Forest management and soil carbon stocks in Swedish boreal forests

Impacts of harvesting, fertilization and tree species choice

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DOCTORAL THESIS
Umeå 2026

Acta Universitatis Agriculturae Sueciae
2026:14

Cover: Soil sampling on a beautiful day. Photo: Marcus Larsson

ISSN 1652-6880
ISBN (print version) 978-91-8124-211-9
ISBN (electronic version) 978-91-8124-231-7
https://doi.org/10.54612/a.6k93ov123l

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Print: Original Tryckeri, Umeå 2026

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Abstract

This thesis explores the link between forest management and carbon (C) sequestration, particularly belowground. It investigates C effects of a forest management system shift, going from unmanaged to rotational forestry and two different forest management practices, and their related effects on soil C stocks. The studies are based on experimental data from extensive field trials in Sweden, aiming to account for both site-to-site heterogeneity and long-term effects. The impact on soil C stocks in older unmanaged forests in relation to rotational even-aged management, especially on mineral soil, was examined in Paper I. The long-term legacy effects from standard forest fertilization practices on soil C accumulation, tree growth, N-cycling and biodiversity was examined in Paper II. The potential of using tree species choice as a tool to increase the soil C stock was examined in Papers III and IV. Together these two studies focus on the above and belowground C inputs and their interaction with heterotrophic respiration and the belowground microbial community, as well as the tree species effect on total ecosystem C stock.

In all studies, the majority of C stock changes from the studied management practices occurred in the biomass of the living trees, followed by moderate responses in the soil organic layer. In contrast, the mineral soil exhibited very limited responses in relation to the forest management practices examined in this thesis. Overall, the results suggest that a more comprehensive view of forest management could be used, in which aboveground and belowground C stocks are evaluated simultaneously, shifting the traditional focus from aboveground biomass towards total ecosystem C management. Such a reframing would make it possible to incorporate information about the relationships between above- and belowground ecosystem compartments into existing forest management practices, thus widening the range of solutions applicable to the challenge of optimizing the carbon sequestration capacity of boreal forests.

Keywords: boreal forest, forest management, harvesting, forest fertilization, tree species, ecosystem carbon stock, soil organic carbon, forest growth

Skogsskötsel och markens kolförråd i svenska boreala skogar

Abstract

Denna avhandling utforskar sambanden mellan skogsskötsel och kolinbindning, med särskilt fokus på marken. Den undersöker ett skogsskötselssystemskifte när trakthyggesbruk appliceras i obrukad skog samt två skogsskötselmetoder och deras effekter på markens kolförråd. Studierna bygger på experimentella data från omfattande fältförsök inom Sverige, där målet har varit att ta hänsyn till både lokal trakteterogenitet och långtgående effekter. Effekterna på markens kolförråd, speciellt i relation till mineraljorden, när trakthyggesbruk sker i äldre, obrukade skogar undersöktes i artikel I. De långsiktiga effekterna från konventionell skogsgödsling på ackumulering av markkol, trädtillväxt, kvävecykeln och biologisk mångfald undersöktes i artikel II. Potentialen att använda trädslagsval som ett verktyg för att öka markens kolförråd undersöktes i artikel III och IV. Tillsammans hanterar dessa två studier kolinflöden både ovan och under mark samt deras samspel med heterotrof respiration och markens mikrobiella sammansättning, liksom trädslagens effekt på ekosystemets totala kolförråd.

Oavsett studie var den övervägande delen av förändringarna i kolförrådet relaterat till trädens biomassa, följt av medelstora förändringar i markens organiska skikt. Mineraljorden uppvisade i stället mycket begränsade förändringar och stod emot den absoluta majoriteten av effekterna från de skogsskötselmetoder som undersöktes i denna avhandling. Resultaten tyder dock på att ett mer omfattande förhållningsätt till skogsskötsel med fördel skulle kunna användas, där kolförrådet ovan - och under mark utvärderas samtidigt, vilket skulle flytta det traditionella fokuset från trädens biomassa till en total ekosystemsförvaltning av kol. En sådan inramning skulle göra det möjligt att väga in information om viktiga samband mellan dessa ekosystemkomponenter i befintliga skogsskötselmetoder, vilket kan öppna upp nya lösningar med syfte att ytterligare optimera kolbindningskapaciteten i boreala skogar.

Nyckelord: boreal skog, skogsskötsel, avverkning, skogsgödsling, trädslag, ekosystemets kolförråd, markens organiska kol, skogstillväxt.

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Larsson, M.*, Dahl, J., Lundmark, T., Gundale, M.J., Lim, H., Nordin, A., 2025. Conversion of unmanaged boreal forest to even-aged management has a stronger effect on carbon stocks in the organic layer than the mineral soil. Forest Ecology and Management 578, 122458. https://doi.org/10.1016/j.foreco.2024.122458

II. Larsson, M.*, Strengbom, J., Gundale, M.J., Nordin, A., 2024. Diminishing legacy effects from forest fertilization on stand structure, vegetation community, and soil function. Forest Ecology and Management 563, 121967. https://doi.org/10.1016/j.foreco.2024.121967

III. Larsson, M.*, Gundale, M. J., Spitzer, C. M., & Nordin, A., 2025. Boreal tree species selection enhances forest carbon stocks through above- rather than below-ground changes. Forest Ecology and Management, 596, 123060. https://doi.org/10.1016/j.foreco.2025.123060

IV. Larsson, M.*, Bizjak-Johansson, T., Gundale, M. J., Spitzer, C. M., & Nordin, A., 2025. Inherent litter properties influence decomposition rates to a greater degree than local soil environment (submitted)

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The contribution of Marcus Larsson to the papers included in this thesis was as follows:

I. Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

II. Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

III. Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

IV. Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

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Abbreviations

C	Carbon
N	Nitrogen
SOC	Soil organic carbon
ha	Hectare
Mg	Mega gram (1 metric tonne)

1. Introduction

1.1 Background

Forests and their associated ecosystem services have been essential throughout human history, providing food, building material, fuel and everything in between (Roberge et al., 2020). Today forest ecosystems are not only essential, but they also serve as a tool to mitigate climate change by capturing atmospheric CO_2, and offer a renewable alternative to many fossil-fuel related products (FAO, 2025). These multitudes of essential services put demands on the forest ecosystem to supply increasing amounts of raw material and services to a multitude of stakeholders (FAO, 2025). The boreal forest (Fig. 1) encompasses approximately 30 % of the Earth's forest cover (Thiffault, 2019) and also store about one third of the global forest carbon (C) pool, of which the majority often can be found in the soil (Pan et al., 2011; Stendahl, 2017). However, due to long cold winters, short summers and low supply of available nitrogen (N), boreal forests have relatively slow biomass growth in contrast to many other forest biomes, meaning any management decision made today will have consequences for decades or even centuries to come.

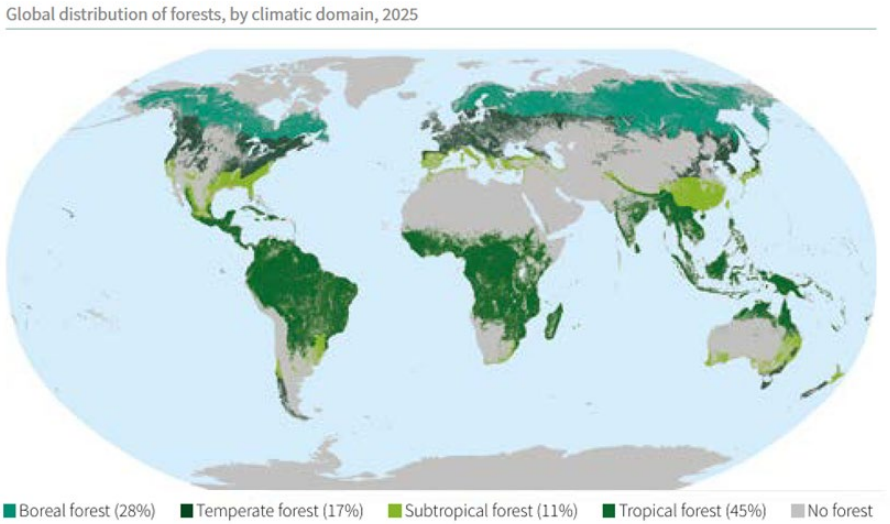


Figure 1. Global area distribution of boreal forests and other forest biomes (FAO, 2025).

Sweden has 28.0 million hectares of forest, of which 23.6 million hectares are classified as productive forest land, defined as forest producing at least 1 m^3 of woody biomass ha^{-1} y^{-1} (Nilsson et al., 2025). Almost all of this forest area is located within the boreal region and from the 1950s onwards, even-aged forestry based around clear-cuts and mandatory regeneration (legally required since 1904), has been the dominant forest management system within the country (Roberge et al., 2020). The management system is normally based around four phases: *Establishment phase*: Where about 80 % of new establishments are performed using soil scarification followed by planting, commonly with seedling material from nurseries. Although, due to natural regeneration the majority of stands end up as a mixture of both planted and naturally generated seedlings (Albrektson et al., 2012; Roberge et al., 2020). *Juvenile phase*: Marks the period during which the forest stand has an average height of approximately 1.3 to 7 meters. The dominating management practice within this phase is pre-commercial thinning, marking the first, and arguably most important, forest structure shift of the entire rotation (Albrektson et al., 2012). *Thinning phase*: Marks the period between the juvenile phase and the harvesting phase, during which commercial thinning is the dominant management practice. The practice is aimed at focusing the not yet realized growth-potential of the stand into fewer trees, thus optimising the commercial value of each tree within the stand. Depending on the type of thinning, goals of the forest owner and forest structure, the biomass removal is usually between 20-40% (Albrektson et al., 2012). *Harvesting phase*: Marks the end of a forest rotation (and the beginning of the next) during which the forest is harvested. The harvesting is required by law (SVL, 2025) to take environmental considerations into account, often further strengthen by environmental certification schemes (e.g., FSC, 2026). The Swedish forestry act also regulates the required minimum forest stand ages required for clear cutting, which are normally based on tree species, site productivity and geographical location within the country (SVL, 2025). For Scots pine and Norway spruce stands, these limits vary from 45 years in the most productive spruce forests of southern Sweden to 100 years in less productive forests in the northern parts of the country (SVL, 2025), rotation times can however be far longer.

