Forest Ecology and Management 447 (2019) 67–76

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Ecosystem carbon stocks and their temporal resilience in a semi-natural beech-dominated forest

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ARTICLE INFO

Keywords:
Old-growth
Unmanaged forest
Climate change mitigation
Suserup Forest
Biomass
Dead wood
Litter
Mineral soil

ABSTRACT

Forest management, including setting aside non-intervention forests, is currently debated as a measure to efficiently mitigate climate change. Temperate, old-growth forests are rare and the long-term effect of setting aside forest reserves, e.g. for habitat conservation, on forest carbon stocks and carbon sequestration remains uncertain. In this study, we assessed the five principal forest carbon pools in a semi-natural, temperate forest in Denmark and evaluated the changes in biomass and dead wood carbon stocks over 20 years. We also benchmarked the current carbon stocks against those in managed beech-dominated forests in the same region. In the most recent inventory, carbon stocks totalled 395 Mg ha^{-1} of which 47% was in above-ground live biomass, 11% in below-ground biomass, 9% in dead wood, 2% in the forest floor, and 31% in the top 75 cm of the mineral soil. Compared to similar, but managed forests in the same region, carbon stocks in above- and below-ground biomass as well as in dead wood were notably larger. However, analyses of above- and below-ground biomass and dead wood carbon stocks showed remarkable stability during the past 20 years, despite major disturbances in terms of windthrows and various pathogens. Despite the overall stability of carbon stocks we observed some significant spatio-temporal changes. Notably, the observed dynamics illustrate a general retreat of *Q. robur* and increasing dominance of *F. sylvatica* under a small-scale disturbance regime. The forest floor and soil carbon stocks averaged 131 ± 4 Mg ha^{-1} and were very similar to those of managed beech-dominated forests, suggesting little potential for soil carbon sequestration from setting forests aside as unmanaged. Our study has implications for selection of adequate forest management strategies to efficiently mitigate climate change as it confirms the large and persistent carbon stocks in old-growth forests compared to managed forests, but offers no evidence of continued carbon sequestration in old-growth forests.

1. Introduction

It is estimated that about 10% of current global anthropogenic CO_2 emissions, making up the second largest source, can be attributed to land-use change (IPCC, 2014; Le Quéré et al., 2016). It follows that any comprehensive policy to mitigate increasing atmospheric CO_2 and in turn climate change, includes management of ecosystem carbon stocks. In accordance with Canadell and Raupach (2008), carbon emissions from forests can be mitigated through four major forest related activities: (i) increasing forest area through afforestation or reforestation, (ii) increasing carbon stocks in existing forests, (iii) increasing the use of wood for energy and materials to avoid fossil-fuel CO_2 emissions, and (iv) reducing emissions from deforestation and forest degradation. The resulting effect on CO_2 emissions of these activities depends on feedback loops between (ii), (iii), and (iv). For example increasing the use of wood as substitution for materials and energy will lower fossil-fuel emissions but also lower carbon stocks in existing forests. Oppositely, setting aside non-intervention forest for habitat protection may increase forest carbon stocks but increase fossil-fuel emissions. An adequate selection among different strategies of forest management is necessary to facilitate informed decisions on setting forests aside as non-intervention areas.

The accumulation of biomass and dead wood as well as larger carbon stocks in soils in some old-growth forests (Mund and Schulze, 2006; Vesterdal and Christensen, 2007) has led to suggestions that non-intervention forests may serve as efficient sinks for atmospheric CO_2 (Knohl et al., 2003; Thomsen, 2011). In this context, large carbon stocks are often misinterpreted as a sign of large rates of carbon sequestration and hence removals of atmospheric CO_2. However, as non-intervention forests mature, they are commonly expected to reach a steady state where carbon sequestration equals emissions from ecosystem respiration (e.g. Odum, 1969). Consequently, the effect of non-

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https://doi.org/10.1016/j.foreco.2019.05.038
Received 10 April 2019; Received in revised form 13 May 2019; Accepted 15 May 2019
Available online 29 May 2019
0378-1127/

intervention forests on atmospheric CO_2 may be limited but dependent on the potential magnitude of carbon stocks. A synthesis of carbon-flux studies suggested that "old-growth forests" may sequester carbon in spite of being several centuries old (Luyssaert et al., 2008) and hence that such forests may play an important role in climate mitigation. In contrast, several authors have argued that the mitigation potential of non-intervention forests is small and limited in time, especially when also considering substitution effects on emissions from fossil fuels and carbon intensive materials (Eriksson et al., 2007; Klein et al., 2013; Lippke et al., 2011; Taeroe et al., 2017).

The contrasting reports regarding the effect of non-intervention forests on carbon sequestration can partly be ascribed to the fact that only few forests in Europe have sufficient continuity to exhibit steady state or near steady state conditions. Hence, there are only few examples to support case studies of baseline carbon stocks for different forest ecosystems and inform on the effect of forest management on ecosystem climate change mitigation potentials (Ammer et al., 2018). In Denmark, the intensively studied Suserup Forest (e.g. Emborg et al., 1996; Heilmann-Clausen et al., 2007; Larsen et al., 2010; Vesterdal and Christensen, 2007) has a documented forest continuity of more than 6,000 years (Hannon et al., 2000) and has been only slightly affected by human intervention during the last 200 years. Consequently, Suserup Forest is more developed in terms of steady state conditions than many other European forest reserves, which have more recently started to recover from former exploitation.

In the present study, we assessed all five principal forest carbon pools in Suserup Forest: above- and below-ground biomass, dead wood, forest floor and mineral soil. We evaluated species-specific, spatial, and temporal changes in ecosystem carbon stocks to evaluate the resilience of carbon stocks in relation to ecosystem dynamics. The current carbon stocks were benchmarked against those in managed beech-dominated forests in the same region. We hypothesize that in non-intervention forest such as Suserup Forest: (1) absence of harvesting would lead to larger carbon stocks in above- and below-ground biomass as well as in dead wood, (2) absence of harvesting would lead to larger soil carbon stocks due to higher input of organic matter, particularly in form of woody debris, and that (3) continued ecosystem carbon inputs would lead to persistent net carbon sequestration and consequently in a significant increase in forest carbon stocks over time.

2. Materials and methods

Suserup Forest is a 19.2 ha semi-natural, nemoral beech (*Fagus sylvatica* L.) dominated forest located on central Zealand (UTM zone 32: E661870, N6139930). The climate is cool-temperate with mean annual temperature of 8.8° and a mean annual precipitation of 674 mm, quite evenly distributed across the year, although the majority falls during late summer and autumn (average climatic data 2001–2010, Wang, 2013). The parent material is a nutrient rich, calcareous glacial till with approximately 20% clay and the soil has been classified as an Inceptic Hapludalf (Vejre and Emborg, 1996).

