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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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Abstract

Background: 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.

Methods: 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.

Results: 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.

Conclusion: 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.

Keywords: Basic cations, *Fagus sylvatica*, Forest history, Nitrogen, Paired plots, *Pinus sylvestris*, Productivity effect, Soil organic carbon, Tree species effect

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Background

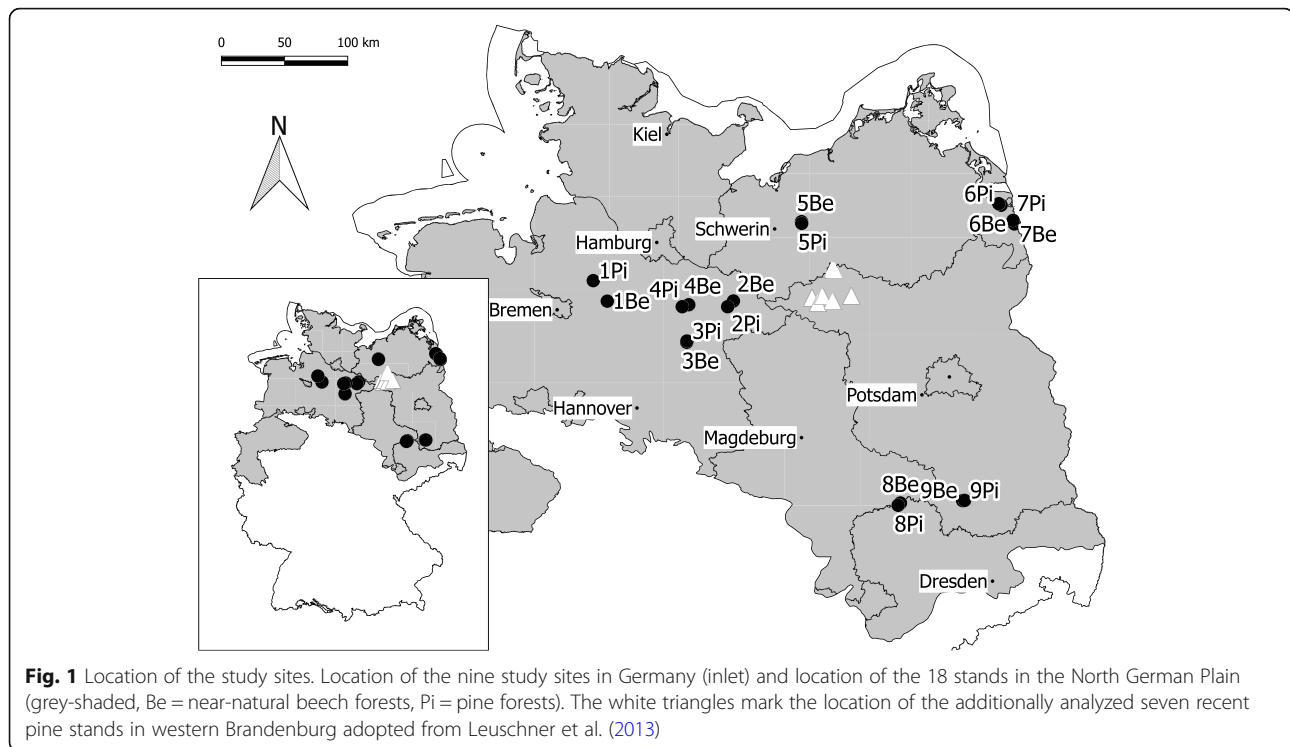
The sequestration of atmospheric carbon dioxide in soils as stable organic matter is discussed as a means of mitigating anthropogenic climate warming (Spalding et al. 2012). Forest soils store one third (c. 720 Pg) of the global organic carbon (C) (Schlesinger 1991, Price et al. 2012) and thus are an 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 (Polonski & 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 (Förster 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 larger 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.

Materials and methods

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 to 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 × 1 km grid data of temperature and precipitation interpolated by Deutscher Wetterdienst (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

Table 1 Location and characteristics of the nine study sites

Site	Location	Forest type	Latitude (°N)	Longitude (°E)	Age (year)	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

groundwater influence. The soil types were spodosystric 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).

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 Arbeitskreis Standortkartierung 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 cm³ 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 × 9 stands × 5 depths × 10 stand-level replicate plots). The soil samples were stored in plastic bags and kept at 4 °C in the laboratory.

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(H₂O)) 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, elemental, 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 BaCl₂ 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 × 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.

Statistical analysis

The data analysis was conducted with R, version 3.6.3 (R Core Team 2020) in the framework of the tidyverse package (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 × 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 Jr, 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 (Table 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,

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

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.

Results

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 (sites 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).

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 (BaCl₂-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 (Figs. A3a and A3b 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