While the four phases of the even-aged management system outline the general structure and progression of a forest rotation, a wide range of forest management options can be used to address the challenge of optimizing the carbon sequestration capacity of boreal forests. These options span financial and environmental objectives and include strategies and practices aimed at reducing the risks of damages from wind, fire, and pests. Disturbances that are expected to increase under future climate change (Patacca et al., 2023). Analysis using the net present value, which is a function of time, revenue, cost and discount rate (normally set between 2-5%), is commonly used as a tool to prioritise between different financial outcomes (Ekvall and Bostedt, 2009). The analysis makes it possible to discount the value of different implemented management practices, controlling for the fact that they are made at different time intervals during stand development. Yet, in practice each forest stand is subject to many environmental and socio-economic factors, which may override the importance of the net present value considerations (Ekvall and Bostedt, 2009).

Most available management tools and options are also often applied in accordance with the traditional aim of forest management, to optimize the quantity and quality of aboveground biomass production. Although, since the majority of C stored in productive boreal forests within Sweden can be found in the soil (Stendahl, 2017), a link between aboveground productivity and belowground C accumulation has been suggested (Mayer et al., 2020; Noormets et al., 2015). Improved management of the belowground soil C stock could therefore increase the climate benefits of the boreal forest biome, shifting the traditional focus of forest management from aboveground biomass towards a total ecosystem C management. However, there are still some substantial knowledge gaps regarding how different forest management practices in the boreal region influences soil C across different sites, soil layers and over longer timescales (Gundale et al., 2024; Mayer et al., 2020), which complicates the implementation of such a shift. The discrepancies are in part caused by the large spatial variation (e.g., hydrology, soil clay content, etc.) in soil organic carbon (SOC) within sites, which complicates the accurate estimation of site averages (Hoffmann et al., 2014). In addition, a variety of sampling techniques are also often used to estimate SOC, limiting direct comparability among studies (Vanguelova et al., 2016). Furthermore, boreal areas remain relatively understudied compared to other forest regions, making region generalization more difficult (James and Harrison, 2016; Luyssaert et al., 2007; Xu et al., 2014).

In this thesis I aim to use paired stands comparisons, repeated measurements combined with long term datasets, and common garden experiments in an attempt to address some of the above-mentioned uncertainties. I present high-quality empirical data and associated conclusions on soil C stocks in relation to one forest management system shift and two forest management practices. All three considered to have a high potential of impacting both belowground and aboveground C responses in boreal forests: Conversion of unmanaged boreal forest to even-aged management, nitrogen (N) fertilization, and tree species choice.

1.2 Conversion of unmanaged boreal forest

In Sweden the dominant forest management system is based around even-aged rotational harvest, followed by mandatory re-establishments (Roberge et al., 2020). The forest rotation length is defined as the number of years between two final fellings (i.e. two clear cutting events). However, older and “larger” areas of unmanaged forests can still be found, mainly in the north-western parts of Sweden (Fig. 2). Forests such as these have been shown to store greater amounts of C than young managed forests (Gleixner et al., 2009; Gundale et al., 2024; Nord-Larsen et al., 2019), both in standing biomass and soil (Luyssaert et al., 2008; Paw U et al., 2004; Zhou et al., 2006), and can also be associated with higher levels of what is considered stable mineral C (Gundale et al., 2024; Kumpu et al., 2025). The suggestion that old unmanaged stands could be preserved to maintain large C stocks is therefore well represented among scientists (Knohl et al., 2003; Luyssaert et al., 2008; Naudts et al., 2016; Zhou et al., 2006). Young, fast-growing managed stands are instead known to achieve higher rates of C uptake compared to older unmanaged stands and studies suggest that long-term forest management improves the C balance in boreal forests due to avoided emissions, that C sink lost to harvest can recover within a couple of decades (Peichl et al., 2023; Pukkala, 2017), and C stores can recover before the end of a rotation. From a management viewpoint these arguments are not entirely compatible, which has led to a controversial debate on how to best utilize (Bellassen and Luyssaert, 2014), and/or incorporate older unmanaged forests as components in policy frameworks to mitigate climate change (Lundmark et al., 2014; UNFCCC, 2016).

Figure 2. Picture from the north-west of Sweden displaying border between an old, unmanaged forest and an old, unmanaged forest that was harvested and re-generated. Photo by Jenny Dahl (2017).

While the arguments are not entirely compatible, there is a degree of consensus around how changes in soil C from harvesting propagates down through the soil profile. The biggest effects are often present in the organic layer and seems to scale with intensifying harvest practices (Achat et al., 2015). The mineral soil is usually affected to a lesser degree, and is also regarded as more stable, potentially over millennial timescales, due to organic matter binding to mineral surfaces, fungal necromass or stabilization within soil aggregates (Adamczyk, 2021; Wiesmeier et al., 2019; Yang et al., 2020). Consequently, most studies on average show decreasing SOC trends in response to harvesting, due to losses in the organic horizon (Gundale et al., 2024; Nave et al., 2010), but only a few studies have shown a significant loss of SOC in mineral soil layers (James and Harrison, 2016). It is however still unclear to what degree even-aged management in older unmanaged forests destabilizes the more stable mineral soil C pool, as relatively few studies have simultaneously quantified soil C stock in unmanaged vs. managed stands. This uncertainty is also further magnified as different countries use different definitions on what constitutes an unmanaged forest. In fact, most countries do not directly identify or distinguish unmanaged forests (or old growth/primary/pristine forests) from other forest types in their national forest inventories, making it difficult to assess the general impacts of a forest management system shift in such areas (Bernier et al., 2017; Eriksson et al., 2023).

1.3 Fertilization (N addition)

About 40 000 ha of Swedish forest is fertilized annually ("Åtgärder i skogsbruket," 2023) and while this is less than half of the suggested yearly potential (Bergh and Hedwall, 2013; Falkeström et al., 2018) it only represents a small part of the available productive forest land (c. 23 million ha in Sweden). The incentives are clear, a standard fertilization practice (Fig. 3) of adding 150 kg N ha^{-1} once or twice during a forest rotation can increase tree growth by approximately 10 – 20 m^{3}sk ha^{-1} during a 10 year period (Drott et al., 2025), and timber harvest profitability by up to 15 % (Jacobson and Pettersson, 2010). The increase in biomass growth is however not the only effect: increased N concentrations in needles, potential effects on N leaching, changes in understory diversity, and alterations to soil C cycling processes are all common outcomes of forest fertilization (Mayer et al., 2020;

Nohrstedt, 2001). From a climate change mitigation perspective, the increase in forest productivity and the alteration to soil C cycling processes (which usually leads to an increase in soil C accumulation) are both beneficial as they lead to a reduction of atmospheric CO2 (Friedlingstein et al., 2020; Hyvönen et al., 2008; Johnson and Curtis, 2001; Jörgensen et al., 2021).

Figure 3. Fertilization by tractor, schematic picture (Jacobson et al., 2005).

The increase in belowground C accumulation is mainly due to the increased production of above and belowground plant litter and shifts in the soil microbial community, which can hamper soil organic matter decomposition (Forsmark et al., 2021; Haas et al., 2018; Jörgensen et al., 2022; Maaroufi et al., 2019, 2015). The majority of results demonstrating impacts of N additions on soil carbon accumulation in boreal forests however stem from experiments using either large doses of N applied a single time, or small doses added repeatedly during long periods of time (Forsmark et al., 2020; Huang et al., 2011; Hyvönen et al., 2008; Maaroufi et al., 2015; Olsson et al., 2005). The effects from "standard" forest fertilization practices are often considered to last no more than ten years (Nohrstedt, 2001); and only a few studies have examined longer-term effects. These studies however showed increased growth of young trees in stands fertilized with standard N doses during the previous forest generation, as well as changes in the species composition of the ground vegetation and soil N (From et al., 2015; Strengbom and Nordin, 2012, 2008). It therefore remains unclear whether standard forest fertilization practices also can result in long-term increases in soil C storage. Thus, to enable for forest owners to make better informed decisions regarding standard fertilization practices within the boreal forest region, a need for improved understanding of the strength and longevity of eventual legacy effects are necessary. Any related negative effects, such as the potential to induce vegetation changes that negatively affect biodiversity (Bobbink et al., 2010, 1998; Midolo et al., 2019) should also be kept to a minimum.

1.4 Tree species selection

The vast majority (80%) of Swedish forestland consists of conifers, mainly *Pinus sylvestris* and *Picea abies* in roughly equal measures, followed by *Betula sp.* (Fig. 4), at 12 % and 14 other species with less than 2 % each (Krekula et al., 2018; Roberge et al., 2020). As planting of seedlings are the most commonly used re-establishment method (approx. 80%), the tree species selection during regeneration roughly follows that of the country distribution, where *Pinus sylvestris* is seen as more suitable on low fertility sites and *Picea abies* is often planted on more nutrient rich sites (Roberge et al., 2020). There is however a possibility to choose different tree species, which (if done right) has the potential to optimise and diversify the above ground biomass production. For example, introduced exotic tree species such as *Larix* and *Pinus contorta* have been shown to have a substantially higher mean biomass production relative to native species (Krekula et al., 2018). Utilizing this potential could both increase the climate change mitigation effect, lower regional risk of biotic damages, and also lead to higher economic gains. All of which are suggested to be positive outcomes from using a broader tree species distribution (Sverige, 2025). The practice could also provide the opportunity to manipulate the size and/or stability of the belowground C stock (Mayer et al., 2020). Which would give forest managers yet another tool for enhancing boreal forests' climate change mitigation potential.

Figure 4. *Betula pendula* plot in tree species experiment outside Vindeln. Photo by Marcus Larsson (2022).

