groundwater recharge, to mitigate climate change. The mitigation potential of forests is large compared to grass- or wetland (Griscom et al., 2017).

In terms of C sink performance, the C pool under beech was smaller than under pine, but when above- and belowground biomass and soil C pool are considered together, beech stands store more C than pine plantations. Consequently, cultivation of beech could increase the C sink capacity of forests in northern Germany (Chapter 2, Leuschner et al., 2022). This storage capacity can be additionally increased by a reduction/omission of forest management and long rotation periods (Knohl et al., 2003; Mayer et al., 2020; Meyer et al., 2021). Moreover, groundwater recharge is greater and warming is less under beech stands compared to pine stands, thus beech stands provide further important ecosystem services (Leuschner et al., 2022). Furthermore, it can be assumed that the reduced influence of increasing temperature on the SOC pool is smaller due to lower temperature within the forest stand (De Frenne et al., 2019; Leuschner and Ellenberg, 2017).

However, despite the many advantages of beech reported above, it should be taken into account that it is considered as a drought sensitive tree species. The projected climate changes may lead to a decline in growth and thus a reduction in biomass accumulation (Albert et al., 2018; Lo et al., 2019; Trotsiuk et al., 2020; Vanhellemont et al., 2019). The growth trend of beech varies regionally but shows no relationship with MAP. Here, we were able to identify the direction of change in June precipitation between periods 1960-1988 and 1989-2017 as the most important factor influencing the direction of the growth trend. Beech exhibits negative growth trends in regions where June precipitation has decreased. In areas where June precipitation increased, a positive growth trend was observed, indicating that summer precipitation, especially in June, has an outstanding influence on the growth trend (Chapter 4). This is in line with findings of Knutzen et al. (2017), Stolz et al. (2021) and Weigel et al. (in preparation) in the North German Lowlands as well as Čufar et al. (2008) who described June as the most important month for ring formation in beech, showing that MAP alone is not sufficient for the selection of suitable areas for beech cultivation. Beech appears to recover well from mild to moderate droughts due to remarkable plasticity in the hydraulic system, while it is damaged during severe droughts with exceptionally high atmospheric saturation deficit so that already drought induced mortality was observed in southern Germany and elsewhere in Europe (Leuschner, 2020; Rothenbühler, 2021; Schuldt et al., 2020; Zimmermann et al., 2021). In the context of an increasingly arid summer in large parts of Central Europe and Germany, it can be assumed that beech has a silvicultural future only in areas with increasing June precipitation, such as the coastal regions in Mecklenburg-Western Pomerania (Chapter 4, Banzragch et al., in revision).

It remains to be clarified to what extent beech is suitable as a tree species, whether in monocultures or in mixed stands, to provide ecosystem functions and services like carbon sequestration, groundwater recharge and timber production under climate change.

5.3 General conclusion

For this dissertation thesis, empirical data on neighboring pine and beech stands were collected and analyzed. The results intend to contribute to future forestry decisions in the North German Lowlands in the context of climate change.

The results of this study suggest that neither pine nor beech forests are unconditionally sustainable forest communities for future forestry in the North German Lowlands. Even though pine stores more C in the soil than beech and actually shows positive growth trends on most sites across the study region – which can be attributed to a positive influence of higher temperatures in spring – a beech stand stores more C overall. In addition, pine is expected to suffer from rising temperatures and increasing drought in the future (Chapter 3, Stolz et al., 2021). Multiple studies have shown that pine stands have characteristics that are counterproductive in the context of predicted climate change (Leuschner et al., 2022). Based on the results of the present and other studies (e.g., Leuschner et al., 2022), a forest conversion away from the extensive pine plantations is recommended.

It is important to note that climate warming has a negative impact on beech growth, as found in this study. The negative growth trends in areas with decreasing June precipitation underpin the drought sensitivity of beech in accordance with previous empirical work (Walthert et al., 2021; Zimmermann et al., 2021). In sum, beech as a tree species naturally occurring in the lowlands in large parts, can only be recommended in coastal regions with sufficient June precipitation for the future.

Currently, no reliable statements can be made about the optimal choice of tree species for the predicted climate. It is diversely discussed which tree species will be the right choice in order to both increase biodiversity as well as the climate change mitigation potential (Ammer et al., 2008; Geßler et al., 2006; Leuschner, 2020; Metz et al., 2020).

Based on the results of this study, it is not advisable to mix beech with pine trees on large scales, even though positive effects of mixed stands have already been observed (Metz et al., 2020, 2016; Pretzsch et al., 2016, 2015). Currently, there are no consistent results on the extent to which different tree species mixtures would facilitate the cultivation of beech in the future (Ammer, 2019). However, climatic factors may override the positive effects of admixture (Bosela et al., 2018; Metz et al., 2020). It is to be assumed, however, that in the long run beech, even as a native species, will show enhanced growth decline (Albert et al., 2018; Bosela et al., 2018; Jump et al., 2006; Kasper et al., 2022; Weigel et al., in preparation), and dieback events (Rothenbühler, 2021; Schuldt et al., 2020) due to a drier climate as well as shifts in distribution range (Hanewinkel et al., 2013). To achieve the goal of a diverse forest ecosystem that will be stable in the future and provide ecosystem services and functions, research into alternative tree species plays an important role.