The forest cover of Suserup Forest dates back to before 4200 BC (Heilmann-Clausen et al., 2007). According to management plans dating back to the 1850s, the forest was managed as a minimal intervention forest. Suserup Forest was formally conserved for biological and recreational reasons in 1925. Although the conservation plan did not fully exclude fellings, only few trees were harvested until 1961, when the protection status was changed to non-intervention forest. Previous studies have shown that the forest may be stratified into three parts (Emborg et al., 1996, Figure 1): Part A characterized by minimal human intervention during more than 200 years, Part B that was affected by grazing until 1792 followed by human seeding of oak around 1820, and Part C characterized by more wet soils in the riparian zone along the lake side. A detailed description of the history of Suserup Forest can be found in Heilmann-Clausen et al. (2007) (Fig. 1).

Today Suserup Forest is a mixed deciduous forest with an average basal area of 37.5 $m^2\,ha^{-1}$. Beech (*Fagus sylvatica* L.) is the dominating species and takes up 53% of the basal area. Other important species are pendunculate oak (*Quercus robur* L., 18%), European ash (*Fraxinus excelsior* L., 18%), common alder (*Alnus glutinosa* L., 7%), and sycamore maple (*Acer pseudoplatanus* L., 2%). Differences in former management and soil conditions reflected in the stratification of the forest into parts A, B and C are still visible in the forest. For instance there is a larger proportion of large *Q. robur* and ingrowth of *A. pseudoplatanus* in the eastern part (Part B).

3. Inventories and calculations

The first inventory of Suserup Forest was initiated in 1992 (Emborg et al., 1996) and focused on forest structure and dynamics in old-growth deciduous forests. The inventory was repeated in 2002 and 2012 with the same focus as in the first inventory, but including also other aspects of undisturbed forests. Changing focus during the two decades of inventories has led to an increase in the intensity of the inventory related to the five basic carbon pools (above- and below-ground biomass, dead wood, forest floor, and mineral soil) over time.

3.1. Tree biomass

When the study of Suserup Forest was initiated in 1992, the forest was divided into a regular grid of 50 × 50 m (Fig. 1) and the grid intersections were marked with iron pipes. Within each 0.25 ha grid cell (at the plot edges some grid cells were less than 0.25 ha), all trees with $dbh \geqslant 29$ cm were measured for diameter at breast height (*dbh*, 1.3 m above ground) and individual tree positions were obtained by measuring their distances perpendicular to the grid lines with a steel measurement tape. Trees with $dbh<29$ cm but $\geqslant 3$ cm were callipered at breast height and recorded in 2 cm diameter classes for each species. Height measurements were obtained on a random sample of trees from across the forest, including 482 height measurements of beech, 214 of ash, 31 of pendunculate oak and 215 of various other species. The measurements were repeated in 2002 according to the above-mentioned procedures including positioning of ingrowth with $dbh \geqslant 29$ cm since 1992 and dead wood (standing and lying). In 2002 height measurements were not conducted and trees with $dbh<29$ cm were only measured in three 100 × 100 m blocks of the original grid.

When measurements were repeated in fall 2012/spring 2013, the original grid was maintained as a practical subdivision of the research area, but tree positions were captured with a Trimble GPS Pathfinder Pro XRS receiver mounted with a Trimble Hurricane antenna and a Trimble Geo Beacon for real time differential correction, fitted into a backpack. This equipment is expected to yield sub-one meter precision even under dense canopies. All standing live or dead trees with $dbh>5$ cm were cross callipered at breast height and a random sample of 290 trees were measured for height.

Based on the pairwise measurements of *dbh* and height, species-specific diameter-height relationships ($h_{ij} = (dbh_{ij}/(\alpha_1 + \alpha_2 \cdot dbh_{ij}))^{\alpha_3} + 13$, where h_{ij} and dbh_{ij} are the height in dm and diameter in mm of the *i*th tree of the *j*th species) were estimated using non-linear regression to calculate the height of trees not measured for height. As it is expected that the diameter-height relationship may differ across the forest, we sampled the 30 nearest trees measured for height as basis for estimating local relationships.

Individual tree above- and belowground biomass was estimated using the measured *dbh*, measured or estimated total tree height, and species-specific biomass equations for the most abundant species (beech, pendunculate oak, sycamore maple, birch, common alder, and lime) (Nord-Larsen et al., 2017). In case of tree species for which no local biomass equations were available, individual tree volumes were first estimated using species-specific volume equations (Madsen, 1987) and aboveground biomass was subsequently estimated using species-specific basic densities (Moltesen, 1988) and expansion factors for beech (Skovsgaard and Nord-Larsen, 2011). For all calculations (both

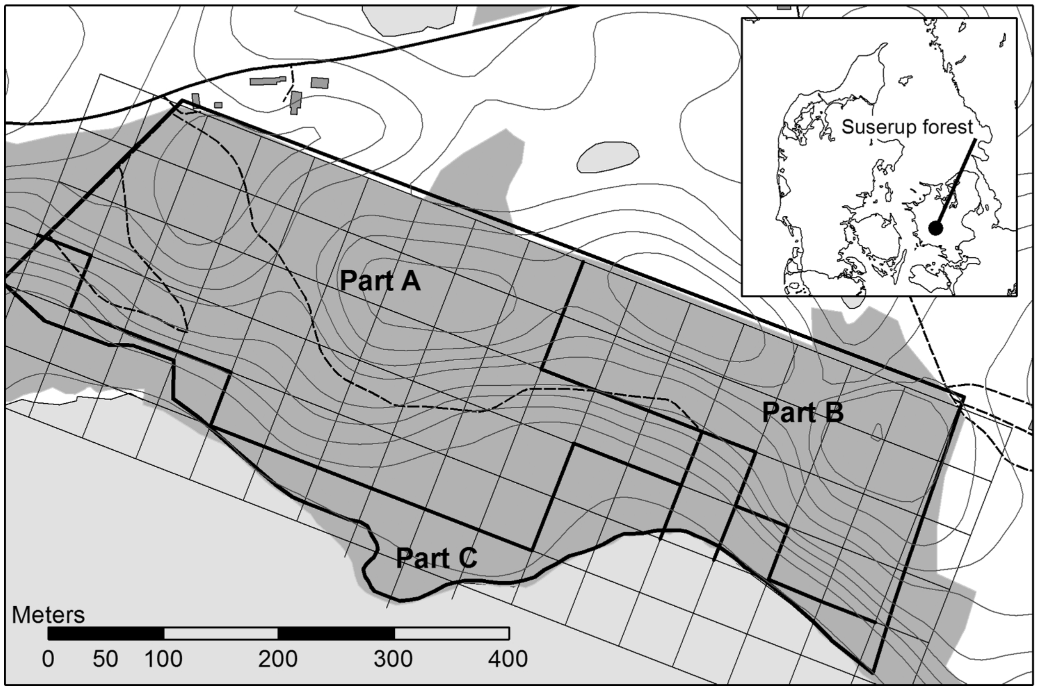

Fig. 1. Suserup Forest. The original 50 × 50 m sample grid is shown on the map. The western part of the forest is less disturbed than the eastern part, which was affected by grazing.

