

Article

The Impact of Thinning and Clear Cut on the Ecosystem Carbon Storage of Scots Pine Stands under Maritime Influence in Flanders, Belgium

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Abstract: A shift in management to improve the ecological function of mature plantations of exotic species can have important effects on the ecosystem climate mitigation potential. This study investigated the effect of two common forest management strategies for Scots pine (*Pinus sylvestris* L.) stands on the C storage after 15 years of management. Two pairs of forest stands on poor sandy soil and under the maritime influence in Brasschaat, Belgium, were observed as case studies. The observed forest management strategies were (i) thinning and group planting of oak saplings (*Quercus robur* L.) and (ii) clear cut, followed by replanting of young oak. For each stand, all forest C pools (aboveground biomass, belowground biomass, litter, and mineral soil) were determined. Results showed, surprisingly, no significant difference in the whole ecosystem C stock for both forest management strategies after 15 years of management. However, after the clear cut and the new plantation, the C in the top 30 cm layer of the mineral soil increased, while it decreased on the forest floor. For thinning with group planting, the C stocks reduced within the 10–30 cm soil layer without impact on the total soil C. Therefore, the shift in management did result in a different allocation of the belowground C, particularly after a clear cut. The results are not only relevant for the study region but also for managed Scots pine forests in neighboring regions of the Atlantic zone of Western Europe.

Keywords: forest ecosystem carbon stocks; forest management; Scots pine; pedunculate oak; clear cut; thinning; sandy soil; maritime climate; coastal area

1. Introduction

Forests store about 50% of the terrestrial carbon (C), making them a very important component within the global C cycle [1,2]. Annually, about 40–60% of the C assimilated by forests through photosynthesis is allocated to biomass [3–5]. Part of this biomass dies, falls as litter, and is then partly broken down by decomposers, which return C to the atmosphere (heterotrophic respiration). The remaining part of the litter is incorporated in a recalcitrant litter C pool and soil organic matter. A fraction of the C in the soil organic matter (in particular the microbial products) also enters the mineral soil. The recalcitrant litter, the soil organic matter and the mineral soil store the majority of the belowground C of forest ecosystems [3,5–7].

The amount of C stored in a forest depends on the environmental (e.g., climate) and site conditions (e.g., soil hydrology). This explains the high C stocks in tropical forests (climate promoting forest productivity) and boreal forests (climate and hydrology delaying decomposition) [8]. However, temperate forests also store an important proportion of the C globally present in forest ecosystems, i.e., ca. 10–14% [9,10]. In temperate forests, the C storage crucially depends on factors related to the forest management, such as the tree species planted, the amount of wood and other materials that is removed from the site or the age of the forest (rotation time) [1,5,11].

For a long time, forest management in the Atlantic and Central European temperate zone focused mainly on the economic function of commercial wood production [12]. In Flanders, Belgium, monocultures of exotic evergreen species (e.g., *Pinus sylvestris* L., *Pinus nigra* subsp. *laricio* (Poiret) Maire, *Picea abies* (L.) H. Karst.) often dominated the forest cover because of their high production and adaptability to suboptimal site conditions [5,12–15]. The classical management of these types of stands was based on a short rotation time (ca. 40–50 years) and a final clear cut [12]. In the past three decades however, other forest functions, such as biodiversity conservation, recreation, air quality control, and climate mitigation, received more attention, resulting in a change of forest management policy [12]. The conversion of evergreen monocultures to mixed or deciduous stands of native species (e.g., pedunculate oak) became one of the applied interventions aiming to improve the forest services. For Flanders, the forest inventory of the Agency for Nature and Forest [16] indicated indeed an increase in the share of hardwood (+3%) and mixed stands (+6%) between 1997–1999 and 2009–2019 at the expense of coniferous stands (−10%). However, we still do not know the impact of interventions improving the ecological function of forests on other ecosystem services such as climate mitigation. Studies focusing on the indirect effects of forest management shifts on the ecosystem C cycles are therefore timely and needed.

This study examines the effect of two typical management strategies of Scots pine (*Pinus sylvestris* L.) stands on the ecosystem C stocks. The first management strategy combined classical thinning regimes (every 5–8 years) with planting of saplings of pedunculate oak (*Quercus robur* L.) in understory gaps (group planting). A gradual transition was therefore established by harvesting pine for wood production and replacing it with a native deciduous species. The light and space created by the thinning allow the understory to develop, giving the planted saplings, but also other trees that grow spontaneously, more opportunities to grow and thereby becoming seed trees for the newly developed broadleaved stand in the long term [17–20]. According to previous studies [21,22], an increasing intensity of thinning results, as expected, in an increasing loss of C in the aboveground biomass, but it has generally no significant impact on the C storage in the mineral soil while it can have a negative impact on the forest floor C. However, in the literature, the reported effect of thinning on the belowground C storage is not always consistent, making further research on this topic necessary [11]. The second management strategy was clear cut followed by installing a new saplings plantation of oak. Clear cut is an intensive forest management technique to harvest wood, that can also be used to realize a fast forest conversion [11,12,23]. However, due to the abrupt changes in the soil (with large C losses) in site micro-climate and in the landscape following the clear cut, the application of this management method is questioned [11,23]. Studies showed that clear cut can result in a decrease in C storage mainly in the forest floor, but also in the mineral soil [11,24,25]. Scots pine is a widely cultivated species in Europe. Sites with similar management and environmental conditions (e.g., soil, climate) are commonly found not only in the studied region (Flanders), but also in other vast areas in Europe with maritime climate and coastal influence.

We put forward two hypotheses. The first is that the aboveground part of both reference pine stands store more C than the stands that underwent the studied management regimes, since the C storage increases with time, and the new management was associated with larger wood removal than the reference management [5,14]. The

second hypothesis is that the belowground part of the reference pine stands would also store more C than the other stands. In fact, with the new management, the soil and the forest litter floor are expected to lose more C, due to the thinning (decreasing the input of litter) and the clear cut (stimulating the degradation of organic materials due to disturbance and increased irradiation) [11,20,25,26].

2. Materials and Methods

2.1. Site Description

The study area is located in Brasschaat, Antwerp, in the Campine region of Belgium. The climate is temperate maritime, with an average annual temperature of 11 °C and an average annual precipitation of 938 mm (data for period 1991–2020). The coldest and warmest months during this period have a mean temperature of, respectively, 4 °C and 19 °C [27]. The study area is part of the Atlantic biogeographic region of Europe, originally dominated by broadleaved deciduous forests, but today extensively covered also by introduced evergreen coniferous species [28]. In the study region, the soils are strongly leached, nutrient-poor podzol types, originated under heather ecosystems [29].

Two study cases were used to investigate the impact of the two management regimes described above (i.e., thinning and group planting, clear cut, and new plantation) on the ecosystem C stocks when applied to Scots pine stands on sandy soils for ca. 15 years. In the first, the ecosystem C stocks of an extensively managed Scots pine stand (reference stand 1) were compared to the C stocks of a Scots pine stand with regular thinning and group planting of oak (thinned stand). In the second, the C stocks of a Scots pine stand under regular thinning (reference stand 2) were compared to the C stocks of a young oak stand planted after clear cut of a pine stand very similar to the former one (clear cut stand).

First study case—thinning with group planting. The two stands investigated in this regard are situated in De Inslag (51° 18' N, 4° 31' E, Figure 1a) and were planted in 1929 with Scots pine. After a similar (extensive) management and a last thinning in 1999 (removing about 30% of the trees [29]), one stand was further extensively managed with minimal intervention (De Inslag Ref., 1.76 ha, [30]). On the other hand, the other stand (1.80 ha) underwent a more intensive management with three thinnings in 2005, 2012 and 2015 (De Inslag Thin.). Following the yield tables, it was estimated that each thinning removed about 8% of the standing trees [31]. The thinning targeted the less vigorous trees following the “future trees” strategy [12]. Furthermore, in the latter stand, in 2012, pedunculate oak saplings were planted in understory gaps (group planting) generally in groups of 19–27 trees [19]. Rhododendron (*Rhododendron ponticum* L.) was also removed to decrease competition with the young, planted oaks [18,32]. In both stands the understory mainly consisted of young trees and shrubs. The soil in De Inslag is classified as a Endogleyic Hypobrunic Albic Hypoluvis Arenosol (Hyperdystric) according to the World Reference Base (WRB) for Soil Resources or medium wet (Zdg) to wet sandy podzol (Zeg) following the local Belgian classification [30,33]. De Inslag Ref. is intensively investigated within ICOS Belgium [30,34].