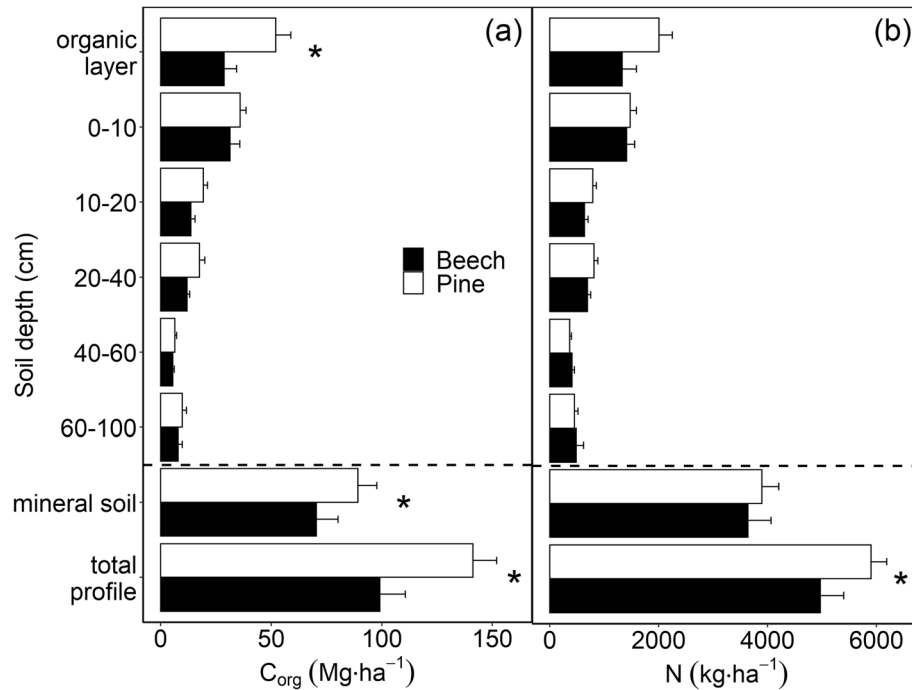


Fig. 2 Soil pool of organic carbon and total nitrogen. Pool of organic C (a) and total N (b) in soil profiles to 100 cm depth (data for 60–100 cm were computed by extrapolation) under beech (black bars) and pine stands (white bars). Total profile refers to mineral soil plus organic layer. Significantly 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

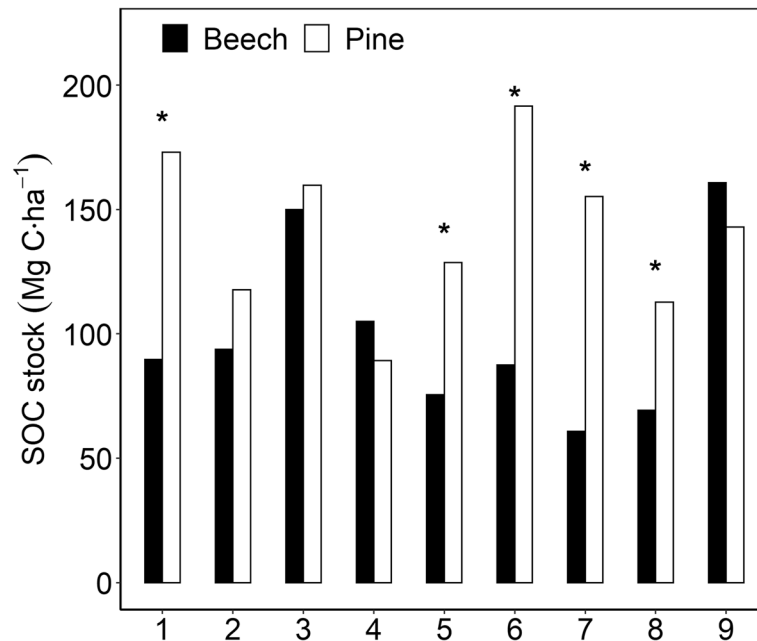


Fig. 3 Mean stocks of soil organic carbon in the mineral soil and organic layer. SOC stocks in the mineral soil (0–100 cm, data for 60–100 cm were computed by extrapolation) and the organic layers of the each nine beech (black bars) and pine stands (white bars) at the sites 1 to 9 (given are the means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