live and dead trees), biomass was converted to carbon by assuming a carbon concentration of 47% in accordance with IPCC guidelines (IPCC, 2006). The procedure is identical to that used with the Danish National Forest Inventory (Nord-Larsen and Johannsen, 2016).

3.2. Dead wood

In 1992, dead trees were registered and measured for assessment of forest habitats, but measurements were insufficient to allow for carbon stock estimation. In 2002 and 2012, standing and lying dead wood was sampled using line transect sampling from 15 and 35 transects, respectively. Dead wood was only sampled in the upland parts (in 2002 only Part A, in 2012 Parts A and B), excluding the wet riparian part close to the lake (Part C). The transects were 50 meters long and 10 m wide (to allow measurements of standing dead wood). All pieces of lying dead wood >10 cm intercepted by the transects were callipered and the degree of decay was recorded according to a scale previously used for Suserup Forest (Vesterdal and Christensen, 2007). Standing dead wood was calipered at breast height and the total height of broken stems was measured using a clinometer.

Lying dead wood mass was estimated according to Husch et al. (2002, p. 243-245), using species specific wood basic densities (Moltesen, 1988) and a species specific reduction factor to account for lost carbon in decayed wood. The decay reduction factors were estimated from 236 samples of dead wood collected in Suserup Forest and representing different tree species and decay classes. The four decay classes were assessed visually for the samples similar to the field assessment and included: (1) Wood without or with only minor decay (<10% of the wood). A pointed object can penetrate 1–2 mm into the wood, (2) Some structural change on 10–25% of the wood. A pointed object can penetrate less than 1 cm into the wood. (3) 26–75% of the wood is decayed. A pointed object can penetrate 1–5 cm into the wood. (4) 75–100% of the wood is heavily decayed. A pointed object can penetrate more than 5 cm into the wood. Basic density of the samples was estimated from the sample volume and dry weight. Volume of the samples was measured using pycnometry and dry weights were obtained after drying at 103 °C until constant weight. We calculated the average basic density for each decay class and estimated the decay reduction factor as the ratio between the average basic densities of the decayed and un-decayed samples.

Standing dead wood mass of unbroken stems was estimated using the same approach as for live trees, with the exception of applying the aforementioned reduction factors. For broken stems, volume of the standing part was estimated using stem taper functions for beech, oak and ash (Madsen, 1987), and biomass was calculated by applying the species-specific wood basic densities and decay reduction factors.

3.3. Forest floor and mineral soil

Forest floor and mineral soil carbon were only assessed from a spatially representative sample in the 2012 inventory of Suserup Forest, although a minor study was conducted in 2007 (Vesterdal and Christensen, 2007). Soils were sampled in Parts A and B of the forest using a systematic sampling approach. Sampling points within Parts A and B were placed in the centre of every second column of the original 50 × 50 m grid covering the forest. This strategy resulted in 22 plots sampled within Part A and 11 plots sampled within the smaller Part B. We only sampled the upland parts of the forest and excluded the wet riparian part close to the lake (Part C).

Soils were sampled in late May 2013 in circular plots (r = 2 m) with four samples from the cardinal points (N, S, E, W) and one sample from the centre of the plot. Forest floors were sampled within a frame of 25 × 25 cm (Vesterdal et al., 2008) and included all materials accumulated on top of the mineral soil. The mineral soil was sampled in the same spot where the forest floor had been removed by coring down to 75 cm. Soil samples were pooled in the field for the layers 0–10, 10–25, 25–50 and 50–75 cm.

Bulk density and stone content of mineral soils were measured in four plots in Parts A and B, respectively. Samples were extracted from mini soil profiles using bulk density rings (100 cm^3) in the layers 0–10, 10–25 and 25–50 cm. Bulk density in the layer 50–75 cm was estimated by use of a Danish pedotransfer function based on carbon concentration and soil type (Vejre et al., 2003).

In the laboratory, forest floors were dried at 55°C and weighed. A sub-sample was dried at 105 °C to correct for moisture content. The material was subsequently finely ground by a ball mill following a cutting mill (Retsch SM2000 and Retsch MM2, Retsch, Germany). The mineral soil was sieved (2 mm) and this fine fraction was finely ground by an electrical mortar (Retsch RM100, Retsch, Germany). We tested the presence of inorganic carbon in the deepest soil samples (25–50 cm and 50–75 cm) by addition of 1 M HCl. If effervescence was observed and/or pH was ⩾ 6 (14% of all samples), carbonate removal prior total carbon analysis was performed by adding a solution of 6% (w/v) H_2SO_3 to ground soil samples. Addition of H_2SO_3 continued until it no longer yielded a reaction and samples were thereafter allowed to dry (Skjemstad and Baldock, 2006). Total organic C and N concentrations were determined on oven dried (60 °C) ground samples by dry combustion, based on the Dumas method (Matejovic, 1993) using a FLASH 2000 EA NC Analyzer (Thermo Fisher Scientific, Waltham, MA, USA).

Forest floor carbon content was calculated by multiplying C concentrations with forest floor mass. The forest floor mass was calculated based on dry weight (105 °C). The bulk density calculations for the three upper mineral soil layers were done according to:

$$\rho_i = \frac{W_{<2mm},\ i}{Vol_{auger,i} - Vol_{>2mm,i} - Vol_{roots,i}},$$

where ρ_i denotes the bulk density in g cm^{-3} of the ith soil layer, $W_{<2mm,i}$ is the dry weight of the fine fraction in grams and $Vol_{auger,i}$, $Vol_{>2mm,i}$, $Vol_{roots,i}$ correspond to the volumes (cm^3) of the auger section, the coarse fraction and roots, respectively. Mineral soil carbon stocks of a given soil layer i was calculated according to:

$$SOC_i = \rho_i\left(1 - \frac{Vol_{auger,i} - Vol_{<2mm,i} - Vol_{roots,i}}{Vol_{auger,i}}\right)d_i C_i,$$

where SOC is the soil organic carbon (Mg ha^{-1}), d is the soil layer depth in cm and C is the carbon concentration in mg g^{-1}. In accordance with the standard approach, carbon content in the coarse fraction (>2 mm) was neglected as this fraction contains insignificant amounts of carbon.