The general idea is that groups of different tree species have different resource acquisition strategies associated with their functional traits, also referred to as the "plant economics spectrum" (Reich et al., 1997). These variations in plant function can correspond to differences in soil C accumulation through “species” differences in biomass decomposition rate. One end of the spectrum corresponds with “acquisitive” strategies, indicating high resource capture that supports rapid growth (e.g. high specific leaf area and/or high leaf nutrient content) and, as a consequence, often higher decomposition rates. These traits are normally found in early-successional tree species such as *Betula pendula* or *Pinus sylvestris*. The other end of the spectrum corresponds with resource “conservation” strategies, instead associated with slow growth (e.g. high levels of structural defence, low specific leaf area and/or high lignin content), and, as a consequence, often slower decomposition rates. These “conservation” strategies are normally found in late-successional species, such as *Picea abies* (Díaz et al., 2016; Gundale et al., 2024; Liski et al., 2003; Prescott, 2010; Zhang et al., 2008). However, despite decades of research (Mayer et al., 2020; Prescott and Vesterdal, 2013), the mechanisms by which different tree species accumulate SOC remains difficult to tease apart from site-specific factors (Mayer et al., 2020). Further testing in well-designed experimental systems such as common gardens are necessary to understand if and how certain tree species are beneficial to sequestration of soil C, and in which forms and soil layers (Mayer et al., 2020). Although, long term results indicates that the decay rate of different types of litter (and litter from different species) may converge over time (Berg and Ekbohm, 1993; Prescott et al., 2004), meaning trait differences between species might not matter as much as quantity of litter input, or local environmental conditions.

1.5 Research objectives

The overall objective of this thesis was to explore how different forest management practices commonly applied in the boreal forests of Sweden affect soil C stocks, and to provide insights into how these practices could be used to enhance the climate change mitigation potential of boreal forests. The impact of a shift to even-aged management in older unmanaged forests on soil C stocks, particularly in mineral soil, was examined in **Paper I**. Eventual long term legacy effects from standard forest fertilization practices (e.g.150 kg N ha^{-1}) on soil C accumulation, tree growth, N-cycling and biodiversity was examined in **Paper II**. **Papers III** and **IV** instead examined the potential of tree species choice as a tool to increase the soil C stock. Together these two papers focus on the above and belowground C inputs and their interaction with heterotrophic respiration and the belowground microbial community, as well as the tree species effect on total ecosystem C stock.

2. 2 Materials and methods

2.1 Study sites

Conversion of unmanaged boreal forest to even-aged management

The study (**Paper I**) includes 23 sites (Fig. 5) in north-west of Sweden (Västerbotten and Norrbotten County), lat. 65-66º, long. 16-20º, 200–630 m above sea level. The region is located just downslope from the Swedish mountain range and has large areas of intact unmanaged forests that have never been utilized for even-aged management. However, most of the forested area has historically been selectively cut with varying proportions of large diameter trees removed and/or been subject to stand replacing fires. At each site managed (even-aged management initiated by clear-cutting) and unmanaged stand pairs were identified.

Figure 5. The distribution of sites used in the study. Each site consisted of paired unmanaged and managed forest stand. The white dot marks the town of Arvidsjaur.

Each managed stand was assumed to have been equivalent to the adjacent unmanaged stand prior to clear-cutting. The managed stands had a mean site index of 14.4 (H100, m) and tree ages ranged between 14 and 54 years old (average age 27 years). The unmanaged stands showed a mean site index of 13.9 (H100, m) and tree ages ranged between 106 and 223 years (average age 163 years). Nine of the managed stands were dominated by Norway spruce (*Picea abies* (L.) Karst and 14 by Scots pine (*Pinus sylvestris* L.), while 14 of the unmanaged stands were dominated by Norway spruce, and 9 by Scots pine. All selected sites were dry or mesic site types lying on moraine or river sediments, with soil textures ranging from silty to sandy.

Forest fertilization and related legacy effects

Data used in this study (**Paper II**) was gathered from 21 forest stands, each sized between 4.7 and 22.4 ha., spread out over an 8500 ha forest land area in the middle boreal zone (Ahti et al., 1968) in central Sweden (62◦58 "N, 16◦40"E, Bispgården, Fig. 6). The studied stands either had, or had not, been subjected to N fertilization before harvest and regeneration. Control (C) stands (n = 7) were never fertilized, N1 stands (n = 7) were fertilized with 150 kg N ha^{-1} once in 1985, and N2 stands (n = 7) were fertilized with 150 kg N ha $^{-1}$ in both 1977 and 1985; thus, the study included 7 stands for each treatment. Fertilizer N was added as granules of ammonium nitrate (NH_4NO_3) spread by tractor or aircraft.

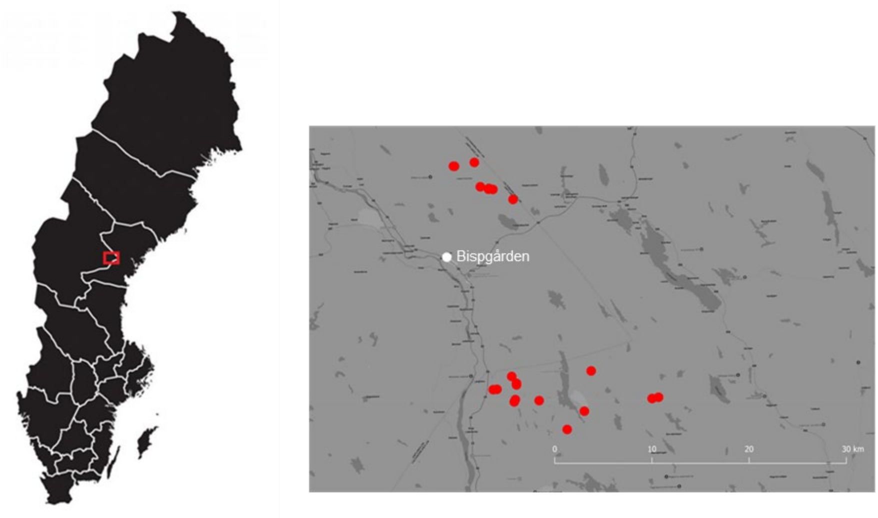


Figure 6. Distribution of the stands. Each treatment included N = 7 stands, giving a total of 21 stands. The white dot indicates the village of Bispgården.

The initial stand selection done in 2008, see From et al., (2015). Care was taken to select the stands with similar initial productivity indices, elevation, temperature sum (growing degree days; Womach, 2005), slope (forest floor incline from 1 (<10 % inclination) to 5 (>50 %), tree species composition, soil conditions and stand age at the time of stand selection, table 1.

Table 1. Number of stands per treatment, site index (SI), elevation (above sea level, a.s.l.), temperature sum (GDD) and forest floor slope. The stands were fertilized once in 1985 (N1) with 150 kg N Ha^{-1}, twice (N2), both in 1977 and 1985 with 150 kg N Ha^{-1} or never fertilized (C).

Stands (n)	**Control**	**N1**	**N2**	***F*-value**	***p*-value**
	7	**7**	**7**		
Site index (H100), m)	20.6 ± 0.2	19.7 ± 0.3	20.4 ± 0.3	3.00	0.08
Elevation a.s.l (m)	334 ± 21	358 ± 20	334 ± 17	0.54	0.59
Temperature sum (GDD)	937 ± 6	900 ± 22	923 ± 11	1.59	0.23
Slope (1-5)	2.00 ± 0.22	1.86 ± 0.26	1.72 ± 0.18	0.41	0.67

Note: Table adapted from (From et al., 2015).

The annual precipitation in the area is between 500 and 600 mm per year, and the atmospheric background N deposition ranges from 1.6 to 2.4 kg ha^{-1} year^{-1} (Karlsson and Hellsten, 2022). All stands used in the study had mesic site conditions with Udic moisture regime and soils were Typic Haplocryods developed on glacial till with an organic surface layer (O-horizon), sometimes also referred to as plant litter layer, where the upper part is relatively undecomposed and the lower parts were strongly humified (Driessen, 2001; From et al., 2015; Strengbom and Nordin, 2008). All stands were harvested by clear-felling between 1997 and 2000, subjected to soil scarification, and then planted with identical seedling stock of either *Pinus sylvestris* or *Picea abies* at a density of 2200–2300 seedlings ha^{-1}.

Tree species selection

Two common garden experiments (**Papers III** and **IV**) were utilized in these studies, one located in northern Sweden and one located in central Sweden. The northern site, Svartberget (64°15′N 19°47′E), was established in 1992 and consisted of 10 tree species, divided over 30 plots and 3 blocks. The central site, Garpenberg (60°18′N 16°17′E), was established in 1995 and consisted of 8 tree species, divided over 20 plots and 3 blocks. All species present on both sites are common in the boreal region, including four species native to Sweden, *Betula pendula*, *Pinus sylvestris*, *Larix sukaczewii* and *Picea abies*. The remaining species are considered exotic species in Sweden, (*Abies lasiocarpa*, *Abies sibirica*, *Picea glauca*, *Picea mariana*, *Pinus banksiana*, *Pinus contorta* and *Pseudotsuga menziesii*). There were three replicate plots for each species at Svartberget, (i.e., a complete block design), whereas at Garpenberg *Betula pendula* and *Larix sp*. were only present in two blocks (i.e., an incomplete block design; Fig. 7). In total 6 species (*Betula pendula*, *Larix sp*., *Picea abies*, *Picea glauca*, *Pinus contorta* and *Pinus sylvestris*) were common between both common garden experiments.