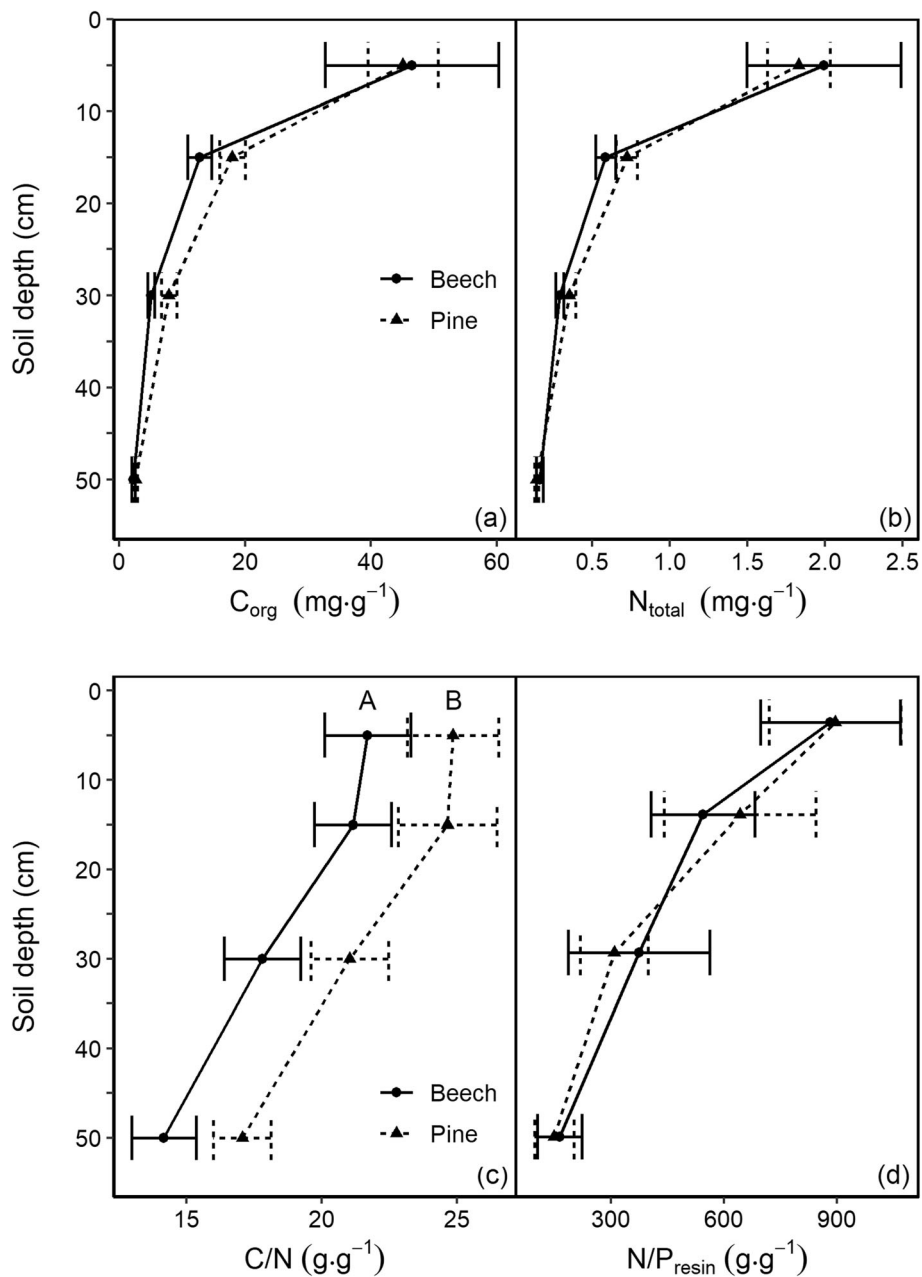


Fig. 4 Soil concentrations of organic carbon, total nitrogen, C:N ratio, and $N:P_{\text{resin}}$ ratio. Mean concentration (and standard error) of (a) organic C, (b) total N, (c) C:N ratio and (d) $N:P_{\text{resin}}$ ratio in mineral soil profiles under beech (solid line) and pine stands (dotted line). 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

pine in the organic layer (3.1 vs. 3.6; difference significant).

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 $148.9 \text{ Mg}\cdot\text{ha}^{-1}$, which is about 27% higher than in recent pine stands ($116.8 \text{ Mg}\cdot\text{ha}^{-1}$) and 50% higher than in ancient beech stands ($99.1 \text{ Mg}\cdot\text{ha}^{-1}$) (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. $33.9 \text{ Mg}\cdot\text{ha}^{-1}$, Fig. 7c). Total N pools were also higher in the

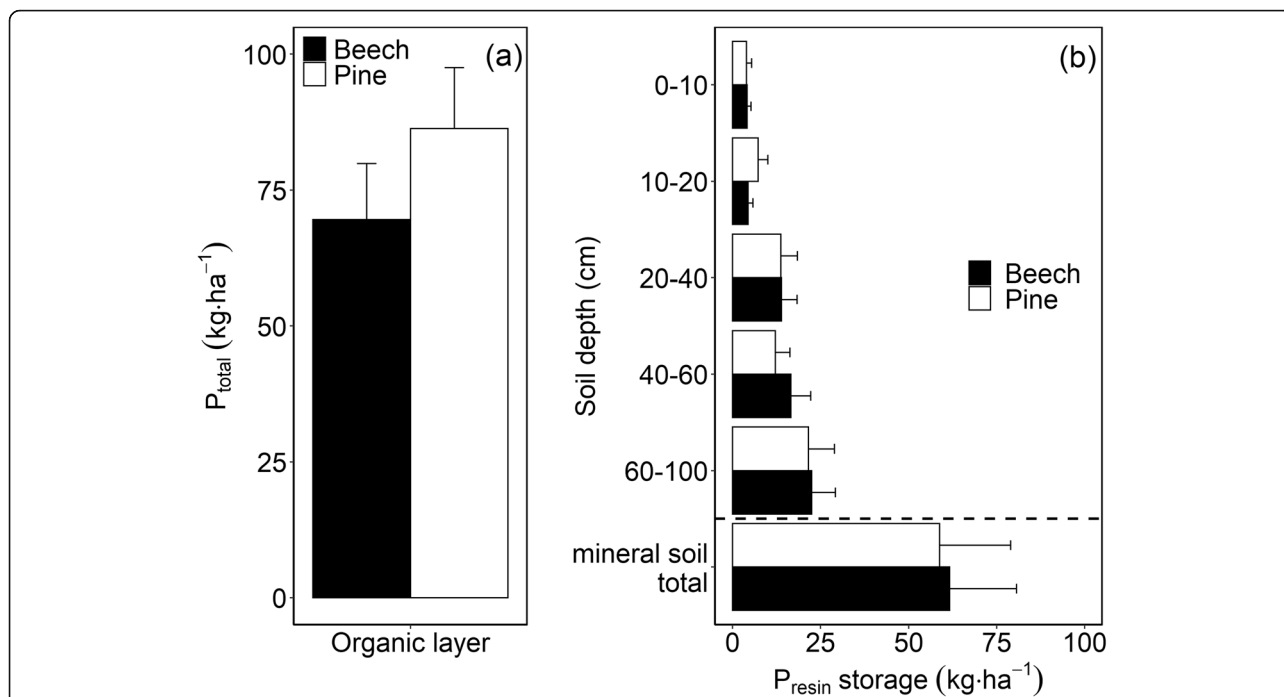


Fig. 5 Soil pool of phosphorus in the organic layer and in the mineral soil. Total pool of phosphorus in the organic layer of beech (black bar) and pine stands (white bar) (a), and pools of plant-available P (resin-P) in mineral soil profiles to 100 cm depth (data for 60–100 cm were computed by extrapolation) 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