Soil carbon stocks in Suserup Forest were compared to forest floor and mineral soil carbon stocks in 19 NFI plots with beech-dominated managed forests on similar soil type (Alfisols) in the same region (central and southern Zealand). The mean stand age of the 19 plots was 82 years (range 30–142 years). Soil sampling in the NFI plots was based on exactly the same methods (soil layers and equipment used) and carried out in 2009–2010. Forest floor and mineral soil were sampled in ten points within the circular NFI plots with a radius of 15 m. Sample preparation, carbon analysis and calculation of forest floor and mineral soil carbon stocks followed the same procedures as in case of Suserup Forest samples with the only exception that bulk densities of all four mineral soil layers were estimated based on pedotransfer functions (Vejre et al., 2003).

4. Results

In 2012, carbon stocks totalled 395 Mg ha^{-1} of which 47% was in above-ground live biomass, 11% in below-ground biomass, 9% in dead wood, 2% in the forest floor, and 31% in the top 75 cm of the mineral soil. The overall distribution of carbon among the five principal pools was however subject to some spatial and temporal variation across the 20 years of measurements in Suserup Forest.

4.1. Biomass carbon

The average total biomass carbon stock in Suserup Forest in 2012 was 230 Mg ha^{-1} of which 45 Mg ha^{-1} or 19.6% was stored in below-ground biomass. The largest share of biomass carbon was stored in beech (56.6%) followed by oak (15.2%), ash (16.5%), and sycamore maple (6.8%) (Fig. 2, Table 1).

The carbon stock varied considerably among different parts of the forest (Table 2). The coefficient of variation between 50 × 50 m cells across the forest was 18.9%, reflecting differences in the growing conditions and species mixtures. The carbon stock in biomass was highest in the eastern part of the forest (Part B, 261 Mg ha^{-1}) and lowest in the riparian strip near the lake (Part C, 205 Mg ha^{-1}).

During the three inventories conducted in 1992, 2002, and 2012, the total biomass carbon stock changed from 213 Mg ha^{-1} in 1992 to 230 Mg ha^{-1} in 2012, corresponding to an 8% increase between 1992 and 2012, made up of a 7% decrease between 1992 and 2002 and a 16% increase between 2002 and 2012 (Table 1). For beech there has been a gain of carbon in diameter classes <60 cm and a loss in diameter classes ⩾ 60 cm, while for oak we observed a loss of carbon in most diameter classes (Fig. 3). For ash we observed both gains and losses across the diameter classes during the 20 year period while for sycamore maple there has been a general gain in carbon stocks.

4.2. Carbon stock in dead wood

In 2012, the carbon stock in dead wood amounted to 35 ± 5 Mg ha^{-1} (Table 2) of which 61% was lying on the ground (not shown). The major part of the dead wood was beech (43%) and oak (36%) (Fig. 4). The dead wood carbon stock varied considerably among transects, illustrating the uneven distribution of dead wood in the forest. Despite the large variation in dead wood carbon among transects, the carbon stock estimates varied very little among the two parts of the forest (A and B) ranging between 34 ± 7 and 36 ± 6 Mg ha^{-1}. Since the first measurement in 2002 the dead wood carbon stock in Part A had increased by 37%.

4.3. Forest floor and mineral soil

Forest floor carbon stocks were very similar within the two parts of the forest, and the carbon stock averaged 6.9 ± 0.6 Mg ha^{-1} (Table 2). Mineral soil carbon stocks were relatively similar within the four sampled layers but there was a trend of lower carbon stocks in the three layers within 0–50 cm in Part B. Soil carbon stocks in the entire sampled soil profile were slightly higher in Part A (134 ± 6 Mg ha^{-1}) than in Part B (125 ± 7 Mg ha^{-1}), but the difference was not significant ($P = 0.29$, Fig. 5).

Forest floor and mineral soil carbon stocks did not differ from the respective average carbon stocks in 19 managed beech-dominated NFI plots in central and southern Zealand (135 ± 3 Mg ha^{-1}). Mineral soil carbon stocks were slightly larger in the top 0–10 cm mineral soil in the managed beech forests but then slightly lower in 25–75 cm than in Suserup Forest (Fig. 5).

5. Discussion and conclusions

5.1. Biomass carbon stocks

In Suserup Forest the average biomass carbon stock in 2012 totalled 230 Mg ha^{-1}, corresponding to 3.5 times the average for Danish forests (65 Mg ha^{-1}, Nord-Larsen et al., 2019) and 1.5 times the average of beech forests within the same region (153 Mg ha^{-1}, Nord-Larsen et al., 2019)). Obviously, the much smaller average regional biomass carbon stock reflects that many of the forests are in the early stages of the forest cycle, where ecosystem production exceeds respiration, resulting in accumulation of carbon stocks. When considering beech forests older than 100 years, biomass carbon stocks in managed forests are similar to those in Suserup Forest (Fig. 6).

Similar results were obtained in a study of managed and non-intervention forests in Germany. In a regular shelterwood system, similar to common practices of beech management in Denmark, biomass carbon stocks peaked at 231–233 Mg ha^{-1} around an age of 100 years, but averaged 149–160 Mg ha^{-1} across the full rotation (Mund, 2004). In the same study, carbon stocks averaged 179 Mg ha^{-1} in forests