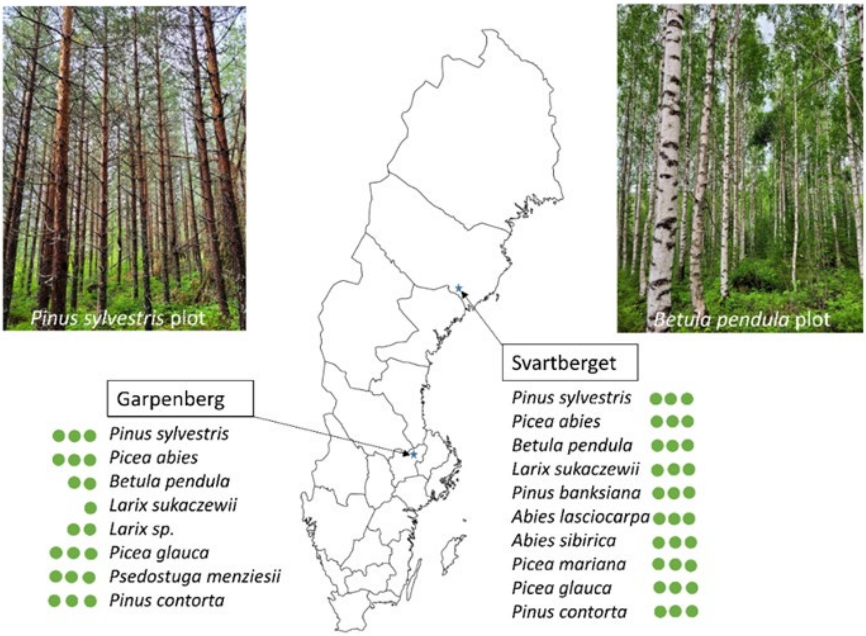


Figure 7. Map showing the locations of the two field sites in Sweden. Tree species monocultures present at each site are listed and the number of green dots indicate the number of replicate plots of each species found at the site. Photos are of one replicate plot of two species, source: (Spitzer et al., 2025).

At establishment all plots were scarified and planted using a seedling spacing of 2 m, resulting in 289 seedlings per plot. Both sites had a similar site index (SI), defined as the average height that the dominant trees of a particular species will attain at a specific reference age. Svartberget had an SI value of 22 (H100) and Garpenberg had an SI value of 23 (H100). The average growing season temperature during 2018–2022 was 13.3◦C at Svartberget and 15.9◦C at Garpenberg (Swedish Meteorological and Hydrological Institute, "SMHI", 2025). The soil is a relatively shallow podzol developed on glacial till (moraine). For more information about the site properties, see **Paper III**, Table 1.

2.2 Methodological considerations

2.2.1 Soil sampling

Organic horizon

The organic horizon was sampled in a similar fashion across all experiments (**Papers I**, **II**, **III** and **IV**), utilizing a plot level grid sampling and a cylindrical (diameter 10 cm) soil corer. The exception was the fertilization experiment (**Paper II**), where the organic layer was sampled along a transect at each stand. The collected material was put in paper bags and after transport to the lab sieved (2 mm mesh) and then dried at 70 C° for at least 36 h, then stored in room temperature awaiting analyses. Replicate samples were pooled at the plot level to obtain one value of concentration per element and stand. The samples were later milled, and total C and N concentrations were analysed using an isotope ratio mass spectrometer (DeltaV,Thermo Fisher Scientific, Bremen, Germany) and an elemental analyzer (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). C and N stocks in the organic layer were calculated by multiplying the C and N concentrations with the combined dry weight of the pooled samples from each stand. The values were then then upscaled to Mg ha^{-1} using the combined cross-sectional area of the subsamples in each stand. A slightly different approach was used in the harvesting study (**Paper I**) due to difficulty bringing all sampled material back to a road suitable for transport. Instead, a composite sample was used and C stock in the organic layer was calculated with the aid of bulk density functions (equation 18, Nilsson and Lundin, 2006), and the thickness of the organic layer.

Mineral soil

In the fertilization and tree species study (**Papers II, III** and **IV**) the mineral soil was sampled at two 10 cm increments 0-10 cm and 10-20 cm, using a metal core sampler (diameter 1.59 cm). The collected material was pooled at the plot level, sieved (2 mm mesh) and then dried at 70 C° for at least 48 h, and later stored at room temperature until analysis. The samples were later milled, and total C and N concentrations were analysed using an isotope ratio mass spectrometer (DeltaV,Thermo Fisher Scientific, Bremen, Germany) and an elemental analyzer (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). In the fertilization study (**Paper II**) only C/N ratio of the mineral soil was analysed, and in the tree species study (**Papers III** and **IV**) C stock in the mineral soil was calculated with the aid of bulk density functions, equation 31 from Nilsson and Lundin, (2006). In the harvesting study (**Paper I**) the mineral soil was collected from soil pits with individual non-volumetric samples from multiple depth increments (0-10, 10-20, and 20-50 cm). All subsamples from each layer were pooled plot-wise, giving one composite sample for each soil layer and plot. Carbon stock was calculated with the aid of collected bulk density samples using the excavation method (Gatea et al., 2018) where a ca. 15 cm diameter hemispherical pit was excavated, a soft mesh cloth was inserted in the pit and then filled with 2 mm plastic granules. The volume of the granules was then determined, and the excavated soil was sieved (2 mm). Collected samples were transported back to the lab, dried at 70º C for 48 hours, sieved again (2 mm) and weighed. The mass of the processed samples was then divided by the volume of plastic granules used to fill the pit, yielding bulk density estimates (g cm^{-3}).

Stoniness

Stone and boulder content (SB) was estimated using the rod penetration method, where an iron rod with a diameter of 10 mm was driven through the soil until it reached a stone or boulder (Viro, P.J., 1952). This was done at a number of predetermined points in a grid pattern at each site. The mean penetration depth was calculated as volumetric content of stones and boulders in percent using Viro (1952) modified by Stendahl et al., 2009, using the regression equation $SB = 82.5 - 2.75*Si$, where Si is the mean penetration depth of the predetermined sample points.

Soil N mineralization and soluble N

The buried bag (**Paper II**) technique (Eno, 1960; Gundale et al., 2011) was used to investigate N mineralization in all stands. Between June 15-18, 2021, seven samples from the entire O-horizon in each replicate stand (i.e. 147 samples in total) were collected with a cylindrical (diameter 10 cm) soil corer along 45 m transects passing through the centre of each stand. The depth of the O-horizon (ca. 5-15 cm) made sampling of the entire horizon possible for all 49 samples. After gently removing large roots and the top layer of easily identifiable plant material, half of each sample was put in a plastic bag, put into a cooler and transported back to the lab for analysis. The other half was put into another plastic bag and buried in the organic horizon in situ. The buried cores were then collected 85 days later (14-15 of September), transported to the lab in a cooler, and processed for analysis. All samples were sieved (2 mm mesh) and then extracted in 1 mol KCl and analysed for NH_4 and NO_3 using an Auto Analyzer 3 spectrophotometer (OmniProcess, Solna, Sweden). Net mineralization was calculated as the difference in NH_4-N and NO_3-N (mg g^{-1} dry weight [DW] soil) between the June and September sample times. Before statistical analyses, sub-replicate samples of NH_4-N and NO_3-N from the same stands were pooled to obtain one single value of mineralization per stand, with these stand level values serving as true replicates.

Resin ion-exchange capsules (PST-1, Universal Bioavailability Environment/Soil Test, MT, USA) were used to estimate the amount of soil mobile NH_4-N and NO_3-N (mg $capsule^{-1}$) in all stands. Between the 15-18 of June 2021, six capsules were buried just beneath the bottom of the organic horizon along a transect through each stand center. Later the same year, between the 14-15 of September, all capsules were retrieved, put in plastic bags, and transported to the lab for analysis. In the lab, the ion-exchange capsules were brushed off to get them as clean as possible, and then placed in 50 ml Falcon tubes. Ten ml of 1 mol KCl was then pipetted into the tubes, followed by 30 min agitation. This process was repeated 3 times, resulting in a total of 30 ml sample extracts. The NH_4-N and NO_3-N concentration on these extracts were analysed using an Auto Analyzer 3 spectrophotometer (OmniProcess, Solna, Sweden). Before statistical analysis sub-replicate samples from the same stands were pooled to obtain one single value per stand.

2.2.2 Ground vegetation and plant foliar chemistry

In the fertilization experiment (**Paper II**) the vegetation was scored using a modified version of the point intercept method (Jonasson, 1988). The ground vegetation (vascular plants, bryophytes and lichens) was analysed at 200 random points along a 45 m transect through the centre of each stand. At each point a stick was placed (4 mm in diameter) and the number of contacts each species made with the stick was counted. In addition, fresh foliage material from 4 different plant species, *Vaccinium myrtillus*, *Picea abies*, *Deschampsia flexuosa* and *Pleurozium scheberi* were also collected along the transects. These four species are common and represent four different groups of plants, i.e., dwarf shrubs, trees, grasses and mosses. For *Vaccinium myrtillus, Deschampsia flexuosa*, and *Pleurozium scheberi* fresh foliage material (leaves) were collected from seven random places along each transect while current year shoots from *Picea abies* were gathered from five different trees on or close to the transects. The material was immediately dried in paper bags in room temperature and then dried at 40 C° for 48 h in the lab. The material was then milled and analysed for total N and C concentrations (g/g dry mass) using an isotope ratio mass spectrometer (DeltaV,Thermo Fisher Scientific, Bremen, Germany) and an Elemental analyser (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). In the harvesting experiment (**Paper I**) the ground vegetation and litter layer on top of the samples from the organic horizon were instead collected at nine pairs of unmanaged and managed sample plots, and transported the material back to the lab for determination of C content. The ground vegetation and litter were not analysed individually, due to difficulty in separating them.