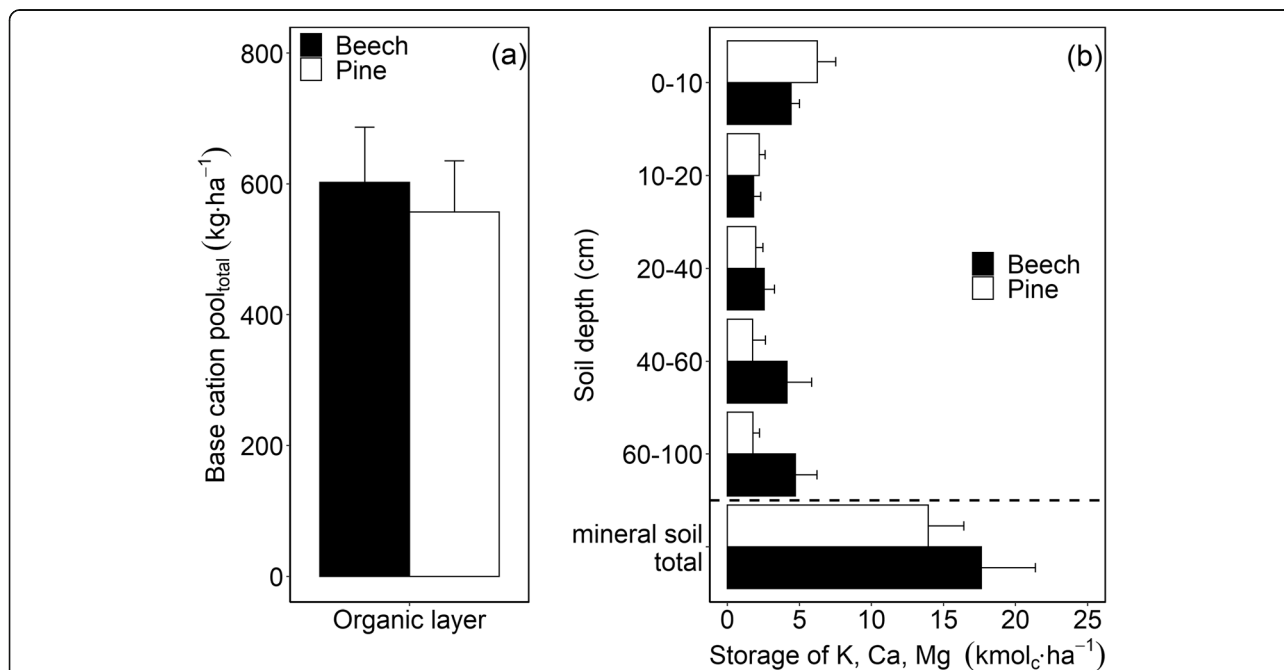
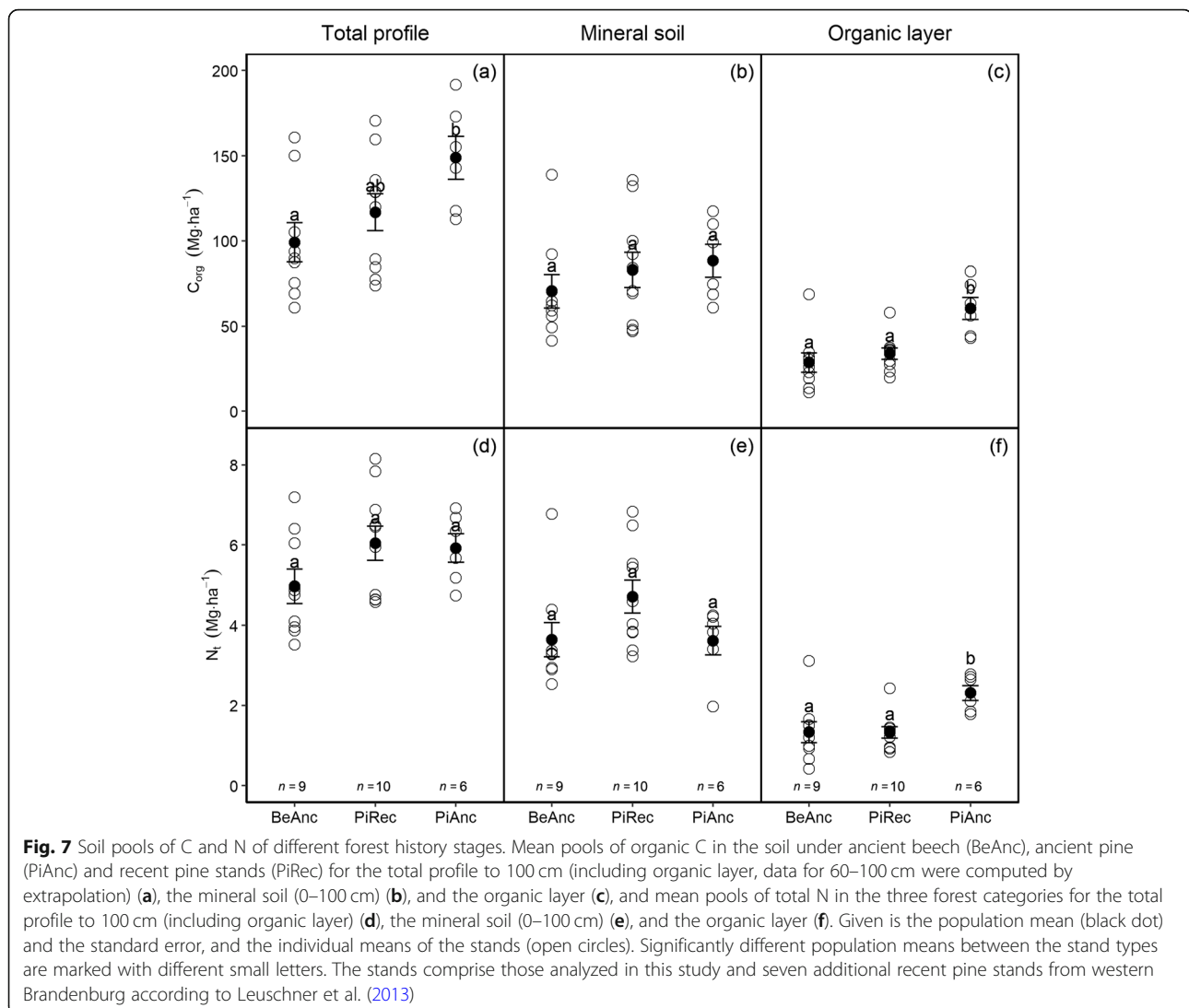