Second study case—clear cut with replanting. The two stands investigated here are a mature Scots pine stand and a young pedunculate oak stand planted after a clear cut, in De Mik (51° 18' N 4° 33' E, Figure 1b). In the first stand (Mik Ref.), pine was planted in 1943 on rows of artificially elevated ground (ca. 0.5 m) on a parcel of 3 ha. For the study only 1.5 ha was considered. Six thinnings followed until 2015. The second stand (Mik Oak; 1.52 ha) was planted in 1922 with pine and was clear cut in 2006 at an age of about 80 years (similar to the age of Mik Ref. at the time of measurements). Subsequently, young oak trees were planted with a density of 2500 trees ha⁻¹. In 2017, pre-commercial thinning halved the tree density. In the Mik Ref. the understory consisted of grasses (mainly purple moor-grass, *Molina caerulea* L. Moench), while in the oak stand little understory was present. The soil is an Abrutic, Gleyic Arenosol (Dystric) following the WRB, also

classified as a medium wet to wet sandy podzols with a clay-sand substrate (w-Zdg, w-Zeg to w-Zfg) following the Belgian classification [33].



Figure 1. Aerial photos of the study sites. (a): De Inslag with the reference pine stand (dashed line) and the thinned pine stand (solid line); (b): De Mik with the reference pine stand (dashed line) and oak stand planted after the clear cut (solid line). Screenshot from [35].

An overview of the different characteristics of all four studied stands is presented in Table 1. Note that De Inslag and De Mik are less than 3 km apart from each other at bird's eye view.

Table 1. Stand characteristics in winter 2020–2021.

	De Inslag Ref.	De Inslag Thin.	Mik Ref.	Mik Oak
Total basal area ($\text{m}^2 \text{ha}^{-1}$)	31.0	26.5	23.2	23.9
Dominant species	<i>P. sylvestris</i>	<i>P. sylvestris</i>	<i>P. sylvestris</i>	<i>Q. robur</i>
Basal area dominant species ($\text{m}^2 \text{ha}^{-1}$)	26.8	20.2	22.5	18.9
Stand age (years)	91	91	77	14
Density (trees ha^{-1})	375	184	255	1225
Tree height (m, mean \pm SE)	17.9 \pm 0.7	20.5 \pm 0.7	18.1 \pm 0.5	12.4 \pm 0.2
Diameter breast height (cm, mean \pm SE)	31.1 \pm 1.4	37.3 \pm 1.7	33.2 \pm 1.0	14.0 \pm 0.3

2.2. Data Collection

The data were collected December–March 2020–2021. To determine the ecosystem C stocks at each studied stand, the following main components of the ecosystem were considered: the phytomass, the litter, and the mineral soil [30]. Phytomass was further divided into aboveground biomass of the overstory, understory, and belowground biomass. Trees were considered as part of the understory when their stem diameter (measured at 5 cm aboveground) was smaller than 5 cm. Litter was divided into forest floor and dead, woody debris. The mineral soil was sampled in three layers (0–10 cm, 10–30 cm, and 30–60 cm) [30].

In every stand, four center points were randomly chosen to mark the plots. Using these center points, three concentric circles with different radii were marked. In the first circle with a radius of 15 m (R_{15} plot), we determined the C pools (i) in the aboveground biomass of the overstory and (ii) the coarse roots with a diameter greater than 5 mm. The second circle had a radius of 5.6 m ($R_{5.6}$ plot). Coarse, woody debris with a diameter greater than 10 cm was determined in these plots. In the third circle with a radius of 2.8 m ($R_{2.8}$ plot) we determined the C storage in the understory and in the fine woody debris. To do so, in each wind direction and in the center of the plot, the vegetation was harvested in subplots ($n = 5$) of 0.3×0.3 m or 1 m^2 depending on the homogeneity and abundance of the understory present. For each site, in one of the four $R_{5.6}$ plot, 16 points were randomly selected to collect the samples for the C pools in (i) forest floor, (ii) the fine and medium

roots (with a diameter less than 5 mm) and (iii) the mineral soil. An overview of the plots in which the components were observed is presented in Figure 2.

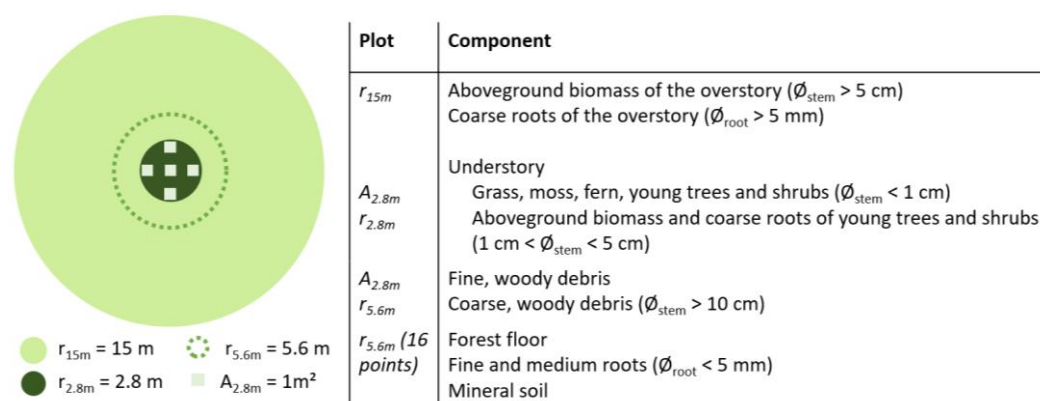


Figure 2. Overview of the different measuring plots and the components measured. \varnothing indicates the diameter

2.3. Measurements of Phytomass

2.3.1. Aboveground Biomass of the Overstory

The aboveground biomass of the overstory was determined using allometric relations (see Section 2.7.1) using data of height (H), diameter at breast height (DBH, at 1.30 m height) and species of each tree in the 15 m radius plots [30,36]. To determine the tree height (m), Field-map was used (IFER, Jilove u Prahy, Czech Republic). This was equipped with a rangefinder and an inclinometer to measure the height of the trees using trigonometry. The DBH (cm) was calculated by measuring the circumference manually with a measuring tape.

2.3.2. Understory

The understory consisted of grasses, mosses, ferns, shrubs and young trees with a stem less than 5 cm in diameter, $\varnothing < 5$ cm, measured 5 cm above ground. The biomass of young trees with a stem diameter between 1 cm and 5 cm was determined using allometric relations derived from the literature (Appendix A, Table A1). The height, stem diameter measured 5 cm above ground were determined as described above for the overstory. The biomass of the Rhododendron was determined using a relationship between biomass and volume determined in this study (Appendix B).

The biomass of the grasses, mosses, ferns, shrubs, and young trees with a diameter of less than 1 cm, was determined using destructive measurements [30,36]. Living and dead standing biomass was collected and further separated into (i) grasses, mosses and ferns and (ii) shrubs and young trees ($\varnothing < 1$ cm). The dry biomass was determined after drying at 70 °C for at least 48 h. For the data analysis, the average of the five subplots was used for each plot (see $A_{2.8m}$ in Figure 2).