2.2.3 Tree growth

Living and dead tree biomass in the harvesting study (**Paper I**) were estimated from four circular sample sub-plots (7-meter radius), with at least 20 meters between sub-plot centers (Fig. 8). Trees with diameters >100 mm within the 7-meter sample sub-plots and trees with a diameter of 40-99 mm within 3.5 meters from the sub-plot centers were included in the study. Sample trees were used to measure both height and age (stem cores at 1.3 meters). In the managed stands only the main tree layer was included when establishing stand age. Dead wood with a diameter over 100 mm and height or length of more than 1.3 m that was classified as “hard dead wood” (more than 90 % of the stem consisting of hard non-decomposed wood, according to Nilsson et al., 2008a), was registered in each sub-plot, whereas other decay stages of dead wood were not included in the sampling. Carbon in living trees for all tree species, (*Pinus sylvestris*, *Picea abies*, *Betula spp.*, *Salix caprea* and *Populus tremula*) were then calculated using Marklund's biomass functions (Marklund, 1988). For calculations of *S. caprea* and *P. tremula* C content, the functions for birch were used, but adjusted according to the density of the wood. Biomass of coarse roots down to 2 mm were calculated for *P. sylvestris* and *P. abies* only, using allometric functions by Marklund, (1988), and adjusted by 6% based on Petersson and Ståhl, (2006). Other tree species were assumed to be minor contributors to these pools due to their low abundance in all plots. Carbon contents were assumed to be 50% of dry mass in all living biomass, and measured values were upscaled to Mg C ha^{-1}. Biomass of dead wood was calculated based on volume estimates according to Näslund (1940) and density of the dead wood (spruce 0.29, pine 0.31 and broadleaves 0.37 g cm^{-3}). The amount of C in dead wood was assumed to be 50 % (Russell et al., 2015) and measured values were upscaled to Mg C ha^{-1}. Each measured biomass pool within the plots were then added together, resulting in total Mg C ha^{-1}.

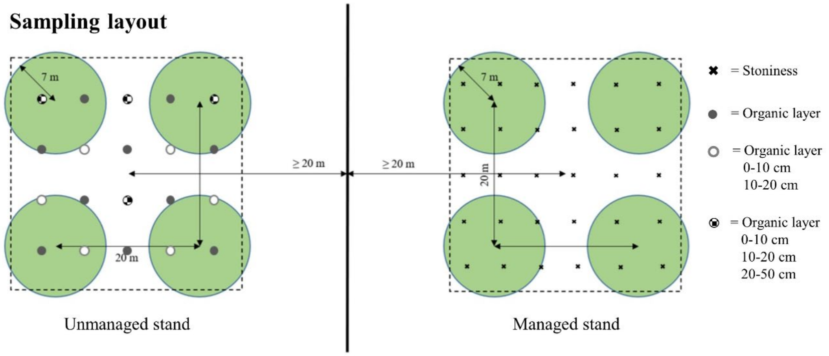


Figure 8. A depiction of sampling at each site utilizing a paring consisting of an unmanaged stand with an adjacent managed stand. All sampling was performed within 0.1 ha plots. Living trees and dead wood were sampled within the green circular sub-plots. Stoniness, soil samples, ground vegetation and litter layer, were collected on points located on a grid within the plots marked with dashed lines. *Note:* Both stoniness and soil sampling

were performed in all plots, the figure only depicts them separately for clarity.

In the fertilization study (**Paper II**) a full site inventory was utilized to measure tree growth. The stands were inventoried by using a square grid randomly positioned over the entire 8500 ha forest area on the map. Each grid cell was 100 x 100 meters in size and all grid cell intersections contained within each of the 21 stands on the map were inventoried using circular (r = 5.64 m) plots, located during the inventory process with GPS. If a plot randomly landed on a nature conservation set-aside patch originating from the previous stand, it was excluded from sampling. After the removal of these specific sub-plots, a total of 253 sub-plots were inventoried across the whole experiment, divided among the different stands. Each stand was thus inventoried using the same "resolution" but the number of inventoried plots per stand varied depending on the size of the stand (4 plots in the 2.34 ha smallest stand, and 25 plots in the 26.4 ha biggest stand). In every plot, tree species and diameter at breast height (1.3 m) was measured for all trees taller than 1.3 m The height of the tree closest to the plot centre, and one tree in every cardinal direction closest to half the radius of the plots was also measured, i.e., 5 samples trees in total within each plot (Gundale et al., 2014). If two trees were equally close to the cardinal points, the clockwise positioned trees were used. For all variables, sub-replicate values from the same stands were pooled to obtain one true replicate value of average DBH and height per stand. Thus, for all statistical analysis, the stand was considered the unit of replication.

Forest inventory at the tree species experiment (**Paper III**) was performed at both sites by randomly selecting 20 trees in each plot and measuring tree height and diameter. Stems per hectare were calculated by total count of trees in each plot and scaling this value to the hectare level. The aboveground biomass was then calculated using the data from the forest inventory and the appropriate biomass equation. To convert stem volume to biomass for tree species native to Sweden, except *Larix sp.*, Marklund's biomass functions were used (Marklund, 1988). For *Larix sp.*, equation 136 in Zianis et al., (2005) was utilized. For all other tree species, the biomass equation from Jenkins et al., (2003) was utilized, with different constants used for each species (**Paper III**, supplemental 2). Only functions constructed for total aboveground biomass were considered and selected for the calculations.

2.2.4 Soil C input, output

Litter fall

Litter fall (**Paper III**) was collected using circular (48 cm in diameter) litter traps with a mesh bottom (Fig. 9) Three traps per plot were installed and emptied twice: once after snowmelt and again in late summer. The traps were placed ≥ 1m from the nearest tree, at a maximum distance of 10 m from the plot center, and at least 10 m from the nearest adjacent trap. This approach was used to effectively sample the center of each plot, while avoiding edge effects and litter inputs from adjacent plots. The collected litter was pooled at the plot level, transported to the lab, and dried at 70° C for at least 48 h. The litter was then sorted into leaves or other detritus (e.g. twigs), saving only leaves or needles from the tree species native to the plot. The samples were then weighed, and a subsample was milled and analysed for total N and C concentrations (g/g dry mass) using an isotope ratio mass spectrometer (DeltaV, Thermo Fisher Scientific, Bremen, Germany) and an elemental analyzer (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). After analysis, the C and N concentrations were multiplied with the combined dry weight of the pooled samples from each plot, and then upscaled to Mg ha^{-1} using the combined area of the litter traps used in each plot. Coarse and woody debris (sticks, branches, bark cones etc.) from each species was collected between 2022 and 2023. A 2 × 2 m square in the center of each plot was cleared of any debris, then marked and left for one year. After this period, any new material entering the plot was collected, dried at 70 °C for 48 h, and then weighed. The weight of the samples was then upscaled to Mg ha^{-1} using the plot area. For upscaling, the C content of the coarse and woody debris biomass was assumed to be 50 %.

Figure 9. Litter trap, tree species experiment outside Vindeln. Photo by Marcus Larsson (2021).

Fine root production

Ingrowth cores (**Paper III**) adapted from (Forsmark et al., 2021) was used to measure fine root production, the method is extensively used in ecosystem studies (Brunner et al., 2013) and the cores (5 cm wide and 20 cm long) were made from nylon mesh (Sintab Product, AB Sweden) with 2 mm mesh openings. In early summer, fine-root ingrowth cores were installed vertically at the centre of each of the four sides in every plot (Fig. 10), at a minimum distance of 3 m from the plot edge and at least 70 cm away from the closest tree. Each core was filled with sieved (2 mm) mineral soil from a pit at the center of the same plot where it was installed (which was packed in the cylinder to approximately the same bulk density as the surrounding soil), and then buried within the mineral soil to a depth of 20 cm. The removed organic layer was placed back on top of the cylinder which was then left to incubate. Two years after installation (with an incubation time of 24 months), the root-ingrowth cores were collected. The incubation time of 24 months was chosen to allow for two full growing seasons, which both minimized the initial disturbance effect and root biomass turnover during the measurement period (Brunner et al., 2013; Finér et al., 2011). After collection, the root-ingrowth cores were transported to the lab, the soil was removed, and the root biomass from individual ingrowth cores was pooled at the plot level. The pooled root biomass was then dried at 70°C for at least 48 hours and sorted, removing everything except fine roots from the tree species native to each individual plot. The remaining biomass was weighed and then upscaled to Mg ha^{-1} y^{-1} using the combined volume of the root ingrowth cores installed in each plot. The C content of the fine root biomass was assumed to be 50 % (Nilsson et al., 2008b; Spitzer et al., 2025), and the values were adjusted for stoniness of each plot.

Figure 10. Installation of root ingrowth cores, tree species experiment outside Garpenberg. Photo by Marcus Larsson (2021).

Decomposition rate

To measure decomposition rate (**Papers III** and **IV**) for each tree species, litter bags made from a nylon mesh with 100 µm openings (Sintab Product, AB Sweden) was used (Fig 11). The mesh size was chosen to allow for microbial processes and fungal ingrowth, but to exclude soil macrofauna. In total 600 bags were used in tree species experiment (**Paper III**), with half of them filled with tree species litter gathered from litter traps the year before, and half filled with material from the organic layer (i.e. “humus-layer”). At the beginning of autumn all bags were filled with 3 grams of dry mass and were then gently put back in the field just beneath the organic layer, at the intersection with the mineral soil, and in the same plot as their respective litter origin. Consequently, 6 litter bags and 6 humus bags were placed in each plot. A year later all bags were collected and brought back to the lab, dried in 70° C for at least 48 h, and weighed to allow calculation of mass loss. Values from individual bags were pooled at the plot level before statistical analysis.

Figure 11. Decomposition bags used in the tree species experiment outside Garpenberg. Photo by Marcus Larsson (2022).

To measure tree species specific interactions between decomposition rate and the belowground microbial community (**Paper IV**) 672 decomposition bags in conjunction with a reciprocal litter transplant approach were used (i.e. 2 litter types × 2 sites × 3 blocks × 4 tree species origins × 4 tree species destinations × 4 decomposition bags per plot). One block at Garpenberg was however missing *Betula pendula* and *Larix* (the plots were never established), resulting in an incomplete block design. This resulted in 96 fewer bags from this block, i.e., in a total of 672 bags. At the beginning of autumn all bags were filled with 3 grams of dry mass and were placed in the field just beneath the organic horizon, at the intersection with the mineral soil. Bags were placed in the same plot from which the litter was collected, as well as three adjacent plots of the other tree species within the block. One year later all bags were collected and brought back to the lab, dried in 70° C for at least 48 h, and weighed to allow calculation of mass loss. Values from individual bags were pooled at the plot level before statistical analysis.