Fig. 6 Soil pool of base cations in the organic layer and in the mineral soil. Total pool of base cations (Ca, K, Mg) in the organic layer of beech (black bar) and pine stands (white bar) (a), and pools of exchangeable base cations in mineral soil profiles to 100 cm depth (data for 60–100 cm were computed 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

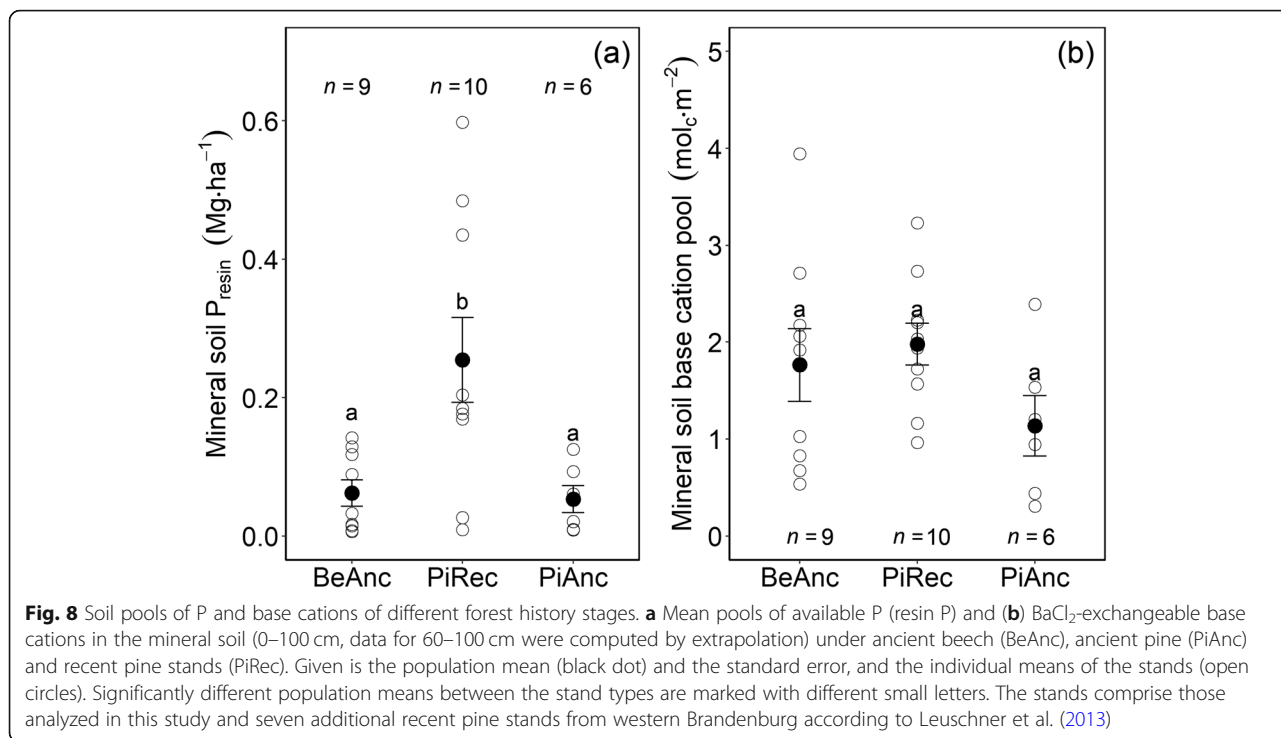


organic layer of ancient than recent pine stands, while the mineral soil N pool tended to be larger in recent pine stands (Fig. 7e and f). Consequently, the profile total N pools differed not significantly among the stand types, but were in tendency larger in recent and ancient pine than beech stands. 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).

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 were of minor

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	–	–	–	×	–
	OL	–	–	×	×	–
	MS	–	–	–	–	–
N pool	total	–	–	–	–	–
	OL	–	–	–	×	–
	MS	–	–	–	–	–
P _{resin} pool	MS	–	×	–	×	–
BC pool	MS	×	–	–	–	–

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 (×) remained

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).

Discussion

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; 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).

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 $\text{g}\cdot\text{g}^{-1}$ higher in pine than beech with N concentrations of 8–9 $\text{mg}\cdot\text{g}^{-1}$ in beech and 5–7 $\text{mg}\cdot\text{g}^{-1}$ 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 $\text{g}\cdot\text{g}^{-1}$ 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). Whatever 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 & McLaugherty 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.

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 re-accumulation 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 $\text{Mg C}\cdot\text{ha}^{-1}$) from recent to ancient pine stands (> 230 years of continuity) and a smaller (non-significant) increase in the mineral soil (Figs. 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.

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 above-ground 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 years); 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

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40663-021-00330-y>.

Additional file 1.

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Authors' contributions

CL and HC conceived the research idea. MD took the samples in the field and was responsible for laboratory analyses. MD and RW conducted the data evaluation and statistical analysis. MD wrote the manuscript together with CL and RW and HC contributed critically to the writing. The author(s) read and approved the final manuscript.