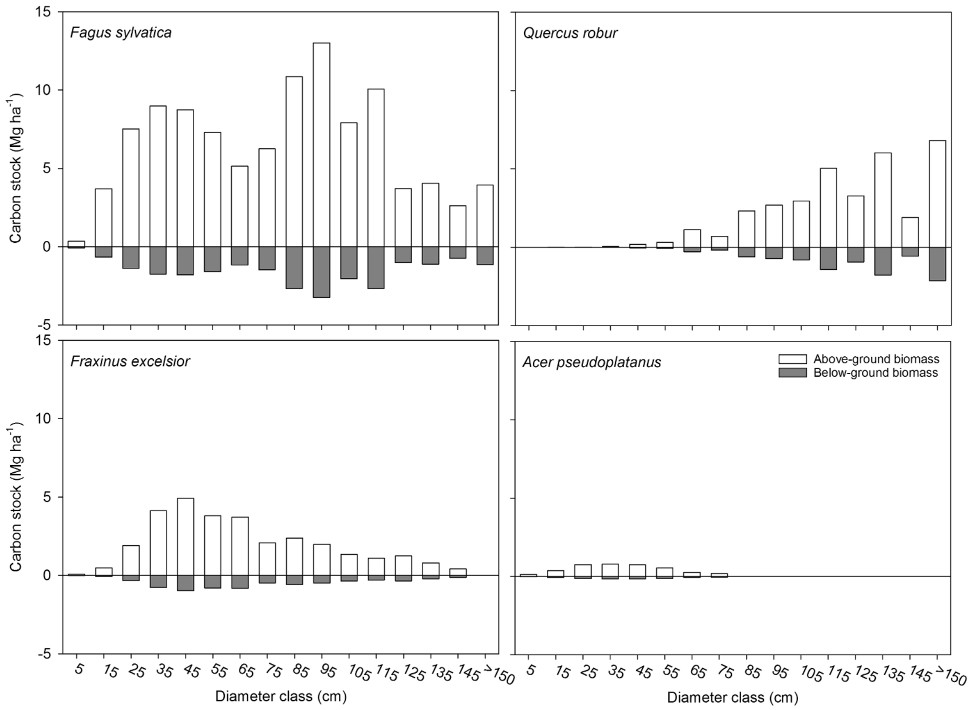

Fig. 2. Biomass carbon stocks in Suserup Forest in 2012. Belowground carbon stocks are shown as negative figures in grey.

managed by a selection system in Revier Langula (Germany). Although this was substantially larger than the full rotation average stock observed for the regular shelterwood system, the variation was large (range 154–219 Mg ha^{-1}) and the difference in average carbon stocks between selection forestry and the regular shelterwood system was insignificant (Mund, 2004). Finally, the biomass carbon stock in Suserup Forest was well within the range observed in the non-intervention beech forests in National Park Hainich (Germany) (212.7–285.0 Mg ha^{-1}, Mund, 2004). In the study of managed and non-intervention forests in Germany, Mund (2004) found no significant difference between non-intervention and selection system carbon stocks, while the full-rotation average of the shelterwood system was significantly lower than observed for the non-intervention forest ($P = 0.013$, Mund, 2004).

From the first measurement in 1992, the biomass carbon stock decreased 7% during the following 10-year period, but hereafter increased 16% in the next 10-year period, leading to a total increase in the biomass stock of 8% from 1992 to 2012. The observed fluctuations were likely caused by the catastrophic storm on December 3rd 1999 (Bigler and Wolf, 2007) and a subsequent regeneration of the biomass carbon stock. Considering the magnitude of the damage to the forest in 1999, the rapid regeneration of biomass demonstrates a remarkable resilience of this carbon stock. Despite the periodical changes in the biomass carbon stock, comparison with similar studies of unmanaged forests (e.g. Mund, 2004) corroborates that the biomass carbon stocks in Suserup Forest has reached an approximate steady state characterized by similar rates of biomass growth and mortality, i.e. the biomass stock remains relatively stable.

Regardless of the apparent stability of biomass carbon stocks in Suserup Forest, the average numbers cover substantial spatio-temporal variation. During the past 20 years of inventories there has been an

Table 1
Average growing stock, aboveground (ag), and belowground (bg) carbon stocks in Suserup Forest. Standard deviations among 50 × 50 m cells are provided in brackets.

Year	Variable	Unit	*F. sylvatica*	*Q. robur*	*F. excelsior*	*A. pseudoplatanus*	Other	Sum
1992	Volume	$m^3\,ha^{-1}$	344.4	136.4	106.1	6.4	84.4	677.8
			(125.2)	(70.5)	(45.5)	(8.8)	(51.1)	(135.6)
	Carbon (ag)	Mg ha^{-1}	90.2	40.5	26.0	1.4	11.9	169.9
			(34.2)	(21.8)	(11.9)	(1.7)	(8.6)	(37.3)
	Carbon (bg)	Mg ha^{-1}	21.9	11.6	5.7	0.3	3.1	42.6
			(8.5)	(6.4)	(2.8)	(0.4)	(2.3)	(9.5)
2002	Volume	$m^3\,ha^{-1}$	325.0	130.3	103.7	7.8	60.0	626.9
			(128.0)	(70.1)	(41.5)	(11.2)	(51.1)	(135.9)
	Carbon (ag)	Mg ha^{-1}	83.7	36.2	25.7	1.9	10.7	158.2
			(32.2)	(20.4)	(10.5)	(2.6)	(9.4)	(34.4)
	Carbon (bg)	Mg ha^{-1}	20.3	10.4	5.6	0.4	2.9	39.6
			(8.1)	(5.9)	(2.4)	(0.5)	(2.6)	(8.9)
2012	Volume	$m^3\,ha^{-1}$	371.9	116.2	116.2	13.7	70.2	688.1
			(121.7)	(64.3)	(41.0)	(16.0)	(57.7)	(128.4)
	Carbon (ag)	Mg ha^{-1}	104.1	33.3	30.4	3.8	13.2	184.8
			(33.9)	(18.5)	(10.7)	(4.4)	(10.4)	(34.6)
	Carbon (bg)	Mg ha^{-1}	24.4	9.6	6.7	0.8	3.5	45.0
			(8.4)	(5.4)	(2.4)	(0.9)	(3.0)	(8.9)

Table 2
Carbon stocks in the five major compartments in the three different parts of the forest and for the entire sampled area of Suserup Forest. Standard deviations among 50 × 50 m cells (biomass), transects (dead wood), and sample plots (litter layer and mineral soil) are provided in brackets along with the sample size, i.e (std.dev, n). No sample size has been provided for above- and below-ground biomass as the entire area was sampled.