2.2.5 Soil microbial community

Five soil samples (**Paper IV**) were collected (in summer) from beneath the different tree species within each plot, one in the centre of each plot and 4 positions halfway from the plot border. In each sample position within the plot, the intersection between the organic layer and the mineral soil (bottom 5 cm of the organic layer and top 5 cm of the mineral soil) was sampled. The samples were immediately placed on dry ice and transported to the lab. In the lab, the samples were immediately sieved (Ø 2 mm) using sterilized equipment inside a sterile fume hood and then pooled at the plot level. The samples were stored at -80°C until further analysis. The DNA from soil samples was isolated using DNeasy PowerLyzer PowerSoil Kit (Qiagen) according to the manufacturer's instructions. The quality and quantity of the isolated DNA from all samples were checked using Nanodrop (Thermo Fisher Scientific) and Qubit dsDNA Quantification Assay Kit (Invitrogen) before being sent for sequencing at Maryland Genomics. The samples were analysed using general ITS primers, ITS9MUNngs (5′-TACACACCGCCCGTCG-3′) and ITS4ngsUni (5′-CCTSCSCTTANTDATATGC-3′) (Tedersoo and Lindahl, 2016). Maryland Genomics prepared the ITS full-length amplicon libraries from the sent DNA samples and sequenced the prepared libraries on PacBio Revio SMRT Cell Sequencing run (HiFi/CCS mode, 24-hour movie).

DNA data analysis

The initial steps of data analysis including preprocessing, ASVs generation and taxonomic assignment, were done by Maryland Genomics. First, DADA2 was used on the ITS sequences for trimming, filtering, denoising, removing of chimeras and generating ASVs. Fungal ITS ASVs were then assigned using the UNITE database (Abarenkov et al., 2024). The samples were further processed by using R Statistical Software version (R Core Team, 2024) and the packages phyloseq and Vegan (McMurdie and Holmes, 2013; Oksanen et al., 2025), unless otherwise specified. At the beginning of the analysis, the ITS dataset contained in total 22 samples totalling 3,315,172 reads and 12,558 ASVs. Reads not belonging to the fungal kingdom were removed along with unknown taxa on the phylum level. The entire dataset was then aggregated on the taxonomic level of order. The resulting ITS dataset used for the analysis included 22 soil samples totalling up to 1,575,291 reads and 132 taxa (ASVs).

2.2.6 Statistics

For all statistical analyses utilized in the harvesting and fertilization studies (**Papers I** and **II**), both experiments were treated as completely randomized designs, with each plot (**Paper I**) or forest stand (**Paper II**) serving as the unit of replication. In contrast, the tree species experiments (**Papers III** and **IV**) employed a randomized block design, where each plot served as the unit of replication. All statistical analyses were performed using R software (R Core Team, 2024). The major statistical method of use throughout the statistical analyses have been a linear mixed effects ANOVA, where the random effect has been used account for any eventual variation caused by; pre-commercial thinning (**Paper II**), or environmental factor caused by any site to-site differences (**Papers I, III** and **IV**). Two multivariate (NMDS and PCoA) methods were also used to examine differences in ground vegetation biodiversity (**Paper II**) and soil microbial community composition (**Paper IV**). Response variables were checked for normality and homoscedasticity with the aid of residual plots and if needed the appropriate data transformations where applied. If suitable, Tukey´s post hoc test for pairwise comparison was then used to further the analysis.

For all statistical tests a significance terminology suggested in Muff et al., (2022) has been utilized, where different ranges of p-values are reported on a continuum from “little or no evidence” to “very strong evidence”. A p-value of 0.0001 – 0.001 subsequently equals very strong evidence, a value of 0.001 – 0.01 equals strong evidence, 0.01 – 0.05 equals moderate evidence, 0.05 – 0.1 equals week evidence and a p-value of 0.1 – 1 is considered as no evidence

3. Results and discussion

The overall objective of this thesis was to explore how a forest management system shift and two practices commonly applied in the boreal forests of Sweden affect soil carbon stocks, and to provide insights into how these practices could be used to enhance the climate change mitigation potential of boreal forests. The main results of the individual studies are summarized below and linked to their respective objectives as expressed in the beginning of the thesis.

3.1 Conversion of unmanaged boreal forest

The C present in the mineral soil is often regarded as most stable part of the different soil horizons, potentially over millennial timescales, but it has been unclear to what degree even-aged management in older unmanaged forests destabilizes this C pool. The data provided by this experiment indicate that the mineral soil remains unaffected, also when unmanaged forests are converted into even-aged management. The different number of samples between the ground vegetation (and litter) and the 20-50 cm mineral soil depth compared to the rest of the dataset makes statistical comparisons on total mean ecosystem C difficult. However, comparisons referring only to the means show that total mean ecosystem C was 106.8 Mg C ha^{-1} in unmanaged forest stands, and 69.5 Mg C ha^{-1} in the managed stands. The biggest difference was, not surprisingly, found in the biomass of the living trees, equivalent to 45.4 and 13.4 Mg C ha^{-1} respectively. Comparing only mean SOC (organic layer and mineral soil) the difference was 47.6 Mg C ha^{-1} in unmanaged forests and 43.4 Mg C ha^{-1} in managed forests (Table 2).

Table 2. Mean ± SE C pools sampled in unmanaged and managed forest types. Results are based on averaging all values for each respective layer in both forest types.

	Mg C ha^{-1}		
Compartment	Unmanaged forest	Managed forest	p-value
Living trees	45.4 ± 3.4	13.4 ± 3.3	<0.001 ***
Ground vegetation & litter	12.4 ± 0.7	12.4 ± 2.2	0.994
Dead wood	1.4 ± 0.3	0.3 ± 0.1	<0.001 ***
Organic horizon	21.9 ± 2.1	18.7 ± 1.5	0.054 *
Mineral soil 0-10 cm	6.5 ± 0.7	6.2 ± 0.7	0.461
Mineral soil 10-20 cm	6.4 ± 0.6	5.9 ± 0.5	0.212
Mineral soil 20-50 cm	12.8 ± 2.8	12.6 ± 3.0	0.848
Total aboveground C	59.2	26.1	Unbalanced data
Total belowground C	47.6	43.4	Unbalanced data
Total ecosystem C	106.8	69.5	Unbalanced data

Note: All compartment values are based on samples from 23 paired stands except ground vegetation & litter and mineral soil 20-50 cm, which are based on samples from 9 paired stands.

Statistical analysis of the SOC in different ecosystem compartments showed weak evidence ($p = 0.054$) of a significant decrease of C within the organic layer of 3.2 Mg C ha^{-1}, when comparing unmanaged and managed stands. However, no evidence was found for differences in other measured belowground ecosystem C compartments (Fig. 12).

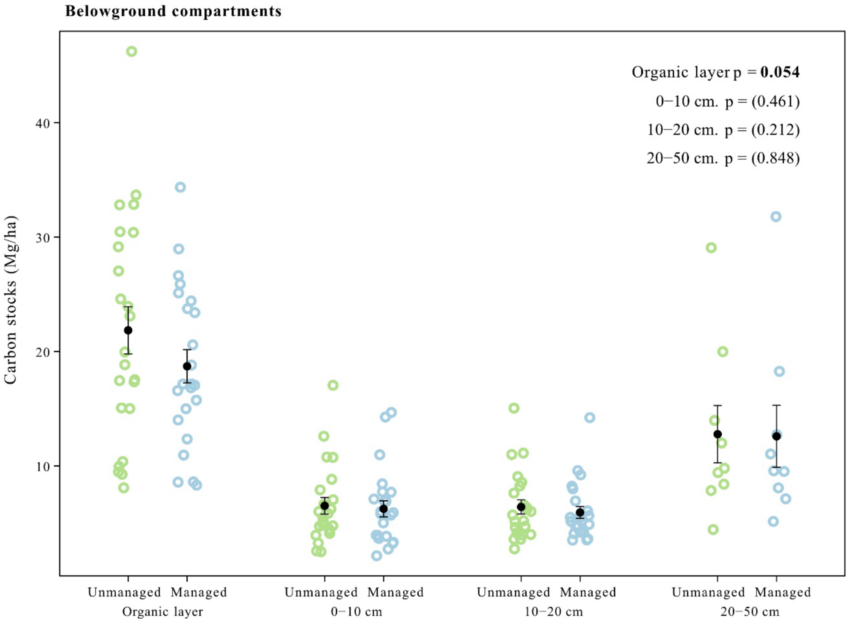


Figure 12. Visualization of SOC ecosystem compartments based on pooled measurements from all sites included in the study. Mean ± SE is indicated by black points and arrows, while the coloured circles showing the full range the measurements. P-values in bold indicating weak evidence or higher, based on comparisons between the two forest types for each measured compartment.

Adding together C in all mineral soil layers (0-10, 10-20 and 20-50 cm) resulted in a non-significant loss of 1.0 Mg C ha^{-1} in managed versus unmanaged forest stands. Hence, only ca. 3% of the total C stock difference between managed and unmanaged forest stands was explained by the mineral soil compartment. This result corresponds well to other studies where mineral soil C is often less affected by harvest than the organic horizon or “humus-layer” (Achat et al., 2015; Nave et al., 2010). Frequent explanations given for this greater stability of C in mineral soil are stabilizing interactions between organic matter and mineral particles within soil aggregates (Mikutta et al., 2006; Torn et al., 1997), or incorporation of C in root-derived compounds and fungal necromass (Adamczyk, 2021; Adamczyk et al., 2019). Both SOC stocks and their rate of change are however known to decrease with latitude (Olsson et al., 2009). Small changes over time might therefore be difficult to observe in high latitudes compared to the southern boreal region (Ågren et al., 2007), thus care should be taken when scaling the results of this study to other parts of the boreal region.