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Availability of data and materials

The dataset used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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References

- Akatsuki M, Makita N (2020) Influence of fine root traits on in situ exudation rates in four conifers from different mycorrhizal associations. *Tree Physiol.* doi.org/10.1093/treephys/tpaa051
- Akselsson C, Olsson J, Belyazid S, Capell R (2016) Can increased weathering rates due to future warming compensate for base cation losses following whole-tree harvesting in spruce forests? *Biogeochemistry* 128(1-2):89–105. <https://doi.org/10.1007/s10533-016-0196-6>
- Ammer C, Bickel E, Kölling C (2008) Converting Norway spruce stands with beech – a review of arguments and techniques. *Austr J Forest Sci* 125:3–26

- Anders S, Beck W, Hornschuch F, Müller J, Steiner A (2004) Vom Kiefern-Reinbestand zum Kiefern-Buchen-Mischbestand. *Beitr. Forstwirtsch. u. Landsch.ökol.* 38: 55–67
- Angst G, Messinger J, Greiner M, Häusler W, Hertel D, Kirfel K, Leuschner C, Rethemeyer J, Mueller CW (2018) Soil organic carbon stocks in topsoil and subsoil controlled by parent material, carbon input in the rhizosphere, and microbial-derived compounds. *Soil Biol Biochem* 122:19–30. <https://doi.org/10.1016/j.soilbio.2018.03.026>
- Angst G, Mueller KE, Eissenstat DM, Trumbore S, Freeman KH, Hobbie SE, Chorover J, Oleksyn J, Reich PB, Mueller CW (2019) Soil organic carbon stability in forests: distinct effects of tree species identity and traits. *Glob Change Biol* 25(4):1529–1546. <https://doi.org/10.1111/gcb.14548>
- Arbeitskreis Standortkartierung (2016) Forstliche Standortaufnahme, 7th edn. IHW Verlag, Eching, Germany
- Berg B, McLaugherty C (2003) Plant litter. Decomposition, humus formation, carbon sequestration. Springer, Berlin
- Binkley D, Giardina C (1998) Why do tree species affect soils? The warp and woof of tree-soil interactions. *Biogeochemistry* 42:73–88
- Binkley D, Valentine D (1991) 50-year biogeochemical effects of green ash, white pine, and Norway spruce in a replicated experiment. *For Ecol Manag* 40(1–2): 13–25. [https://doi.org/10.1016/0378-1127\(91\)90088-D](https://doi.org/10.1016/0378-1127(91)90088-D)
- BMEL (2020) Dritte Bundeswaldinventur 2012. Bundesministerium für Ernährung und Landwirtschaft, Berlin
- Boča A, Van Miegeot H, Gruselle M-C (2014) Forest overstorey effect on soil organic carbon storage: a meta-analysis. *Soil Sci Soc Am J* 78(5):S35–S47. <https://doi.org/10.2136/sssaj2013.08.0332nafsc>
- Bublinec E (1974) Bodenpodsolierung unter Kiefernbeständen. *Nanka o Zemi VIII Pedologica*, Bratislava 8:1–22
- Compton JE, Boone RD (2000) Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. *Ecology* 81(8):2314–2330. [https://doi.org/10.1890/0012-9658\(2000\)081\[2314:LTIOAO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[2314:LTIOAO]2.0.CO;2)
- Core Team R (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria <https://www.R-project.org>.
- Enriquez S, Duarte CM, Sand-Jensen K (1993) Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. *Oecologia* 94(4):457–471. <https://doi.org/10.1007/BF00566960>
- Finér L, Ohashi M, Noguchi K, Hirano Y (2011) Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. *For Ecol Manag* 262(11):2008–2023. <https://doi.org/10.1016/j.foreco.2011.08.042>
- Fischer H, Bens O, Hüttl RF (2002) Changes in humus form, humus stock and soil organic matter distribution caused by forest transformation in the north-eastern lowlands of Germany. *Forstwiss Centralbl* 121(6):322–334. <https://doi.org/10.1046/j.1439-0337.2002.02037.x>
- Förster A, Culmsee H, Leuschner C (2021) Thinned northern German scots pine forests have a low carbon storage and uptake potential in comparison to naturally developing beech forests. *For Ecol Manag* 479:118575. <https://doi.org/10.1016/j.foreco.2020.118575>
- Gessler A, Keitel C, Kreuzwieser J, Matyssek R, Seiler W, Rennenberg H (2006) Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. *Trees* 21(1):1–11. <https://doi.org/10.1007/s00468-006-0107-x>
- Glaser FF, Hauke U (2004) Historisch alte Waldstandorte und Hutewälder in Deutschland. *Angewandte Landschaftsökologie* 61:1–193
- Godbold DL, Hoosbeek MR, Lukac M, Cotrufo MF, Jansens IA, Ceulemans R, Polle A, Velthorst EJ, Scarascia-Mugnozza G, De Angelis P, Miglietta F, Peressotti A (2006) Mycorrhizal hyphal turnover as a dominant process for carbon input into soil organic matter. *Plant Soil* 281(1–2):15–24. <https://doi.org/10.1007/s11104-005-3701-6>
- Grüneberg E, Schöning I, Riek W, Ziche D, Evers J (2019) Carbon stocks and carbon stock changes in German forest soils. In: Wellbrock N, Bolte A (eds.) status and dynamics of forests in Germany. *Ecol stud* 237. Springer nature, pp 167–198
- Hagedorn F, Saurer M, Blaser P (2004) A ¹³C tracer study to identify the origin of dissolved organic carbon in forested mineral soils. *Eur J Soil Sci* 55(1):91–100. <https://doi.org/10.1046/j.1365-2389.2003.00578.x>