Part	Biomass		Dead wood	Forest floor	Mineral soil			
	Aboveground	Belowground			0–10 cm	10–25 cm	25–50 cm	50–75 cm
	Carbon, Mg ha^{-1}							
1992								
A	164.6	40.7	–	–	–	–	–	–
	(29.6, –)	(7.9, –)	–	–	–	–	–	–
B	201.8	52.4	–	–	–	–	–	–
	(22.4, –)	(6.3, –)	–	–	–	–	–	–
C	152.7	37.2	–	–	–	–	–	–
	(55.2, –)	(13.2, –)	–	–	–	–	–	–
Average	169.9	42.6	–	–	–	–	–	–
	(37.3, –)	(9.5, –)	–	–	–	–	–	–
2002								
A	150.4	37.0	24.7	–	–	–	–	–
	(26.3, –)	(6.9, –)	(22.0, 15)	–	–	–	–	–
B	185.5	48.0	–	–	–	–	–	–
	(21.5, –)	(6.3, –)	–	–	–	–	–	–
C	152.6	38.0	–	–	–	–	–	–
	(52.4, –)	(12.9, –)	–	–	–	–	–	–
Average	158.2	39.6	24.7	–	–	–	–	–
	(34.4, –)	(8.9, –)	(22.0, 15)	–	–	–	–	–
2012								
A	183.7	43.7	33.9	6.9	32.4	36.8	39.9	17.9
	(25.6, –)	(7.0, –)	(32.9, 20)	(4.2, 22)	(5.0, 22)	(7.8, 22)	(11.7, 22)	(4.9, 22)
B	208.5	52.5	35.7	7.1	29.6	33.8	34.1	19.9
	(24.9, –)	(7.0, –)	(24.3, 15)	(2.5, 11)	(4.9, 11)	(8.4, 11)	(9.8, 11)	(9.3, 11)
C	164.4	40.6	–	–	–	–	–	–
	(52.2, –)	(12.6, –)	–	–	–	–	–	–
Average	184.8	45.0	34.7	6.9	31.5	35.8	38.0	18.5
	(34.6, –)	(8.9, –)	(29.2, 35)	(3.7, 33)	(5.1, 33)	(8.0, 33)	(11.3, 33)	(6.6, 33)

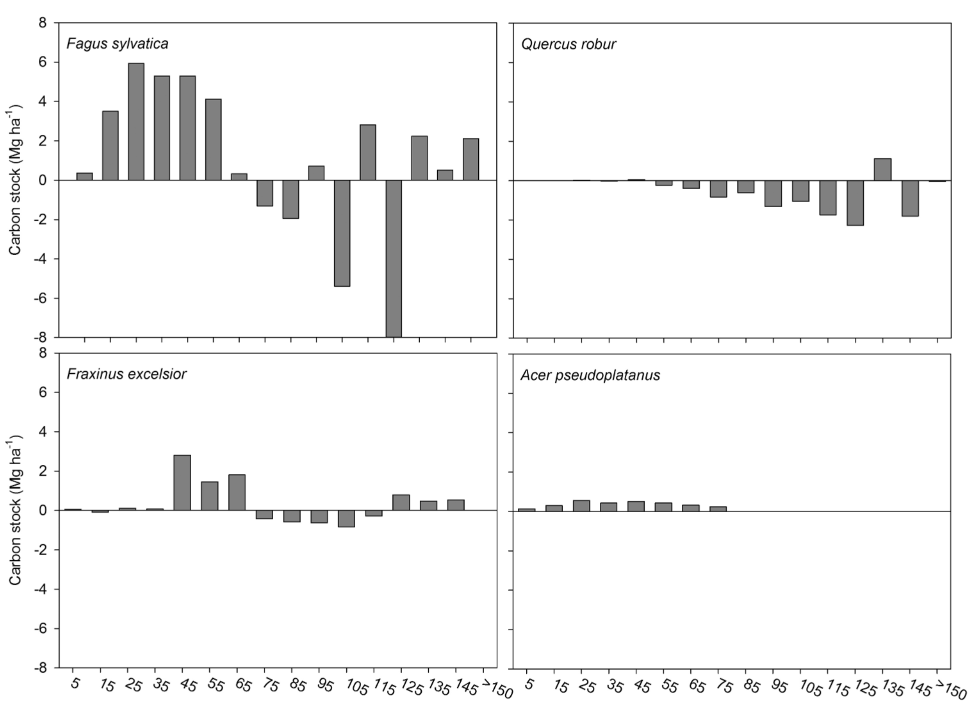

Fig. 3. Change in live biomass carbon pools from 1992 to 2012, for the four most common tree species in Suserup Forest.

unambiguous loss of carbon in *Q. robur* and a gain in *A. pseudoplatanus*, particularly in the eastern and previously grazed Part B of the forest, which is believed to have a shorter history as non-intervention forest than the western part (Heilmann-Clausen et al., 2007). The observed dynamics illustrate a general retreat of *Q. robur* and increasing dominance of *F. sylvatica* under a small-scale disturbance regime where *Q.*