Studies from central Germany and Romania show that e.g., Norway maple (*Acer platanoides* L.), ash (*Fraxinus excelsior* L.) and sessile oak (*Quercus petraea* Matt. Liebl) are particularly suitable for the expected drier and warmer climate (Fuchs et al., 2021; Kasper et al., 2022). It is hypothesized that conversion to drought-resistant oak forests will result in a species-specific reduction in aboveground C storage capacity compared to beech forests (Kasper et al., 2021). In addition, warming will lead to an additional reduction in the SOC pool (Kasper et al., 2021; Melillo et al., 2017). From the current perspective, it will probably come down to a compromise in the choice of sustainable tree species, where a balance between climate sensitivity and productivity has to be found. In this context, further research is needed on which tree species and which mix of species can meet the demands of future forest ecosystems and show possible adaptation potential.

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Danksagung

An dieser Stelle möchte ich mich bei den Personen bedanken, ohne die die Anfertigung und Fertigstellung dieser Arbeit nicht möglich gewesen wäre.

Ich danke meinem Doktorvater Prof. Dr. Christoph Leuschner für die Bereitstellung des Themas, die fachliche Betreuung und die vielen hilfreichen Gespräche. Des Weiteren danke ich Prof. Dr. Ammer für die Übernahme der Zweitbetreuung, sowie Prof. Dr. Seidel für die kurzfristige Übernahme des zweiten Gutachters. An dieser Stelle sei auch den weiteren Mitgliedern der Prüfungskommission Prof. Dr. Hölscher, Prof. Dr. Kreft und Prof. Dr. Bergmeier für ihre Bereitschaft der Mitarbeit gedankt.

Bedanken möchte ich mich auch bei Dr. Dietrich Hertel für seine Hilfe bei der Planung der Feldarbeit, sowie die Möglichkeit ihn bei Fragen oder Problemen immer ansprechen zu können. Ebenfalls für seine Hilfsbereitschaft bei technischen Fragen aller Art möchte ich mich bei Dr. Heinz Coners bedanken. Ein besonderer Dank gilt Dr. Robert Weigel, für seine intensive Unterstützung bei der Datenauswertung und Anfertigung der Manuskripte. Für ihre Hilfe beim Einstieg in die Dendroökologie und die Beantwortung zahlreicher Fragen bedanke ich mich bei Dr. Choima Dulamsuren.

Ein großer Dank geht auch an die TAs der Abteilung, für die Analysen der vielen Bodenproben. Besonderer Dank geht an Mechthild Stange für ihre Hilfe bei der Gewinnung der Bodenproben und die angenehme Zeit während der Feldarbeit. An dieser Stelle möchte ich mich auch bei Marvin Kühne bedanken, der als studentische Hilfskraft unermüdlich zahlreiche Bodenprofile in den norddeutschen Wäldern anlegte, sowie Johanna Steen und Thore Schulz die mich bei der dendrologischen Datenaufnahme und im Labor unterstützten. Die Zeit mit euch im Wald hat mir viel Spaß bereitet.

Ich danke dem Bundesministerium für Bildung und Forschung (Projektnummer: 01LC1314B) für die Finanzierung des WiNat-Projektes und dem gesamten WiNat-Team für die schöne Zeit, außerdem Maria und Nathalie für die Hilfe und schöne Woche in der Rüthnicker Heide. In diesem Zusammenhang bedanke ich mich auch bei Agnes Förster für einen sehr angenehmen Start im Projekt und in der Abteilung.

Darüber hinaus danke ich all den anderen Doktoranden, insbesondere meiner Schreibtischnachbarin Eva, sowie Greta, Katja, Sebastian, Eenee, Esther, Roman, Kerstin, Lisa und Sally für eine wunderbare Zeit, ausgedehnte Mittagspausen und die gemeinsamen Aktivitäten.

Ebenso möchte ich mich bei Michi, Stefan und Bastian für die mentale Unterstützung bedanken. Ich danke auch meinen Mitbewohnern Nadine und Martijn, Hanna, Andreas und Markus für eine WG in der ich mich immer sehr wohl gefühlt habe.

Danke Ulrike für deine Unterstützung, deinen äußerst positiven Einfluss auf mein Leben und die wundervolle gemeinsame Zeit mit dir.

Zum Schluss möchte ich mich bei meiner Familie, insbesondere bei meinen Eltern bedanken, die mir das Studium ermöglichten, mich in meinen Plänen unterstützen und immer für mich da sind. Danke!

Publications in connection with dissertation

Schneider, H., Meyer, P., Aljes, M., Culmsee, H., **Diers, M.**, Förster, A., Leuschner, C. (2023): Wie kann Naturnähe im Wald gemessen werden? Natur und Landschaft 98 (2): 49-57

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