2.3.3. Belowground Biomass

The belowground biomass consisted of the roots of the overstory and of the understory. These were separated in coarse, medium, and fine roots. The *coarse roots* were roots with a diameter larger than 5 mm and were estimated for the overstory and the young trees ($1 < \varnothing < 5$ cm) in each R_{15} and $R_{2.8}$ plot, respectively. For the overstory, allometric relations (see Section 2.7.1) were used [30,36]. Due to a lack of allometric relations for young trees, for each species, their coarse root biomass was derived from data of aboveground biomass and the coarse root/shoot ratio of the mature trees (the ratios

used are presented in Appendix A, Table A1). Bias was introduced by using these ratios (that change with age), but the relative importance of the C stock in the coarse roots of young trees was so small (see Section 3.1.3 in Results) that this approximation had little impact [37].

The *fine and medium roots* consisted of roots with diameter less than 5 mm and were measured in 16 points of one $R_{5.6}$ plot in each site [30,38]. After the removal of the forest floor (see Section 2.4.1), the samples ($n = 16$) were taken with a root auger (\varnothing 7.85 cm, height 14.9 cm) for two layers at depth 0–10 cm and 10–30 cm (> 90% of fine roots reside above this depth [29]). At four of the 16 points, the 30–60 cm layer was also sampled. In the laboratory, the roots were manually picked out of the soil samples [39]. While sorting, dead and live roots were not separated. Thus, fine and medium root biomass also included their litter component. After washing, the roots were sorted into two classes: (a) medium roots, with a diameter between 2 mm and 5 mm and (b) fine roots, with a diameter less than 2 mm. The roots were dried at 70 °C for at least 48 h, after which they were weighed.

2.4. Litter

2.4.1. Forest Floor

The forest floor was considered as the thick layer (ca. 5 cm) consisting of fallen leaves, needles, pinecones, acorns, and partly decomposed organic material. This excludes the dark decomposed humus, which was considered the A-horizon of the mineral soil. Woody debris was collected separately (see Section 2.4.2).

For each stand, at each of the 16 points in the $R_{5.6}$ plot, a square of 0.25 × 0.25 m of the forest floor was collected. The material was then dried at 40 °C for 7 days and weighed [30,38].

2.4.2. Woody Debris

The woody debris was separated in coarse ($\varnothing > 10$ cm) and fine ($\varnothing < 10$ cm) woody debris [36]. Fine woody debris (or *fine wood*, e.g., small branches) was collected for each $R_{2.8}$ plot, in the same five subplots (of 0.09–1 m²) used to collect the understory. It was dried at 70 °C and weighed [36]. The biomass of the coarse woody debris (*coarse wood*, e.g., large branches, logs) was determined in the four $R_{5.6}$ plots. The circumference and length of each wood debris within the plot were measured. To determine the biomass of each piece of coarse wood, the stadium of decomposition was accounted for [30,36]: 1—solid, not rotten; 2—solid in the center, rotting starting on the outside; 3—rotten to the center. For each stadium, 3 to 5 pieces of wood were collected and their volume was determined. After drying at 70 °C, these coarse wood pieces were weighed and the density of the three stadia of decomposition was calculated. By using the length, circumference, and estimated density of the decomposition level, the dry biomass of the coarse wood in each plot was calculated.

In De Mik also (i) broken dead standing trees, (ii) stumps and (iii) dead wood left behind after the pre-commercial thinning of oaks, were also present and thus also considered as coarse woody debris. The biomass was determined as above, from measurements of volume and wood density. For standing dead trees and stumps, the biomass of the (dead) coarse root system (determined with allometric relationships assuming a decomposition level of 1) was also added to the coarse wood.

2.5. Mineral Soil

Soil samples of layers 0–10 cm and 10–30 cm were taken at the same 16 points of one $R_{5.6}$ plot measured for the forest floor and fine root biomass. After removing the forest floor, the samples to measure the soil C were taken with a soil auger. Furthermore, for 4 sampling points (one in each quadrant of $R_{5.6}$ plot) samples from the layer 30–60 cm were also collected.

For each layer and measuring point, two soil samples were taken: one to determine the bulk density and the other to determine the soil C content. To determine the bulk density, a sample was taken using a bulk density auger with Kopecky rings. These samples were dried for 48 h at 105 °C and weighed. The density of the soil was calculated using the dry mass value and the volume of the auger (0.00010 m³) [38]. By multiplying by the thickness of the layer, the mass of soil per surface unit could be calculated. Samples for soil C concentration were collected close to the sampling point of the bulk density with a smaller auger (Ø 2.45 cm). The soil samples for C analysis were dried at 40 °C for about 7 days [38].

2.6. C Content and C Stocks

For the *phytomass and the woody debris* a C content of 0.5 g C per g dry biomass was assumed [30]. The C content of the samples of the *forest floor and mineral soil* was analyzed using dry combustion. The dried samples were first sieved to pass a 2 mm mesh to remove roots and stones. Next, soil samples were ground using a ball mill (Fisher Bioblock Scientific Retsch), whereas dried forest floor samples were ground using a centrifugal mill (Model ZM 200, Retsch GmbH, Haan, Germany) with a sieve of 0.25 mm mesh size. The ground samples were analyzed for C content by dry combustion, based on the Dumas-method using an elemental analyzer (Model FLASH 2000, Interscience, Louvain-la-Neuve, Belgium).

Using the bulk density of the soil and the soil C content (g C g dry mass⁻¹), the C stored in each layer of the mineral soil was calculated (tC ha⁻¹). The C stocks (tC ha⁻¹) in phytomass, forest floor, and woody debris were calculated using the dry mass (t ha⁻¹) and the C content.

2.7. Data Analysis

2.7.1. Allometric Relationships

For Scots pine, allometric equations were available for the study area [40]. For the other species, we used equations determined for other Atlantic or Central European regions and for trees of comparable age as the investigated trees. In case equations for a representative region or age was not available, the relationships of a closely related species were used (these approximations were only applied for young trees of less common species). For all deciduous species, the use of allometric relationships introduced some bias, as some (dead) leaves of the current year were also considered within the forest floor pool. However, litter traps were not available for more accurate estimation and the bias is assumed minor. All details information about the relationships used are reported in Appendix A (Table A1) and B.

2.7.2. Statistics

For the statistical analyses, the software program IBM SPSS Statistics (Version 28.0, IBM Corp., Armonk, NY, USA) was used, while R (Version 4.1.1, R Foundation for Statistical Computing, Vienna, Austria) was used for data visualization [41,42]. The C stocks of all components characterizing phytomass, litter, and mineral soil were compared between the two stands at De Inslag and the two stands at De Mik separately. For C stocks in the fine roots and the mineral soil, the soil layers were considered both separately, as well as aggregated.

When data presented a normal distribution (Shapiro–Wilk test) and homoscedasticity (Levene’s test), an independent, two-tailed t-test was performed. In case of non-normal distribution, the non-parametric Mann–Whitney U-test was applied. When the homoscedasticity was not met, the Welch test was applied. The difference was considered significant when the $p < 0.05$.

This analysis could not be applied to the total C stock of the woody debris, the mineral soil (0–60 cm), total C stock in fine and medium roots (for each layer and in total

depth) and of the total ecosystem C stock, due to different sample size or plot size of the components making up the aggregated values. Testing was therefore based on comparing the means and their standard deviation (SD) [43]. For example, the following equations were used to determine the standard deviation of the mineral soil C stock ($SD_{\text{mineral soil}}$) and of the total ecosystem C stock ($SD_{\text{total ecosystem}}$).

$$SD_{C \text{ mineral soil}} = \sqrt{SD_{C \text{ 0-10 cm}}^2 + SD_{C \text{ 10-30 cm}}^2 + SD_{C \text{ 30-60 cm}}^2}$$

$$SD_{C \text{ ecosystem}} = \sqrt{SD_{C \text{ phytomass}}^2 + SD_{C \text{ forest floor}}^2 + SD_{C \text{ woody debris}}^2 + SD_{C \text{ mineral soil}}^2}$$

With the mean values of an aggregated C stock (e.g., mineral soil, total roots, total ecosystem) of two stands being m_1 and m_2 (with $m_1 < m_2$), and SD_1 and SD_2 their respective standard deviations, the values were considered to be significantly different at $p < 0.05$ when $m_1 + 1.96 \times SD_1 < m_2 - 1.96 \times SD_2$ [43].