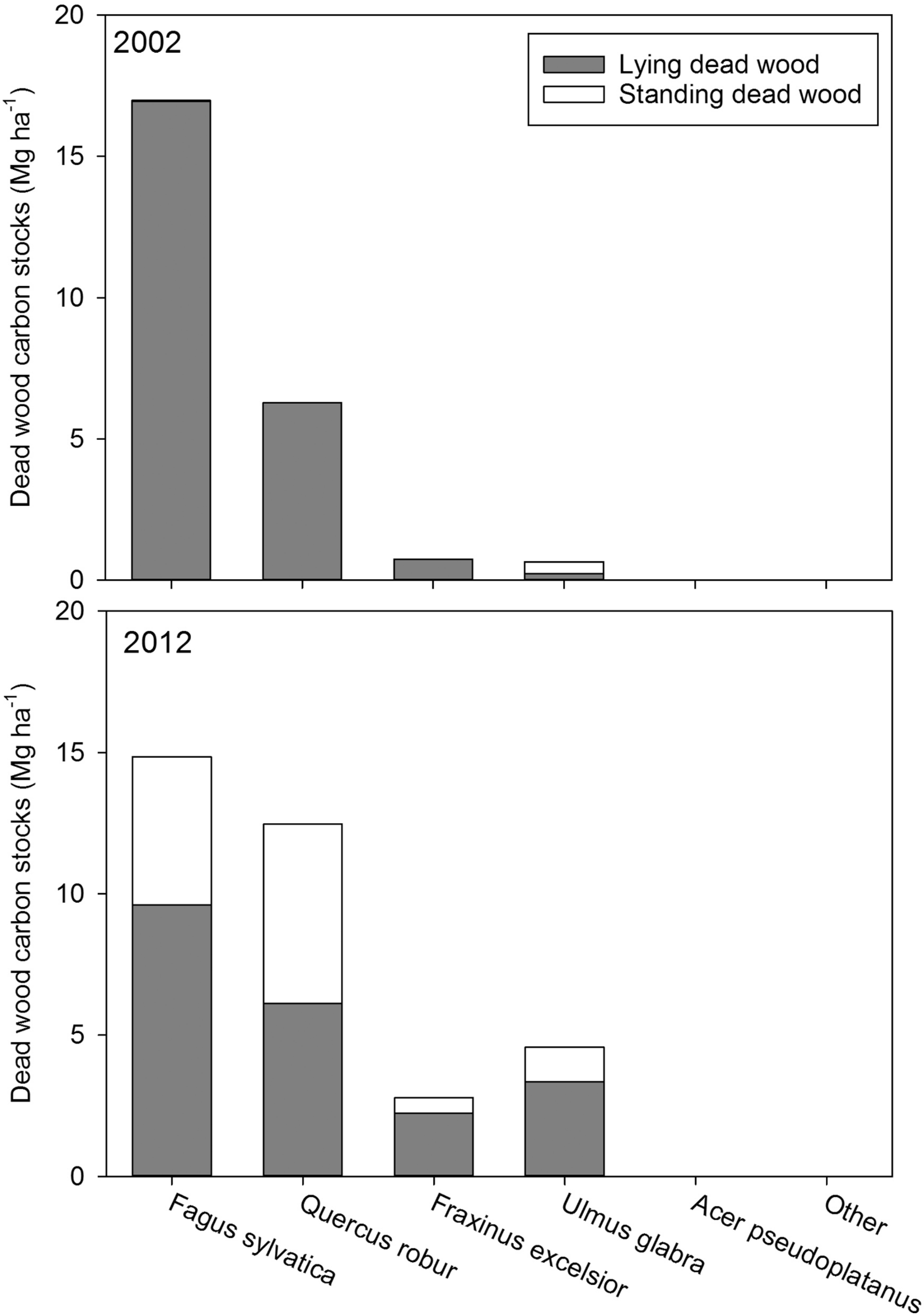

Fig. 4. Carbon stocks in dead wood in Suserup Forest in 2002 and 2012. In 2002, dead wood carbon stocks were only measured in the oldest part of the forest (Part A).

robur is unable to compete with *F. sylvatica* and *A. pseudoplatanus* (Larsen et al., 2010; Meyer, 2005). Currently, Part B of the forest supports a larger average biomass carbon stock than Part A, probably as a consequence of the development of a multi-layered structure in the favourable light environment under the large oak trees. It is however likely that future dominance of *A. pseudoplatanus* and subsequently *F. sylvatica* will lead to a less multi-layered forest structure and a gradual decrease in biomass carbon to reach a level similar to that in Part A.

The biomass carbon stock in 2002 was 197.8 Mg ha^{-1}, which is less than calculated in a previous study (225 Mg ha^{-1}, Vesterdal and Christensen, 2007). The observed difference is due to improvements in the models applied in biomass estimation (i.e. development of new biomass models and expansion functions).

5.2. Dead wood

Compared to Danish forests in general (Nord-Larsen et al., 2019), dead wood carbon stocks in Suserup Forest were 43 times larger, reflecting obvious differences in management as well as species and age composition. Average dead wood carbon stocks in broadleaf forests in the same region (Zealand) as Suserup Forest are 1.5 t ha^{-1} (unpublished material from Nord-Larsen et al., 2019), corresponding to only 4% of the deadwood carbon stored in Suserup. Since the inventory in 2002, the dead wood carbon stock had increased by 10 Mg ha^{-1}. The

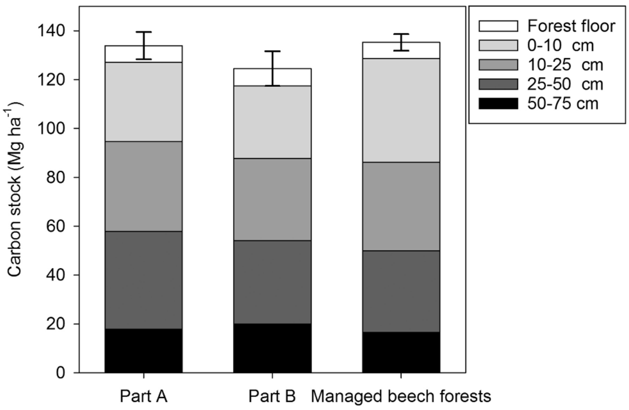

Fig. 5. Total soil carbon stocks and the contribution of individual soil layers in parts A (22 plots) and B (11 plots) of Suserup Forest and similar data from 19 managed beech-dominated NFI plots in central and southern Zealand. Bars indicate standard errors of the total soil carbon stock.

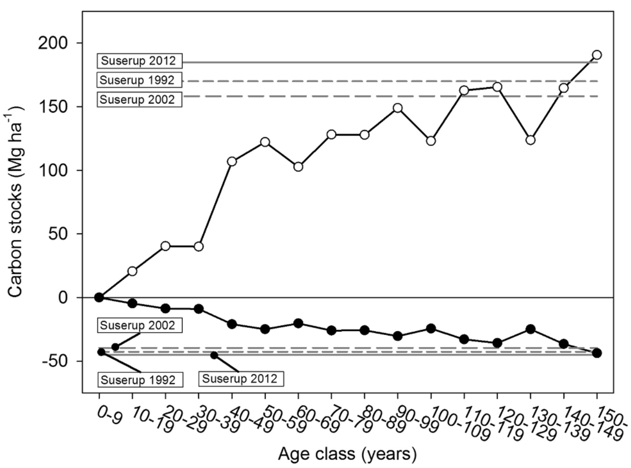

Fig. 6. Above- and below-ground (negative) biomass carbon stocks in Danish beech forests (dots, full lines) compared with Suserup Forest stocks measured in 1992, 2002, and 2012 (grey lines). The reference forest data is collected from a random sample of beech dominated forests (n = 215) as part of the Danish NFI (unpublished data from Nord-Larsen et al., 2019) within the same region as Suserup Forest. Age-classes (midpoints) are the predominant stand age registered at the inventory plots.

increase may be due to recent windthrows in 2005 and 2011 but it seems that beginning senescence of several hundred year old oaks and death of ash trees due to ash dieback (*Hymenoscyphus fraxineus*) have been the main contributors to the increase in dead wood carbon stores.