This experiment provides a snapshot picture of the ecosystem C stocks at the time of the measurements; and further, it utilized a paired comparison and sampling approach that is not well represented in the literature. Based on available knowledge, the experiment is the only one within Sweden where unmanaged stands could be compared directly to stands managed with even-aged management, which helped to control for landscape heterogeneity, an often problematic issue when making forest C stock comparisons (Ortiz et al., 2013; Vanguelova et al., 2016). However, other types of data are also relevant for understanding the long-term climate impacts of forest management. One such datapoint within this experiment is the significant reduction (80 %) of deadwood C stock between unmanaged and managed stands. The C stock reduction in deadwood corresponded to 1.1 Mg C ha^{-1} and from a pure CO2 standpoint this pool is therefore of minor importance. Although from a biodiversity perspective, deadwood represents a major habitat loss and serves as the host to a substantial number of saproxylic beetle and fungal species, including many red-listed species (Birkemoe et al., 2018; Gao et al., 2015). Assessing the climate benefits of forest management in previously unmanaged forest stands thus must take values such as this into account.

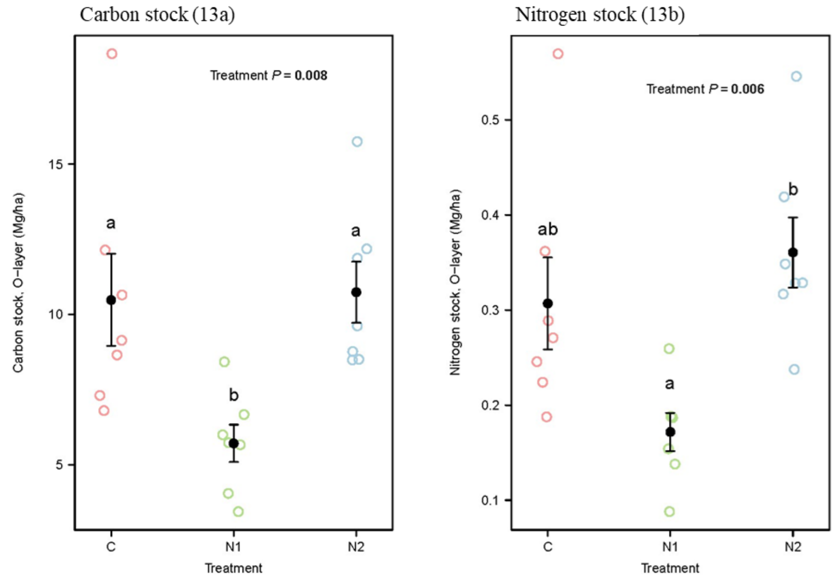
3.2 Fertilization (N addition)

In combination with older measurements (From et al., 2015; Strengbom and Nordin, 2008) the results from this experiment suggests that, while standard practices of N addition (150 kg ha^{-1}) can generate long-term legacy effects, visible across harvesting rotations, these effects will dimmish with time. Effects on tree growth, biodiversity and soil N mineralization and soluble N that were all present in young stands, approximately 10 years after initiation, had all but disappeared at the time of the repeated measurements, 23 years into the current forest rotation. A weak effect ($p = 0.095$) on tree growth (20 % difference between control and N2 treatments) could however still be found (table 3).

Table 3. The means (±1 SE, N=7) for total soil N mineralization rates (NH_4-N and NO_3-N mg g^{-1} DW soil), total capture of N on ion-capsules (NH_4-N and NO_3-N), tree diameter (cm) at breast height (DBH), and tree height (m), for each treatment. Results for p-values are based on a mixed-effects model ANOVA with treatment used as fixed factor and pre-commercial thinning as a random effect factor.

Treatment	**Total mineralization**	**Total soil mobile N**	**DBH**	**Tree height**
	(N mg g^{-1} DW soil)	*(N mg capsule $^{-1}$)*	*(cm)*	*(m)*
C	0.188 ± 0.037	0.109 ± 0.009	5.11 ± 0.592	4.41 ± 0.362
N1	0.170 ± 0.030	0.111 ± 0.008	5.71 ± 0.320	5.30 ± 0.259
N2	0.220 ± 0.060	0.133 ± 0.015	5.18 ± 0.511	5.57 ± 0.370
p-value	0.747	0.356	0.386	0.095

The analysis of legacy effects on soil C stock, which had no analogous older measurements, instead indicated that no clear pattern could be found (Fig. 13). Strong evidence was found showing that soil C stocks differed in the organic layer (p = 0.008), with lower C stock in the N1 treatment compared to the control and N2-treatment (Fig 13a). However, no evidence of this effect was found comparing the control and N2-treatment. Strong evidence (p = 0.006) was also found indicating differences in soil N stocks within the organic layer (Fig 13b), displaying lower N stock in the N1 treatment compared to the control and higher N stock in the N2 treatment compared to both the N1 treatment and the control stands. Comparison of the soils' C/N-ratios, which was measured at three different depths (organic, 0-10 cm, and 10-20 cm depth; Fig 13c), indicated no evidence of any effect between treatments. The differences in C stock hence did not correspond to the increase in number of N additions and are therefore likely related to other factors. A higher foliar N content (p = 0.098) in dwarf shrubs was also found (**Paper II**, fig. 2).



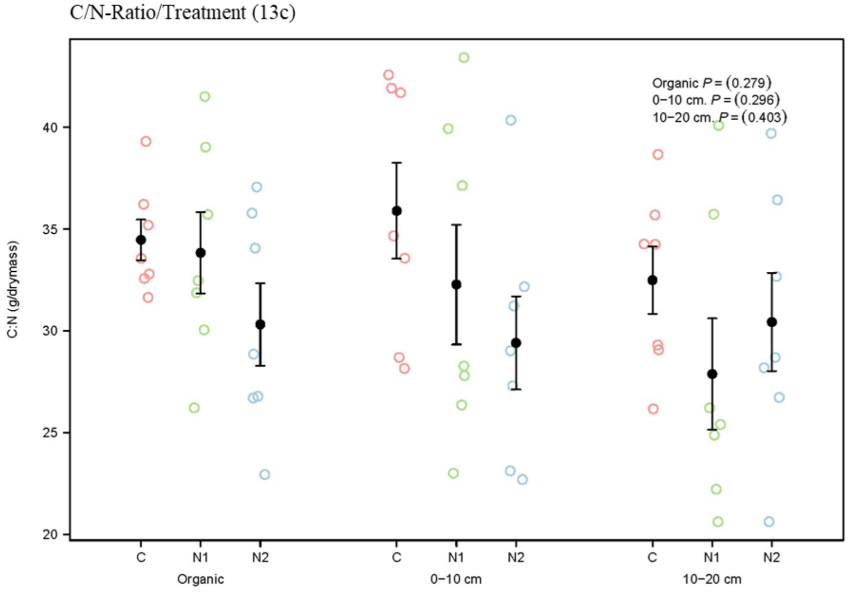


Figure 13. The left figure (graph 13a.) shows the C stock within the organic layer. The right figure (graph 13b.) shows the N stock within the organic layer. The bottom figure (graph 13c.) shows C/N-ratios in three different soil layers for each treatment (organic, 0-10 cm mineral soil depth and 10-20 cm mineral soil depth. Bars represent the different means (±1 SE, N=7).

Initially the relatively large effect size of 20 % difference in tree growth seems like a given candidate for a proven legacy effect. The average effect size was however the same during the last measurements in 2010, while the variation among stands was much smaller, and the effect thus ended up as statistically significant ($p = 0.026$; From et al., 2015). If residual effects from the initial fertilization would still be present, the difference between treatments would likely have continued to diverge instead of remaining the same. Regarding the foliar N and soil (organic layer) N stock differences, experiments from more southern latitudes that do report legacy effects between forest rotations suggests that the forest floor and ground vegetation could act as a nutrient sink for added fertilizer. Later releasing nutrients in subsequent forest rotation and thus increasing forest growth (Subedi et al., 2014). Destruction of the soil organic material instead appears to leave a legacy effect of declining productivity (O'Hehir and Nambiar, 2010). The same type of nutrient sink have been shown to occur in boreal areas (Gundale et al., 2014), and seems to persist between forest rotations, as illustrated by the slightly higher N stock found in the O-horizon in N2 stands present in this experiment.

Based on available knowledge, no other study in the northern boreal zone has evaluated responses this far in time from the fertilization event and this study therefore contributes important information regarding the timespans over which N fertilization affects boreal forests. While most of the measured variables have analogous in other studies (Bobbink et al., 2010; Forsmark et al., 2021, 2020; Högberg et al., 2014, 2006; Pettersson and Högbom, 2004; Sullivan and Sullivan, 2018), the majority of these results are based on much higher fertilization practices than the ones used in operational forest management. Until now, data on long term and/or legacy effects from standard forestry fertilization practices in boreal forest have been missing (Jämtgård et al., 2023). This experiment puts an upper limit on how long these effects may persist before diminishing, and thus addresses a key component of an identified knowledge gap between basic research focused on understanding N dynamics in boreal forests, and the applied knowledge needed to sustainably manage these ecosystems (Sponseller et al., 2016).

3.3 Tree species selection

The data from this study show that a potential to use tree species choice as a tool to increase the soil C stock exists. However, the results also indicate that tree species selection to promote soil C accumulation can be complicated and must be matched to site specific conditions. The largest average SOC stock across the two sites was found for *Pinus contorta*, and while *Pinus contorta* also ranked among the top species in measured above ground tree biomass, the highest above ground C stock was found in *Larix sp*., which also consequently ranked the highest in total ecosystem C stock (Fig. 14). The interaction between species and site showed very strong evidence ($p < 0.001$) for affecting tree biomass C. Furthermore, ecosystem C stock also displayed an interaction effect between species and site, the evidence was however weak ($p = 0.064$), indicating that the strong influence of the tree species on the ecosystem C stock is only weakly related to the site. In contrast, total soil C stock showed very strong evidence ($p < 0.001$) of being affected only by site (Table 4). The rank order between species in relation to their above ground tree biomass C stock also differed between sites, mainly in that *Betula pendula* and *Pinus sylvestris* had a similar aboveground biomass when present on the northern site; while, in the central site *Betula pendula* biomass and annual growth was smaller than those of *Pinus sylvestris*, and more equalled *Picea abies* (**Paper III**, Fig. 3).