3. Results

3.1. Phytomass

3.1.1. Overstory

In De Inslag, the overstory stored at the reference stand 93.3 tC ha^{-1} and at the thinned stand 75.3 tC ha^{-1} , which were not significantly different ($p = 0.15$; Table 2). In both stands, Scots pine contributed to about 85% of the overstory biomass. In the reference stand, the most important species next to Scots pine, was birch (*Betula pendula* Roth; accounting for 10% of the overstorey biomass), whereas in the thinned stand, it was pedunculate oak (7%) (Figure 3).

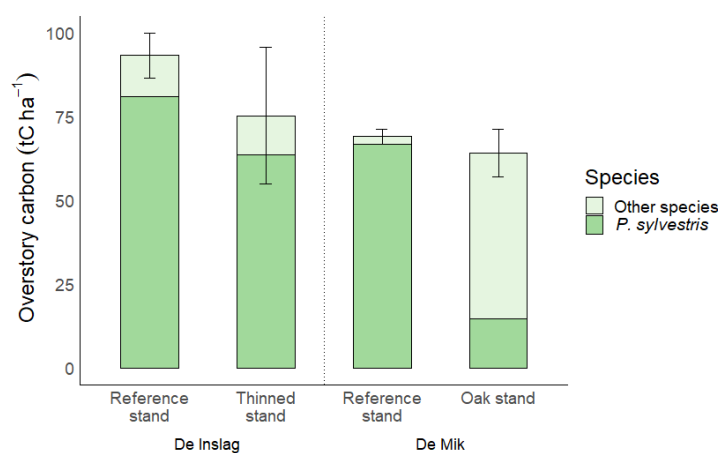


Figure 3. C stocks (tC ha^{-1}) in the aboveground biomass of the overstory of the investigated stands with differentiation between the contribution of Scots pine (dark green) and of the other species (light green).

In De Mik, the C stock in the aboveground tree biomass was 69.1 and 64.2 tC ha^{-1} in the reference and oak stand, respectively (not significantly different; Table 2). At Mik Ref., Scots pine made up 97% of the biomass. At Mik Oak, pedunculate oak made up 77% of the biomass.

Table 2. Overview of the mean values of C stocks (tC ha⁻¹) with standard error (SE; tC ha⁻¹) at the study stands. ‘%’ indicates the percentage relative to the total C storage in the ecosystem for each component. The p-value shows the statistical significance between pairs of stands (De Inslag Ref. vs. De Inslag Thin. and Mik Ref. vs. Mik Thin.); the star (*) indicates when $p < 0.05$, the plus (+) indicates when $0.05 < p < 0.10$. NA indicates not applicable.

	De Inslag Ref.		De Inslag Thin.		<i>p</i>	Mik Ref.		Mik Oak			<i>p</i>
	Mean ± SE (tC ha ⁻¹)	%	Mean ± SE (tC ha ⁻¹)	%		Mean ± SE (tC ha ⁻¹)	%	Mean ± SE (tC ha ⁻¹)	%		
Aboveground biomass											
Overstory	93.3 ± 3.4	34	75.3 ± 10.2	30	0.15	69.1 ± 1.1	22	64.2 ± 3.6	20	0.27	
Understory											
Grass, moss, and fern	0.21 ± 0.05	<1	0.21 ± 0.11	1	1.00	1.38 ± 0.12	<1	0.35 ± 0.06	<1	<0.001 *	
Young trees and shrubs ^a	4.1 ± 2.0	2	4.6 ± 0.7	2	0.81	0	0	0	0	NA	
Belowground biomass											
Coarse roots of overstory	10.8 ± 0.3	4	8.8 ± 1.0	4	0.10	7.8 ± 0.2	2	10.9 ± 0.4	3	<0.001	
Coarse roots of young trees and shrubs	0.88 ± 0.4	<1	1.1 ± 0.2	<1	0.62	0	0	0	0	NA	
Fine and medium roots											
0–10 cm	2.3 ± 0.4	1	1.8 ± 0.3	1	0.37	1.5 ± 0.3	<1	1.8 ± 0.2	1	0.05 +	
10–30 cm	2.1 ± 0.6	1	2.2 ± 0.6	1	0.79	2.1 ± 0.4	1	3.2 ± 0.7	1	0.24	
30–60 cm	3.0 ± 0.9	1	0.71 ± 0.23	<1	0.040 *	1.0 ± 0.1	<1	1.9 ± 0.4	1	0.25	
Forest floor	41.9 ± 2.7	15	44.7 ± 3.7	18	0.54	46.2 ± 2.1	15	21.7 ± 1.0	7	<0.001 *	
Woody debris											
Fine woody debris	2.5 ± 1.2	1	2.6 ± 1.2	1	0.57	0.80 ± 0.16	<1	1.36 ± 0.30	<1	0.08 +	
Coarse woody debris	2.1 ± 1.7	1	3.0 ± 2.8	1	0.89	3.2 ± 1.4	1	5.9 ± 1.7	2	0.27	
Mineral soil											
0–10 cm	44.9 ± 4.8	17	52.7 ± 7.3	21	0.47	50.8 ± 3.5	16	63.8 ± 4.8	20	0.036 *	
10–30 cm	39.7 ± 2.1	15	29.7 ± 2.2	12	<0.001 *	68.1 ± 5.8	21	80.3 ± 3.6	25	0.08 +	
30–60 cm	22.9 ± 3.1	8	22.1 ± 3.8	9	0.88	65.8 ± 7.7	21	60.4 ± 25.6	19	0.85	

^a refers to individuals with a diameter between 1 and 5 cm at 5 cm aboveground (young trees and shrubs with a diameter < 1 cm were not reported as with a negligible stock of < 0.1 tC ha⁻¹).

3.1.2. Understory

In De Inslag, thinning and new planting did not result in a significant difference in C stock in the young trees and shrubs ($1 < \varnothing < 5$ cm) with 4.1 and 4.6 tC ha⁻¹ in the reference and thinned stand, respectively. In the understory, the largest amount of C was stored in this compartment. Young trees and shrubs with $\varnothing < 1$ cm (< 0.1 tC ha⁻¹) and grasses, mosses, and ferns (0.2 tC ha⁻¹), accounted for a negligible part of the ecosystem C stock.

However, the grasses, mosses, and ferns represented the largest share of the understory biomass in De Mik, with values at Mik Ref. (1.38 tC ha⁻¹) significantly larger than at Mik Oak (0.35 tC ha⁻¹) ($p < 0.001$; Table 2). Young trees and shrubs with $\varnothing < 1$ cm and $1 < \varnothing < 5$ cm accounted for a negligible portion of the ecosystem C stock at both stands (< 0.1 tC ha⁻¹).

3.1.3. Belowground Biomass

In De Inslag, C stock in the *coarse roots* of the overstory trees (ca. 9–11 tC ha⁻¹) and the young trees (ca. 1 tC ha⁻¹) were both not significantly different between stands (Table 2). In De Mik, the C stock in the coarse roots of the overstory trees was 7.8 and 10.9 tC ha⁻¹ in the reference and oak stand, respectively, with a significant difference ($p < 0.001$; Table 2). Understory trees were largely absent at De Mik, and thus did not contribute to the belowground biomass.