- Harrell FE Jr, with contributions from Charls Dupont and many others (2020) Hmisc: Harrel Miscellaneous. R package version 4.4–1. <https://CRAN.R-project.org/package=Hmisc>. Accessed 20 Dec 2020
- Heinsdorf D (2002) Einfluss der Bewirtschaftung auf den Kohlenstoffhaushalt von Forstökosystemen im nordostdeutschen Tiefland. *Beitr. Forstwirtsch. u. Landsch.ökol.* 36: 168–174
- Hertel D (1995) Streuabbau in verschiedenen Stadien der Heide-Wald-Sukzession. Diploma thesis, University of Göttingen, Göttingen, Germany
- Hobbie SE, Reich PB, Oleksyn J, Ogdahl M, Zytzkowiak R, Hale C, Karoleswki P (2006) Tree species effects on decomposition and forest floor dynamics in a common garden. *Ecology* 87(9):2288–2297. [https://doi.org/10.1890/0012-9658\(2006\)87\[2288:TSEODA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2288:TSEODA]2.0.CO;2)
- Hou E, Chen C, Luo Y, Zhou G, Kuang Y, Zhang Y, Heenan M, Lu X, Wen D (2018) Effects of climate on soil phosphorus cycle and availability in natural terrestrial ecosystems. *Glob Chang Biol* 24(8):3344–3356. <https://doi.org/10.1111/gcb.14093>
- Houle D, Marty C, Augustin F, Dermont G, Gagnon C (2020) Impact of climate change on soil hydro-climatic conditions and base cation weathering rates in forested watersheds in eastern Canada. *Front For Glob Change* 3:535397. <https://doi.org/10.3389/ffgc.2020.535397>
- Jandl R, Lindner M, Vesterdal L, Bauwens B, Baritz R, Hagedorn F, Johnson DW, Minkinen K, Byrne KA (2007) How strongly can forest management influence soil carbon sequestration? *Geoderma* 137(3–4):253–268. <https://doi.org/10.1016/j.geoderma.2006.09.003>
- Jenkinson DS (1988) Soil organic matter and its dynamics. In: Ward A (ed) Russel's soil conditions and plant growth, 11th edn. Longman, Harlow, pp 564–607
- Kremser W (1990) Niedersächsische Forstgeschichte. In: Heimatbund Rotenburg/Wümme. Rotenburg/W, Germany
- Kuusela K (1994) Forest resources in Europe 1950–1990. Cambridge University Press, Cambridge. <https://doi.org/10.1017/CBO9780511752285>
- Ladegaard-Pedersen P, Elberling B, Vesterdal L (2005) Soil carbon stocks, mineralization rates and CO₂ effluxes under 10 tree species on contrasting soil types. *Can J For Res* 35(6):1277–1284. <https://doi.org/10.1139/x05-045>
- Laganière J, Angers DA, Paré D (2010) Carbon accumulation in agricultural soils after afforestation: a meta-analysis. *Glob Chang Biol* 16(1):439–453. <https://doi.org/10.1111/j.1365-2486.2009.01930.x>
- Lal R (2005) Forest soils and carbon sequestration. *For Ecol Manag* 220(1–3):242–258. <https://doi.org/10.1016/j.foreco.2005.08.015>
- Leuschner C (2001) Changes in forest ecosystem function with succession in the Lüneburger Heide. In: Tenhunen JD, Lenz R, Hantschel R (eds) Ecosystem approaches to landscape Management in Central Europe. *Ecol Stud*, vol 147. Springer, Berlin, Heidelberg, pp 517–568. https://doi.org/10.1007/978-3-662-04504-6_29
- Leuschner C, Wulf M, Bächler P, Hertel D (2013) Soil C and nutrient stores under scots pine afforestations compared to ancient beech forests of the German Pleistocene: the role of tree species and forest history. *For Ecol Manag* 310: 405–415. <https://doi.org/10.1016/j.foreco.2013.08.043>
- Link RM (2020) Corrmorant: flexible correlation matrices based on 'ggplot2'. R package version 0.0.0.9007. <http://github.com/r-link/corrmorant>. Accessed 20 Dec 2020
- Lorenz K, Lal R (2010) Carbon sequestration in Forest ecosystems. Springer, Berlin, Heidelberg. <https://doi.org/10.1007/978-90-481-3266-9>
- Lorenz K, Preston CM, Krumrei S, Feger K-H (2004) Decomposition of needle/leaf litter from scots pine, black cherry, common oak and European beech at a conurbation forest site. *Eur J For Res* 123(3):177–188. <https://doi.org/10.1007/s10342-004-0025-7>
- Meier IC, Knutzen F, Eder LM, Müller-Haubold H, Goebel M, Bachmann J, Hertel D, Leuschner C (2018) The deep root system of *Fagus sylvatica* on sandy soil: structure and variation across a precipitation gradient. *Ecosystems* 21(2):280–296. <https://doi.org/10.1007/s10021-017-0148-6>
- Meyer P, Wevell von Krüger A, Steffens R, Unkrig W (2006) Naturwälder in Niedersachsen – Schutz und Forschung. Bd. 1: Tiefland. Göttingen, Nordwestdeutsche Forstliche Versuchsanstalt
- Milnik A (2007) Zur Geschichte der Kiefernwirtschaft in Nordostdeutschland. *Eberswalder Forstliche Schriftenreihe* 32:14–21
- NW-FVA & NL (2019) Klimaangepasste Baumartenwahl in den niedersächsischen Landesforsten. Nordwestdeutsche Forstliche Versuchsanstalt, Niedersächsische Landesforsten. Aus dem Walde – Schriftenreihe Waldentwicklung in Niedersachsen, H 61
- Pausch J, Kuzakov Y (2018) Carbon input by roots into the soil: quantification of rhizodeposition from root to ecosystem scale. *Glob Chang Biol* 24(1):1–12. <https://doi.org/10.1111/gcb.13850>
- Pérez-Harguindeguy N, Díaz S, Cornelissen JH, Vendramini F, Cabido M, Castellanos A (2000) Chemistry and toughness predict leaf litter