The dead wood carbon stock in Suserup Forest vastly exceeded the stocks observed in the non-intervention beech forests in National Park Hainich (Germany) (3.1–9.3 Mg ha^{-1}, Mund, 2004). The dead wood carbon stock in Suserup Forest was however comparable to that of old-growth beech-oak forests in Bavaria where carbon stocks of coarse woody debris (d>7 cm) ranged between 23.2–30.4 Mg ha^{-1} (Krüger et al., 2017). The relatively low dead wood carbon stocks at National Park Hainich may reflect differences in growth, species composition, disturbance regimes, or decay rates but are most likely caused by differences in former forest use. The non-intervention forest in National Park Hainich was only strictly protected since 1997 and although no regular management was conducted from 1965 large and valuable stems were harvested also during this period (Wäldchen et al., 2011). Considering the longevity of temperate forest trees it is unlikely that the dead wood carbon stock would have reached a steady state.

5.3. Forest floor and mineral soil

An earlier inventory of forest floor and mineral soil carbon based on only four soil pits in Part A of Suserup Forest (Vesterdal and Christensen, 2007) reported a forest floor carbon stock of 4.5 Mg ha^{-1} and 132 Mg ha^{-1} in the entire soil profile to 1 m (estimated total mineral soil carbon stock to 75 cm 123 Mg ha^{-1}). The inventory in 2012 had a much higher spatial resolution and coverage but resulted in comparable forest floor and mineral soil carbon stocks for Part A (6.9 and 127 Mg ha^{-1}, respectively).

We hypothesized that higher input of organic matter to soils, particularly in form of woody debris because of no or limited harvesting, would lead to higher soil carbon stocks in Suserup Forest than in managed forests. However, benchmarking of the soil carbon stocks in Suserup against stocks in 19 beech-dominated forests within the same region did not support the hypothesis of higher SOC stocks in the long-term unmanaged Suserup Forest (Fig. 5).

The similarity in soil carbon stocks between the unmanaged Suserup Forest and managed, beech-dominated forests is well in line with previous reports on SOC stocks in unmanaged and managed forests in Europe and North America. In a study of managed and non-intervention forests in Germany, no differences in forest floor or mineral soil carbon stocks were observed between regular shelterwood management, selection forestry, or non-intervention forest ($P>0.05$, Mund, 2004). However, in the even-aged stands a general decrease in forest floor carbon stocks with increasing stand age was observed until a stand age of about 140 years followed by an increase with increasing stand age both for the entire organic layer and the foliar fraction alone. In a study of unmanaged forests in Germany, Grüneberg et al. (2013) reported more forest floor carbon and more particulate organic matter in the mineral soil which represent forms of carbon that are most labile to disturbances. However, they found no differences in bulk soil carbon stocks. In 130 inventory plots in Germany there was no effect of management system on SOC stocks, i.e. no legacy effect of past and present management (Wäldchen et al., 2013). In USA, Hoover et al. (2012) found more forest floor carbon, but no significant difference in mineral soil carbon stocks, between managed and non-intervention broadleaved forests in New England.

Our results indicated that soil carbon stocks were slightly lower in Part B which was subject to a more recent period (until 1792) of open conditions with animal grazing (Heilmann-Clausen et al., 2007). This difference in soil carbon stocks might reflect lower carbon inputs to the soil through time and more recent disturbance in this part of the forest compared to Part A with longer undisturbed forest continuity. In northern Germany, Nitsch et al. (2018) reported around 15% higher SOC stocks to 55 cm in beech, pine and oak forests with a continuity of >230 years compared to forests with shorter continuity (<200 years). Similar to our case, Nitsch et al. (2018) also observed the largest difference in SOC stocks in subsoils (29–55 cm). Another explorative European study by Maes et al. (2019) also failed to observe any direct effect of former coppice management compared to high forest on topsoil conditions across central Europe.

Collectively, the results suggest that soil carbon stocks are quite resilient, at least in terms of the disturbances related to traditional beech management in Denmark. It is likely that a larger effect of non-intervention forests would be observed if compared to a management scheme with intensive site preparation and shorter rotation, or in case soils were more wet in the undrained non-intervention forest. The effect of recent disturbance (in Part B) was also modest and in line with studies that found only subtle effects as a result of different forest management legacies (Maes et al., 2019; Nitsch et al., 2018; Wäldchen et al., 2013).

6. Ecosystem carbon stock and temporal dynamics

A long term effect of forests in reducing atmospheric CO_2 concentrations requires persistent net ecosystem carbon sequestration. Net primary production should exceed the loss of carbon through heterotrophic respiration. On a global scale, forests exhibit a persistent carbon sink (Pan et al., 2011), whereas signs of carbon sink saturation have been reported for European forests (Nabuurs et al., 2013). Our study shows, that nemoral beech forests may indeed accumulate high amounts of carbon in the five principal pools, particularly in biomass and dead wood. However, a remarkable finding is that except for the dead wood, the accumulation of carbon in the principal pools after more than 6000 years of forest continuity (Hannon et al., 2000) and 200 years of almost no forest management (Heilmann-Clausen et al., 2007) is no larger than that of just 100 year old managed beech forests, and the potential to further accumulate carbon may be limited. Under the assumption that soil carbon stocks in Suserup Forest are stable at the decadal scale, the ecosystem carbon stocks appear to be close to a steady state. This indicates that net ecosystem production (NEP) is approaching zero around 200 years after the forest was left largely unmanaged. This is in line with simulation studies of forests in the Pacific Northwest, where maximum biomass and total biomass and dead wood carbon stores of 319 and 393 Mg ha^{-1} were reached 150–200 years after disturbance (Janisch and Harmon, 2002).

A key issue regarding the role of forests in climate change mitigation is their ability to continue being carbon sinks with increasing age. It is widely acknowledged that carbon sink strength declines with stand age after an initial increase (e.g. Luyssaert et al., 2008; Law et al., 2003), but dispute remains as to whether the carbon sink declines to a negligible rate (Anderson-Teixeira et al., 2013). This study suggests that unmanaged old nemoral beech forests offers a large and stable carbon stock but no significant carbon sink. Another, but related key issue is the trade-off between the ability of forests to sequester and store atmospheric carbon and the ability of forest products to displace fossil carbon. Many studies have addressed the temporal carbon dynamics of forest products (see reviews by e.g. Bentsen, 2017; Buchholz et al., 2016; Lamers and Junginger, 2013; Mund et al., 2015) and reported that in the medium to long term, using forest products to displace fossil products contributes to climate change mitigation. After around 200 years of non-intervention Suserup Forest offers no additional carbon sequestration, and as an unmanaged forest, also no displacement of fossil resources.

Acknowledgements

The project was supported by a grant from the Hartmann Foundation. We wish to acknowledge the efforts of numerous people involved in measuring trees, dead wood, and soil properties in Suserup Forest during more than 20 years.

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