An overview of the C stored in the *fine and medium roots* for the different soil layers in both stands of De Inslag and De Mik is presented in Table 3. Overall, for the aggregated fine and medium roots in De Inslag, the total sampled layer (0–60 cm) stored 4.7 ± 2.6 and 7.4 ± 3.3 tC ha⁻¹ (mean \pm SD) in the thinned and reference stand, respectively, without significant difference between stands. The fine and medium roots accounted for about 50% of the total root C stock. In De Inslag, the C storage in the fine roots was only significantly different for the layer 30–60 cm, with larger C stock in the reference than in the thinned stand ($p = 0.03$). For the medium roots, the C stock of the separated layers was not significantly different between stands. Though, in the layer 0–10 cm, there was a trend toward a larger C stock in De Inslag Ref. ($p = 0.06$; Table 3). In the aggregated fine and medium roots, the C stock showed only a significant difference in the layer 30–60 cm, as in the fine roots, with larger values in the reference stand (3.0 ± 0.9 tC ha⁻¹) than in the thinned stand (0.7 ± 0.2 tC ha⁻¹) ($p = 0.040$; Table 2).

Table 3. Mean values of C stocks (tC ha⁻¹) with standard error (SE; tC ha⁻¹) of the fine (with less than 2 mm in diameter) and medium roots (with diameter between 2 and 5 mm) in different soil layers at the study stands. The star (*) indicates a statistically significant difference between stands at $p < 0.05$, the plus (+) indicates $0.05 < p < 0.10$.

	De Inslag Ref.	De Inslag Thin.		Mik Ref.	Mik Oak	
	Mean \pm SE (tC ha ⁻¹)	Mean \pm SE (tC ha ⁻¹)	<i>p</i>	Mean \pm SE (tC ha ⁻¹)	Mean \pm SE (tC ha ⁻¹)	<i>p</i>
0–10 cm						
$\varnothing < 2$ mm	1.12 ± 0.13	1.08 ± 0.10	0.82	0.78 ± 0.07	1.26 ± 0.09	<0.001 *
$2 < \varnothing < 5$ mm	1.18 ± 0.30	0.67 ± 0.31	0.06 +	0.69 ± 0.30	0.52 ± 0.12	0.57
10–30 cm						
$\varnothing < 2$ mm	0.71 ± 0.08	0.66 ± 0.11	0.84	1.27 ± 0.20	1.38 ± 0.22	0.61
$2 < \varnothing < 5$ mm	1.40 ± 0.56	1.54 ± 0.51	0.83	0.85 ± 0.34	1.86 ± 0.53	0.18
30–60 cm						
$\varnothing < 2$ mm	1.91 ± 0.75	0.53 ± 0.15	0.029 *	0.70 ± 0.27	1.28 ± 0.32	0.15
$2 < \varnothing < 5$ mm	1.12 ± 0.47	0.18 ± 0.14	0.11	0.31 ± 0.27	0.60 ± 0.17	0.25

The total C in the aggregated fine and medium roots in De Mik was 4.6 ± 2.0 and 6.9 ± 2.8 tC ha⁻¹ (mean \pm SD) in the reference and oak stand, respectively, without significant difference between stands. However, in De Mik, the C stock in the fine roots in the layer 0–10 cm was lower in the reference than in the oak stand (0.8 ± 0.1 and 1.3 ± 0.1 tC ha⁻¹, respectively) ($p < 0.001$; Table 3) and a similar trend ($p = 0.05$) was observed in the same layer for the aggregated fine and medium root C stock (Table 2). There were no significant differences in the root C stocks in the layers of 10–30 cm ($1–3$ tC ha⁻¹) and 30–60 cm ($1–2$ tC ha⁻¹) (Table 2).

3.2. Litter

3.2.1. Forest Floor

In De Inslag, the amount of C stored in the forest floor in the extensively managed stand and in the thinned stand was about 42–45 tC ha⁻¹ (the difference was not significant; Table 2). In De Mik, the amount of C stored in the forest floor of the pine stand was twice as large as the amount of C stored in the forest floor of the oak stand ($p < 0.001$; Table 2).

3.2.2. Woody Debris

Regarding the C stored in the coarse woody debris, there was no significant difference between both stands in De Inslag, neither between both stands in De Mik (Table 2). In De Inslag and De Mik, the C stocks of fine woody debris also did not show a significant difference between stands, but Mik Oak presented marginally significant ($p = 0.08$) larger fine woody debris than Mik Ref (Table 2). Overall, in De Inslag, a total of 5–6 tC ha⁻¹ was stored in the dead wood, whereas in De Mik, this amount was about 4–7 tC ha⁻¹ (without significant differences between stands).

3.3. Mineral Soil

In De Inslag, there was no significant difference in C stocks in the total sampled soil (0–60 cm) between the extensively managed stand (107 ± 22 tC ha⁻¹) and the thinned stand (105 ± 31 tC ha⁻¹). In addition, in De Mik, the total C stored in the soil did not differ significantly between the pine stand (185 ± 31 tC ha⁻¹) and the oak stand (205 ± 56 tC ha⁻¹). The results are given with their corresponding SD.

In De Inslag, there was, however, a difference in the layer 10–30 cm, with larger C stock in the extensively managed stand than in the thinned stand ($p < 0.001$; Table 2). This difference was related to C content (C%) and bulk density, which tended to be larger in the reference stand (Table 4). The layers 0–10 cm ($40–55$ tC ha⁻¹) and 30–60 cm (22 tC ha⁻¹) did not present a significant difference between stands. Note that the aggregated layer of 0–30 cm showed no significant difference in C stocks between the extensively managed stand (84.6 ± 5.9 tC ha⁻¹) and the thinned stand (82.5 ± 8.4 tC ha⁻¹) ($p = 0.84$).

Table 4. Characteristics of the mineral soil for each soil layer in each investigated stand. The star (*) indicates the statistically significant difference between stands at $p < 0.05$, the plus (+) indicates $0.05 < p < 0.10$.

	De Inslag Ref.	De Inslag Thin.		Mik Ref.	Mik Oak	
	Mean ± SE	Mean ± SE	<i>p</i>	Mean ± SE	Mean ± SE	<i>p</i>
0–10 cm						
bulk density (g cm ⁻³)	1.18 ± 0.03	1.23 ± 0.02	0.19	1.20 ± 0.04	1.23 ± 0.04	0.37
C content (%)	3.80 ± 0.38	4.36 ± 0.65	0.76	4.30 ± 0.28	5.26 ± 0.39	0.05 +
10–30 cm						
bulk density (g cm ⁻³)	1.28 ± 0.01	1.22 ± 0.03	0.07 +	1.23 ± 0.05	1.21 ± 0.03	0.60
C content (%)	1.55 ± 0.09	1.22 ± 0.09	0.004 *	2.82 ± 0.23	3.39 ± 0.19	0.06 +
30–60 cm						
bulk density (g cm ⁻³)	1.29 ± 0.02	1.17 ± 0.05	0.78	1.45 ± 0.04	1.33 ± 0.04	0.07 +
C content (%)	0.59 ± 0.08	0.64 ± 0.13	0.09 +	1.53 ± 0.22	1.51 ± 0.62	0.97

In De Mik, the layer 0–10 cm presented larger C stock in the oak stand than in the pine stand ($p = 0.036$; Table 2). The C stock in the layer 10–30 cm also tended to be larger in the oak stand than the pine stand (Table 2). In fact, when considering the aggregated layer 0–30 cm, the C stored in the pine stand ($118.1 \pm 7.5 \text{ tC ha}^{-1}$) was significantly lower than in the oak stand ($142.6 \pm 6.5 \text{ tC ha}^{-1}$) with $p = 0.020$. In both layers, 0–10 cm and 10–30 cm, the difference in C stocks between stands was associated with a marginal difference ($p = 0.05$ – 0.06) in C%, with Mik Oak presenting larger values than Mik Ref. (Table 4). In the layer 30–60 cm the C stock did not differ significantly between the two stands (60 – 65 tC ha^{-1}), though the bulk density was marginally larger at Mik Ref. (Table 4).