- decomposition rates over a wide spectrum of functional types and taxa in Central Argentina. *Plant Soil* 218:21–30
- Poeplau C, Don A, Six J, Kaiser M, Nieder R, Benbi D, Chenu C, Cotrufo F, Derrien D, Grand S, Gregorich E, Griepentrog M, Gunina A, Haddix M, Kuzyakov Y, Kuhn A, Macdonald LM, Soong J, Trigalet S, Vermeire ML, Rovira P, van Wesemael B, Wiesmeier M, Yeasmin S, Yevdokimov I, Nieder R (2018) Isolating organic carbon fractions with varying turnover rates in temperate agricultural soils – a comprehensive method comparison. *Soil Biol Biochem* 125:10–26. <https://doi.org/10.1016/j.soilbio.2018.06.025>
- Polomski J, Kuhn N (1998) *Wurzelsysteme*. Haupt Verlag, Bern
- Prescott CE, Vesterdal L (2013) Tree species effects on soils in temperate and boreal forests: emerging themes and research needs. *Forest Ecol Manage* 309:1–3. <https://doi.org/10.1016/j.foreco.2013.06.042>
- Price SP, Bradford MA, Ashton MS (2012) Characterizing organic carbon stocks and flows in forest soils. In: Ashton MS, Tyrell ML, Spalding D, Gentry B (eds) *Managing Forest carbon in a changing climate*. Springer, Dordrecht, pp 7–30. https://doi.org/10.1007/978-94-007-2232-3_2
- Prietzl J (2004) Humusveränderungen nach Einbringung von Buche und Eiche in Kieferreinbestände. *J Plant Nutr Soil Sci* 167(4):428–438. <https://doi.org/10.1002/jpln.200421363>
- Prietzl J, Stetter U, Klemmt HJ, Rehfuess KE (2006) Recent carbon and nitrogen accumulation and acidification in soils of two scots pine ecosystems in southern Germany. *Plant Soil* 289(1-2):153–170. <https://doi.org/10.1007/s1104-006-9120-5>
- Reich PB, Oleksyn J, Modrzyński J, Mirozinski P, Hobbie SE, Eissenstat DM, Chorover J, Chadwick OA, Hale CM, Tjoelker MG (2005) Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. *Ecol Lett* 8(8):811–818. <https://doi.org/10.1111/j.1461-0248.2005.00779.x>
- Roy J, Saugier B, Mooney HA (2001) *Terrestrial global productivity*. Academic Press, San Diego
- Schlesinger WH (1991) *Biogeochemistry. An analysis of global change*, 3rd edn. Academic Press, Waltham, USA
- Schlesinger WH, Bernhardt ES (2013) *Biogeochemistry. An analysis of global change*, 1st edn. Academic Press, San Diego, USA
- Schulp CJE, Nabuurs G-J, Verburg PH, de Waal RW (2008) Effect of tree species on carbon stocks in forest floor and mineral soil and implications for soil carbon inventories. *For Ecol Manag* 256(3):482–490. <https://doi.org/10.1016/j.foreco.2008.05.007>
- Silver WL, Miya RK (2001) Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia* 129(3):407–419. <https://doi.org/10.1007/s004420100740>
- Spalding D, Kendirli E, Oliver CD (2012) The role of forests in global carbon budgeting. In: Ashton MS, Tyrell ML, Spalding D, Gentry B (eds) *Managing Forest Carbon in a Changing Climate*. Springer, Dordrecht, pp 165–179. https://doi.org/10.1007/978-94-007-2232-3_8
- Verheyen K, Bossuyt B, Hermy M, Tack G (1999) The land use history (1278–1990) of a mixed hardwood forest in western Belgium and its relationship with chemical soil characteristics. *J Biogeogr* 26(5):1115–1128. <https://doi.org/10.1046/j.1365-2699.1999.00340.x>
- Vesterdal L, Raulund-Rasmussen K (1998) Forest floor chemistry under seven tree species along a soil fertility gradient. *Can J For Res* 28(11):1636–1647. <https://doi.org/10.1139/x98-140>
- Vesterdal L, Ritter E, Gundersen P (2002) Change in soil organic carbon following afforestation of former arable land. *For Ecol Manag* 169(1-2):137–147. [https://doi.org/10.1016/S0378-1127\(02\)00304-3](https://doi.org/10.1016/S0378-1127(02)00304-3)
- Vesterdal L, Schmidt IK, Callesen I, Nilsson LO, Gundersen P (2008) Carbon and nitrogen in forest floor and mineral soil under six common European tree species. *For Ecol Manag* 255(1):35–48. <https://doi.org/10.1016/j.foreco.2007.08.015>
- Vogel C, Heister K, Buegger F, Tanuwidjaja I, Haug S, Schlöter M, Kögel-Knabner I (2015) Clay mineral composition modifies decomposition and sequestration of organic carbon and nitrogen in fine soil fractions. *Biol Fert Soils* 51(4):427–442. <https://doi.org/10.1007/s00374-014-0987-7>
- von Oheimb G, Härdtle W, Naumann PS, Westphal C, Assmann T, Meyer H (2008) Long-term effects of historical heathland farming on soil properties of forest ecosystems. *For Ecol Manag* 155:1984–1993
- Wickham H, Averick M, Bryan J, Chang W, D'Agostino McGowan L, François R, Grolemond G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Milton Bache S, Müller K, Ooms J, Robinson D, Paige Seidel D, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019) Welcome to the tidyverse. *J Open Source Softw* 4(43):1686. <https://doi.org/10.21105/joss.01686>
- Wördehoff R, Fischer C, Spellmann H (2017a) II. Cluster- und Kohlenstoffstudie Forst und Holz Niedersachsen. Nordwestdeutsche Forstliche Versuchsanstalt, Göttingen
- Wördehoff R, Fischer C, Spellmann H (2017b) II. Cluster- und Kohlenstoffstudie Forst und Holz Schleswig-Holstein. Nordwestdeutsche Forstliche Versuchsanstalt, Göttingen

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