3.4. Total Ecosystem

The total C stock of the study stands is reported in Figure 4. For both De Inslag and De Mik, the total C stock in the ecosystem was not significantly different between stands with different management (Figure 4).

In De Inslag, the aboveground C plus woody debris C represented about 30–38% of the C stored in the ecosystem. On the other hand, soil and roots represented 43–44% of the ecosystem C stock. In the thinned stand, the lower proportion of C in the soil layer 10–30 cm than the extensively managed stand (13% vs. 15%, respectively) was partly compensated by a larger amount of C (even if not significant) in the 0–10 cm layer, so that no difference in C stock in the top 30 cm of soil was recorded. Differences between stands in the relative proportion of C in forest floor, coarse roots and the soil layer at 30–60 cm were also not relevant (Table 2).

At De Mik, only 20–25% of the C was aboveground, whereas the majority (60–70%) was belowground. The relative proportion of C stocks in the aboveground components, in coarse roots and in the deepest soil layer did not vary between stands (Table 2). However, there were differences between stands in the proportion of C in the forest floor and the soil layers until 30 cm (Figure 4). In fact, the pine stand had largest proportion of stored C in the forest floor (15% vs. 7%, for Mik Ref. and Mik Oak, respectively), whereas the oak stand had the largest proportion of C in the top 30 cm of soil (47% vs. 39%, for Mik Oak and Mik Ref., respectively), consisting of mineral soil and fine and medium roots.

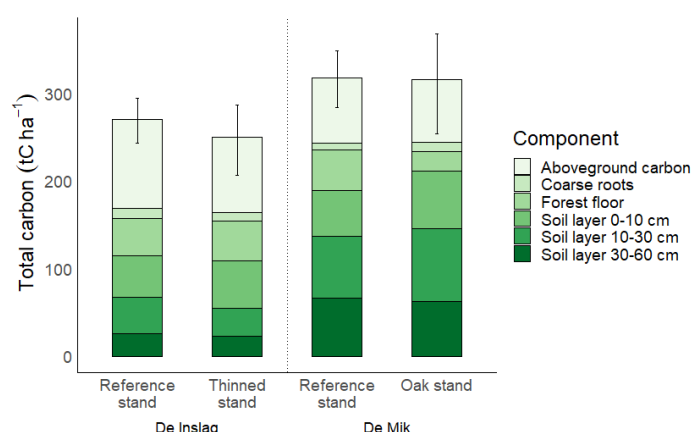


Figure 4. Total ecosystem C storage (tC ha^{-1} ; mean and SD) for the investigated stands, with a separation between components. Note that (i) the aboveground C consists of the aboveground biomass and the woody debris, and (ii) for each soil layer, the C stock of the mineral soil and the fine and medium roots were aggregated.

4. Discussion

4.1. Aboveground Biomass

Thinning can significantly decrease the C stock in overstory biomass, depending on its intensity and the recovery time [21,22,44,45]. However, the results do not show an

impact of thinning on the overstory C stock at De Inslag. This lack of significant effect could be attributed to a less intensive thinning, than in other studies [21,22,44]. Even though the exact data of the trees or wood volume removed was not available, following the standard yield tables it was estimated that only about 18% of the standing trees was thinned in the 15 years before measurements [29]. Another factor partly compensating for the loss of biomass due to the tree harvest could have been the improved growth of the trees left after thinning. This was shown by the difference in the DBH of the pines in De Inslag with an average of 37.3 and 31.1 cm in the thinned and reference stand, respectively. This was observed despite a considerable amount of younger and smaller pine trees in the thinned stand, due to natural regeneration, which reduced the mean DBH and increased the data uncertainty (Figure 3). The oaks planted in 2012 at De Inslag Thin. did not contribute substantially to the overall C storage (ca. 7% of the overstory biomass), but their relevance can be assumed to increase in the next decades as the conversion to an oak forest continues.

Additionally, in De Mik, there was no significant difference in the aboveground C stock between both stands. Generally, younger trees store less C than older ones, and pioneer coniferous evergreen trees grow faster than late successional broadleaved deciduous trees [5,46,47]. However, the standard applied guidelines for the planting and the first thinning assured that, after 15 years, the young oak stand already stored as much C as the ca. 80-year-old pine stand.

Both in De Inslag and De Mik, the understory accounted for a minor contribution to the C storage in the ecosystem. In De Inslag, young trees and shrubs represented the most important C stock in the understory. In De Mik, grasses, mosses, and ferns represented the largest understory C stock in the open Mik Ref. stand, whereas the closed Mik Oak stand had practically no understory. For De Inslag Ref., C storage in grasses, mosses, and ferns in the peak of the 2021 growing season was 0.18 tC ha^{-1} according to ICOS Belgium, which compares well to our results (0.21 tC ha^{-1}). This might indicate that the standing dead understory biomass measured here outside of the growing season was an acceptable proxy of the peak understory biomass. On the other hand, it is possible that the spatial heterogeneity of the understory confounds the results.

4.2. Roots

Both in De Inslag and De Mik, there was no effect of forest management on the C stored in the fine and medium roots in the total sampled depth (0–60 cm). However, in De Inslag, in the layer 30–60 cm, the C stock of the fine and medium roots decreased alongside management intensity. It is likely that the amount of (deeper) pine roots decreased with thinning, and this could not have been compensated by the young oaks. On the other hand, in De Mik, in the layer 0–10 cm, there was a significantly higher amount of roots in the oak stand, which could be attributed to the high tree density. Regarding coarse roots, the significantly lower C storage in the pine stand in De Mik could be the result of a lower coarse root/shoot ratio in the pine stand compared to the oak stand (0.11 and 0.17, respectively). In fact, the root/shoot ratio can decrease with age and with lower stand density ([37] for root/shoot ratio considering total roots).

4.3. Forest Floor

In De Inslag, the effect of different forest management was not noticeable on the forest floor C stock. This could be explained by the similar composition of the litter in both stands, each dominated (for ca. 80–85%) by Scots pine.

In Mik Oak, the litter, and as a result, the forest floor composition, changed with the sudden conversion after the clear cut. The litter of a broadleaved deciduous stand has better quality than the one of an evergreen coniferous stand. As a result, the litter in the former is broken down faster by soil biota than in the latter [6,11]. Pine litter is recalcitrant, partly because of the low pH and low calcium content [46]. Secondly, the soil of pine stands typically contains fewer earthworms, which are important for the breaking down

of litter [46]. Overall, due to the change in litter and soil ecology following the clear cut and the new planting, the C stock of the forest floor in Mik Oak was lower than in Mik Ref. In addition, the clear cut had likely promoted additional breakdown of forest floor organic matter through the increase in insolation, and thus soil temperature, that it created [11].

4.4. Mineral Soil

The amount of C stored in the soil can strongly depend on the intensity and kind of forest management [1,5,48,49]. For example, intensive disturbance of the soil can foster the breakdown of organic matter and, thereby, the loss of soil C [11,48]. However, the effect of thinning on the soil C stocks can be ambiguous, and literature shows that thinning does not necessarily influence the organic C stored in the mineral soil [11,21,50,51]. This corresponds to our observations at De Inslag. In the soil layer of 10–30 cm, however, the C stock in the reference stand was larger than in the thinned stand. A possible reason for this could be a smaller belowground input of C from the trees in the thinned stand, which is corroborated by the smaller amount of roots in the soil layer of 30–60 cm. On the other hand, we note that the C stock in the 0–10 cm layer was, although non-significant, larger in the thinned stand, balancing out the difference in soil C stock when the top 30 cm of soil was considered. Therefore, the different management could induce a modification in the C allocation pattern among pools rather than a net C loss, which warrants further investigation over longer time scales.

In De Mik, the C stock in the topsoil layer (0–30 cm) was larger in the oak than in the pine stand. This is likely the result of a combination of a better quality of the litter (that is more easily broken down) and of better-developed soil ecology, allowing the transfer of the organic matter from the forest floor to the mineral soil [6,46]. Another factor contributing to the larger topsoil C stock in Mik Oak could have been the increased fine rootstock in the layer 0–10 cm. Due to their turnover, more fine roots could result in larger C input into the soil [52]. The relocation of C from litter to the mineral soil did not reach the deepest measured layer of 30–60 cm, which stored the same amount of C in both stands. This could be explained by the young age of the oak stand. Literature reports that modifications in C content in mineral soil layers can occur over long-time scales and that there are still many unknown aspects of these dynamics [11,53].

The total amount of soil C stock was remarkably higher at De Mik when compared to De Inslag. This difference could be attributed to the soil C content (C%), which was larger at De Mik, particularly for the deeper layers of the soil (10–60 cm). Due to the larger clay fraction, it is likely that more water is retained and less soil organic matter is decomposed at De Mik than at De Inslag [54].

4.5. Woody Debris

It was expected that thinning would result in less woody debris due to the lower density of trees, as well as the lower tree competition [12]. This was not reflected in the results for De Inslag. This might be due partly to the fact that, in the reference stand, the forest canopy was very open, so competition between the trees was avoided even in the stand that was not thinned. Additionally, woody debris (crown wood) was left on site after thinning.

In addition, in De Mik, the management strategy did not have a major influence on the C stored in the woody debris. The slightly larger C stock in the fine woody debris in the oak stand could be attributed to the higher amount of branches and the higher tree density at the oak stand, both resulting in higher branch mortality [55].

4.6. Total Ecosystem

For De Inslag Ref. (the only stand with previous measurements), our data match previous C stock assessments. For the mineral soil, the C stock was reported to be 115 tC

ha⁻¹ in layer 0–100 cm in 1999 [29] and 68 tC ha⁻¹ in layer 0–30 cm in the period 2002–2010 [30]. This is similar to the 85 tC ha⁻¹ and 107 tC ha⁻¹ in the 0–30 cm and 0–60 cm layers, respectively, measured in De Inslag Ref. in the current study. The C stock in the overstory biomass was similar in 1999 [29] (90 tC ha⁻¹), 2002–2010 [30] (76–90 tC ha⁻¹), and in this study (93 tC ha⁻¹). Lastly, the litter/forest floor stored 26, 30–34, and 42 tC ha⁻¹ in 1999, 2002–2010, and 2021, respectively. Overall, these observations confirm that our measurement protocol was of satisfactory quality.

In De Inslag, as well as in De Mik, there was no noticeable effect of the different forest management on the C stock of the total ecosystem. This contrasts with the expectation that the forest C stock would decrease after the new management strategies, i.e., thinning or clear cut. According to literature, clear cut can have a large influence on the C stored in the mineral soil and, mainly, the forest floor, with recovering time depending on multiple factors (such as soil type, climate, tree species, etc.) and up to five decades [11,21,25]. In this case study, the C stock has recovered in, at maximum, 15 years.

The management seems to have modified the C allocation pattern in the forest floor and soil rather than the absolute values of the total ecosystem C stock. This was evident at De Mik, where the clear cut and new planting resulted in less C on the forest floor (-7% considering the total ecosystem C stock) and more C in the top 30 cm of soil (+9%). Although less obvious, this effect was also present in De Inslag, where management seemed to influence the C distribution among the topsoil layers.

Based on the similarity in soil and maritime climate influence, the results and insights obtained here are also of relevance for the widespread Scots pine forests in other areas of the Atlantic region (e.g., The Netherlands, the western part of Germany, and Norway) [56,57], but also in the coastal areas of more continental European regions (e.g., southern Baltic coast) [58].

4.7. Methodological Limitations

We need to stress that the belowground sampling was performed only at one plot of about 100 m² at each stand. Therefore, the belowground sampling was not suited to capture the intra-stand belowground spatial variability. Previous research indicated, however, that the variability in C stocks of soil and litter is relatively low at the De Inslag (confidence interval about 6–13% of the mean), but it is larger for fine roots (confidence interval about 30–38% of the mean) [30]. Fine roots data should therefore be treated with caution, as well as the soil data of the 30–60 cm layer, which were analyzed via four replicas only. For the roots, there was no separation made between live and dead roots. Different live vs. dead roots ratios across stands were possible if the management strategy affected the root turnover rate, but this is unknown.

Finally, note that, in our analysis, the four plots per stand from which the aboveground data were derived were considered independent. A more refined approach would have been achieved by selecting multiple stands for each management strategy. However, such stand replicas were not present in the study area.

5. Conclusions

The effect of typical management strategies on Scots pine stands on sandy soil was clarified by investigating gradual thinning with concurrent planting of pedunculate oak, on the one hand, and clear cut followed by a new planting of pedunculate oak, on the other hand. Contrary to the hypotheses, both management methods did not show a significant effect on the total C stock of the ecosystem or above- and belowground C stocks taken separately, but the distribution of C within the ecosystem C pools did change. In particular, after the clear cut and new plantation, important changes in the C stock of the mineral soil (increase) and the forest floor (decrease) could have occurred. The effect of thinning and concurrent planting had less impact on the ecosystem C storage, although modifications in the distribution of the C in the top 30 cm soil layer were observed. Because of the significant ecological and economic value of Scots pine, more information

on the impact of forest management on the ecosystem C stocks of maritime Scots pine forests on poor sandy soils was needed. Therefore, the data presented in this study are of importance.

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Appendix A. Allometric Relations

Table A1. Allometric relations used to calculate the aboveground biomass and biomass of the coarse roots of the overstory trees and understory trees.

Species	Aboveground Biomass (AGB) (kg/Tree)	Biomass Coarse Roots (BGB) (kg/Tree)	Remarks
Overstory (D > 5 cm)			
<i>Acer pseudoplatanus</i> L.	$AGB_{Leaves} = 10^{(-1.1619)+1.2237 \times \text{LOG}(\text{DBH})}$ (Q. robur) [59] $AGB_{Total} = e^{(-2.7018)+2.5751 \times \ln(\text{DBH})} + AGB_{Leaves}$ [60]	$BGB = 0.040113 \times \text{DBH}^{2.227842}$ (Q. robur) [61]	a
<i>Amelanchier arborea</i> Fernald	$AGB_{Leaves} = 10^{(-1.1619)+1.2237 \times \text{LOG}(\text{DBH})}$ (Q. robur) [59] $AGB_{Total} = 0.0927 \times \text{DBH}^{2.5097} + AGB_{Leaves}$ (Q. robur) [62]	$BGB = 0.040113 \times \text{DBH}^{2.227842}$ (Q. robur) [61]	a
<i>Betula pendula</i>	$AGB_{Leaves, Inslag} = 0.80 \text{ kg/tree}$ $AGB_{Leaves, Mik} = 1.06 \text{ kg/tree}$ [63] $AGB_{Branches} = 0.0742 \times \text{DBH}^{2.24}$ $AGB_{Stem} = 0.193 \times \text{DBH}^{2.25}$ $AGB_{Total} = 0.2511 \times \text{DBH}^{2.29} + AGB_{Leaves}$ [64]	$BGB = 0.04582 \times \text{DBH}^{2.23951}$ [61]	AGB _{Total} : De Inslag AGB _{Branches} and AGB _{Stem} : Mik a
<i>Castanea sativa</i> Mill.	$AGB_{Leaves} = 10^{(-1.1619)+1.2237 \times \text{LOG}(\text{DBH})}$ (Q. robur) [59] $AGB_{Total} = 0.0927 \times \text{DBH}^{2.5097} + AGB_{Leaves}$ (Q. robur) [62]	$BGB = 0.040113 \times \text{DBH}^{2.227842}$ (Q. robur) [61]	a
<i>Corylus avellana</i>	$AGB_{Total} = 0.068 \times \text{DBH}^{2.745}$ [65]	$BGB = 0.040113 \times \text{DBH}^{2.227842}$ (Q. robur) [61]	a
<i>Fagus sylvatica</i>	$AGB_{Leaves} = 0.0167 \times \text{DBH}^{2.951} \times H^{-1.101}$ $AGB_{Branches} = 0.0114 \times \text{DBH}^{3.682} \times H^{-1.031}$ $AGB_{Stem} = 0.0109 \times \text{DBH}^{1.951} \times H^{1.262}$ $AGB_{Total} = 0.0306 \times \text{DBH}^{2.347} \times H^{0.590}$ [66]	$BGB = e^{(-4.1302)+2.6099 \times \ln(\text{DBH})}$ [67]	AGB _{Total} : De Inslag AGB _{Leaves} AGB _{Branches} and AGB _{Stem} : Mik
<i>Frangula alnus</i> Mill.	$AGB_{Total} = 0.121 \times \text{DBH}^{2.480}$ [65]	$BGB = 0.040113 \times \text{DBH}^{2.227842}$ (Q. robur) [61]	a
<i>Ilex aquifolium</i>	$AGB_{Leaves} = 10^{(-1.1619)+1.2237 \times \text{LOG}(\text{DBH})}$ (Q. robur) [59]	$BGB = 0.040113 \times \text{DBH}^{2.227842}$ (Q. robur) [61]	a

	AGB _{Total} = 0.0927×DBH ^{2.5097} + AGB _{Leaves} (<i>Q. robur</i>) [62]		
<i>Pinus sylvestris</i> L.	AGB _{branches} = 0.0022×DBH ^{2.9123} AGB _{Leaves} = 0.0045×DBH ^{2.2372} AGB _{Stem} = 0.1227×DBH ^{2.3272} AGB _{total} = AGB _{branches} + AGB _{Leaves} + AGB _{Stem} [40]	BGB = 0.3399×DBH ^{1.4728} [40]	
<i>Prunus serotina</i> Ehrh.	AGB _{Leaves} = 10 ^{(−1.1619)+1.2237×LOG(DBH)} (<i>Q. robur</i>) [59] AGB _{Total} = 0.0927×DBH ^{2.5097} + AGB _{Leaves} (<i>Q. robur</i>) [62]	BGB = 0.040113×DBH ^{2.227842} (<i>Q. robur</i>) [61]	a
<i>Pseudotsuga menziesii</i> (Mirb.) Franco	AGB = e ^{(−1.620)+2.410×ln(DBH)} [66]	BGB = 0.040113×DBH ^{2.227842} (<i>Q. robur</i>) [61]	a
<i>Quercus robur</i>	AGB _{Leaves} = 10 ^{(−1.1619)+1.2237×LOG(DBH)} [59] AGB _{Branches} = 0.0149×DBH ^{2.5994} AGB _{stem} = 0.0722×DBH ^{2.5135} AGB _{Total} = 0.0927×DBH ^{2.5097} + AGB _{Leaves} [62]	BGB = 0.040113×DBH ^{2.227842} [61]	AGB _{Total} : De Inslag AGB _{Branches} , AGB _{stem} : De Mik a
<i>Quercus rubra</i>	AGB _{Leaves} = 10 ^{(−1.1619)+1.2237×LOG(DBH)} (<i>Q. robur</i>) [59] AGB _{Total} = 0.0927×DBH ^{2.5097} + AGB _{Leaves} (<i>Q. robur</i>) [62]	BGB = 0.040113×DBH ^{2.227842} (<i>Q. robur</i>) [61]	a
<i>Salix caprea</i> L.	AGB _{Leaves} = 10 ^{(−1.1619)+1.2237×LOG(DBH)} (<i>Q. robur</i>) [59] AGB _{Total} = 0.0927×DBH ^{2.5097} + AGB _{Leaves} (<i>Q. robur</i>) [62]	BGB = 0.040113×DBH ^{2.227842} (<i>Q. robur</i>) [61]	a
<i>Sorbus aucuparia</i>	AGB _{Total} = 0.164×DBH ^{2.047} (De Inslag) [65] AGB _{Leaves} = 10 ^{(−1.1619)+1.2237×LOG(DBH)} (Mik, <i>Q. robur</i>) [59] AGB _{Branches} = 0.0149×DBH ^{2.5994} AGB _{stem} = 0.0722×DBH ^{2.5135} (Mik, <i>Q. robur</i>) [62]	BGB = 0.040113×DBH ^{2.227842} (<i>Q. robur</i>) [61]	a
<i>Taxus baccata</i> L.	AGB _{branches} = 0.0022×DBH ^{2.9123} AGB _{Leaves} = 0.0045×DBH ^{2.2372}	BGB = 0.3399×DBH ^{1.4728} (<i>P. sylvestris</i>) [40]	

	$AGB_{Stem} = 0.1227 \times DBH^{2.3272}$ $AGB_{total} = AGB_{branches} + AGB_{Leaves} + AGB_{Stem}$ <i>(P. sylvestris)</i> [40]		
Young trees (D > 5 cm)			
<i>Betula pendula</i>	$AGB_{Leaves} = e^{(-1.6938)+1.7455 \times \ln(D)}$ <i>(Q. robur)</i> [68] $AGB_{Total} = (0.259 \times D^{2.132})/1000 + AGB_{Leaves}$ [69]	BGB = 0.16×AGB	
<i>Frangula alnus</i>	$AGB_{Leaves} = e^{(-1.6938)+1.7455 \times \ln(D)}$ [68] $AGB_{Total} = (0.027 \times (D)^{2.769})/1000 + AGB_{Leaves}$ [69]	BGB = 0.21×AGB	
<i>Quercus robur</i>	$AGB_{Leaves} = e^{(-1.6938)+1.7455 \times \ln(D)}$ [68] $AGB_{Total} = (0.027 \times (D)^{2.769})/1000 + AGB_{Leaves}$ [69]	BGB = 0.23×AGB	
<i>Pinus sylvestris</i> L.	$AGB_{Leaves} = e^{(-5.478)+2.494 \times \ln(DBH)}$ [70] $AGB_{Total} = (0.015 \times D^{2.881})/1000 + AGB_{Leaves}$ [69]	BGB = 0.17×AGB	Needles: Eq. from literature uses DBH; here, D was used, resulting in a small error
<i>Sorbus aucuparia</i>	$AGB_{Leaves} = e^{(-1.6938)+1.7455 \times \ln(D)}$ <i>(Q. robur)</i> [68] $AGB_{Total} = (0.143 \times D^{2.064})/1000 + AGB_{Leaves}$ [69]	BGB = 0.23×AGB	
<i>Rhododendron</i>	Biomass per volume-unit (Appendix B): $AGB_{Total} = 68,131.70 \text{ g/m}^3$	Root/shoot = 0.68 [71]	BGB: root/shoot ratio of <i>Phillyrea latifolia</i> L

Dry aboveground biomass (AGB) and coarse roots (BGB) in kg, DBH in cm, stem diameter measured 5 cm above ground (D) in mm. ^a: Coarse roots: allometric relations of roots with diameter > 2 mm. The diameter class of 2–5 mm is counted twice (as coarse roots and as medium roots); compared to the total amount of C in the roots, this error is small.

Appendix B. Calculations of the Allometric Relationships for *Rhododendron*

The amount of dry weight (DW) of stems (or branches) plus leaves of *Rhododendron* was calculated from measurements of volume and density of the stem. Six full stems were harvested from a *Rhododendron* located outside the measured plots. The length and diameter at 5 cm above ground were determined for each stem so that the stem volume could be calculated. The fresh weight was also determined. Next, sub-samples of each stem were taken and weighed, after which they were dried and weighed again. By extrapolation, the DW of the total stem was calculated. Using the DW (g) and the volume (m³) of the stem, the stem density (g m⁻³) was calculated. The average density of *Rhododendron* was 68.132 kg m⁻³. Using this density, DW was determined from measurements of diameter and length for each of the several stems making up the *Rhododendron* shrubs in the measurements plots.

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