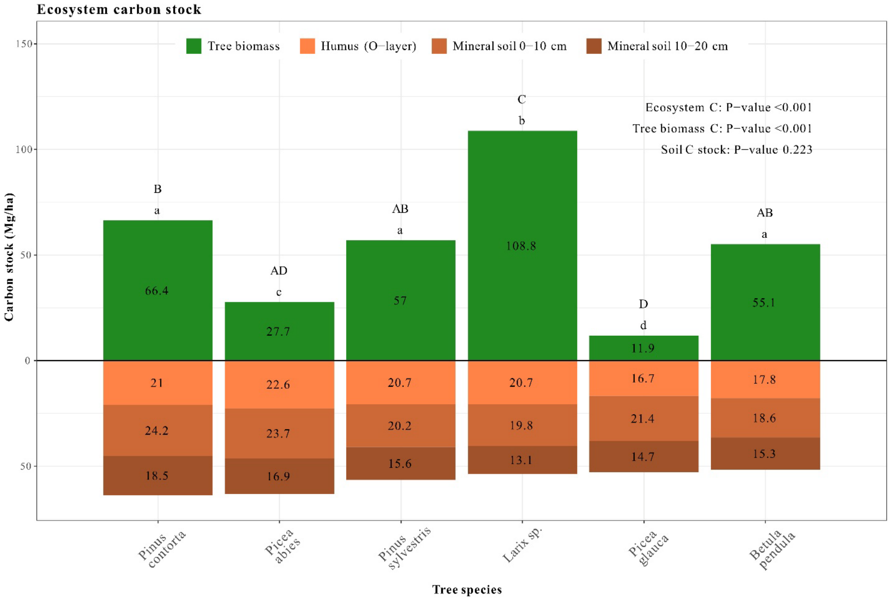


Figure 14. The average amount of C stock in different ecosystem compartments for different tree species at both sites (n = 6 species^{-1}, except *Betula pendula* where n = 5). The species are organized in descending order, starting with the highest belowground C stock. Letters above or below bars indicate significant differences between species. Top capital letters = post hoc test of ecosystem C and bottom letters = post hoc test of tree biomass C.

On both experimental sites, tree species with "acquisitive" traits (*Betula pendula*, *Larix sp.*, *Pinus contorta* and *Pinus sylvestris*) that usually dominate early in forest succession were shown to exhibit higher levels of tree biomass C than "conservative" trait species (Picea abies and *Picea glauca*) that usually dominate later in forest succession (Gundale et al., 2024). This is expected as the experiments are still quite young in relation to the length of a normal forest rotation of 60-100 years in boreal managed forests, and the much longer successional dynamics in unmanaged forest (Nilsson et al., 2022).

Table 4. Results of testing SOC in different ecosystem compartments against tree species and site interaction. Each result is presented with their respective Chisq (X^2) and p-values.

Species & Site interaction			
Ecosystem compartment	Model variables	X^2-value	p-value
Ecosystem C stock	Species	26.182	< **0.001**
	Site	0.990	0.423
	Species:Site	1.668	**0.064**
Tree biomass	Species	172.440	< **0.001**
	Site	87.161	< **0.001**
	Species:Site	6.786	<**0.001**
Total soil C stock	Species	1.382	0.227
	Site	19.024	< **0.001**
	Species:Site	1.450	0.202

The aim to determine if some key variables related to soil C input and output could be used to explain eventual differences in C stock between the tree species in the experiment was not reflected to a large degree by the results. The measured tree species variables (tree biomass, woody coarse debris, litterfall, root growth, litter mass loss and humus mass loss), did not in general translate into differences in soil C. The analysis showed very strong evidence ($p < 0.001$) for a tree species effect on tree biomass, amount of coarse woody debris, amount of litterfall, rate of litter mass loss and rate of root growth. No significant tree species effect was however found in relation to humus mass loss and soil pH. The only tree species variable shown to effect soil C was amount of litterfall, which showed moderate evidence for an effect on C in the deepest layer of the mineral soil. Soil pH was the only other variable shown to affect soil C in different soil layers, as strong evidence was found for an effect on the overall soil C stock ($p < 0.001$), moderate evidence of an effect in the 0-10 cm mineral soil layer ($p = 0.028$) and strong evidence ($p = 0.003$) of an effect on the deepest 10-20 cm mineral soil layer. The variable was however not tree species dependent (**Paper III**, table 2). Some previous studies have also shown that while different tree species can affect SOC accumulation within different soil layers, the total belowground C stock is not always affected (Mayer et al., 2020); and there is some evidence of differences in SOC distribution between conifer and broadleaves species (Mayer et al., 2020). However, when analysing total ecosystem C, the data from this experiment suggests that there is a potential for forest managers to optimally match species with site characteristics to maximize ecosystem C stocks (Augusto et al., 2025).

3.4 Reciprocal litter transplant experiment

This study assessed the relative effects of two mechanisms that have been proposed to influence decomposition rate at the local stand scale (litter quality versus soil environment). The results showed very strong evidence ($p < 0.001$) of differences in decomposition rate due to litter origin (i.e. differences in litter between tree species), while soil destination effects on mass loss exhibited only weak evidence ($p = 0.057$). No evidence for an interaction between litter origin and destination could be found (Table 5). Post hoc analysis of litter origin showed that the *Pinus sylvestris* and *Larix* litter decomposed faster than *Betula pendula* and *Picea abies* (Table 5).

Table 5. Results of statistical analysis of decomposition rate with crossed factors of litter origin and soil destination. Post hoc test of litter origin and soil destination is organized in descending order of mass loss from highest to lowest. Displayed mass loss values of post hoc test are based on estimated marginal means.

Litter mass loss (%)

Model variables	X^2-value	p-value
Litter origin	47.71	< 0.001
Soil destination	7.52	0.057
Interaction	7.63	0.572

Humus mass loss (%)

Model variables	X^2-value	p-value
Litter origin	5.1742	0.159
Soil destination	2.4651	0.481
Interaction	6.6963	0.668

Post hoc litter origin

Litter origin	Mass loss (%)	group
Pinus sylvestris	29.0	b
Larix sp.	27.4	b
Betula pendula	21.7	a
Picea abies	19.5	a

Post hoc Soil destination

Soil destination	Mass loss (%)	group
Betula pendula	26.0	a
Larix	25.0	ab
Picea abies	24.7	ab
Pinus sylvestris	21.9	b

Note: Post hoc test of soil destination is made on the 0.1 significant level instead of the commonly used 0.05 to reflect the weak evidence of ($p = 0.057$).

The analysis of the measured chemical litter traits (C/N-ratio and lignin values) indicated very strong evidence ($p < 0.001$) of litter origin differences for all variables (Table 6). Post hoc tests showed that *Betula pendula* had the lowest C/N-ratio whereas *Pinus sylvestris* litter displayed the highest, all litter origins were also shown to differ significantly in relation to C/N-ratio. The lowest signal % of lignin was detected in *Betula pendula*, which also was shown to differ compared to all other litter origins. The highest value was instead attributed to *Picea abies* which grouped together with *Pinus sylvestris* (Table 6).

The results show that the measured differences in decomposition rate did not line up with the observed differences in litter quality, a contrasting result compared to other studies (Berg and McClaugherty, 2003; Zhang et al., 2008). For instance, litter from *Betula pendula* were shown to have both the lowest C/N - ratio and the lowest signal % of lignin and should as such be regarded as the highest quality litter in this dataset. This was however the litter origin that together with *Picea abies* exhibited the lowest decomposition rate of all species, 21.7 % mass loss, compared to the highest rate of 29 % displayed by *Pinus sylvestris*. The discrepancies could potentially be explained due to different tannin content in different types of litter. Tannins found in higher plants are divided into two classes, condensed and hydrolysable tannins (Kraus et al., 2003), and while gymnosperms, (represented by *Larix sp*., *Picea abies* and *Pinus sylvestris* in the study) only produces condensed tannins, *Betula pendula* are able to produce both types (Kraus et al., 2003). This difference has been suggested as an explanation for higher values of total tannin concentrations found in the humus layer under *Betula pendula* compared to other tree species (Adamczyk et al., 2009), and could lead to a reduction in soil organic matter turnover (Kraus et al., 2003).

Table 6. Statistical results from litter origin differences in chemical litter traits (a) followed by post hoc tests and average trait values for each litter origin respectively (b) and (c). C and N values are based on weight % (g g^{-1} DW) and lignin values are expressed as percentages of the total peak area from the mass spectrometry analysis (signal%). Displayed values of post hoc test are based on estimated marginal means.

a) Litter origin differences

Trait	F-value	p-value
C/N-ratio	11.553	< 0.001
L (Signal %)	9.457	< 0.001

b) Post hoc test (C/N-ratio)

Litter origin	C/N	group
Betula pendula	51.746	a
Larix	69.989	ab
Picea abies	77.377	bc
Pinus sylvestris	98.375	c

c) Post hoc test (Lignin)

Litter origin	(Signal %)	group
Betula pendula	11.666	a
Larix	14.862	ab
Pinus sylvestris	17.097	b
Picea abies	17.402	b

Note: C and N content is not directly comparable with the values for lignin as they are not analysed using the same methods. Lignin is therefore only comparable across species, not other chemical traits.

The fungal microbial analysis of the soil environment showed no differences in alpha (Shannon and Chao1 indices) or beta diversity (PERMANOVA analysis) for any soil destination (**Paper IV**, supplemental table 2). This result was further illustrated by the overlap in the principal coordinate analysis (fig. 15). In contrast to these results, other experiments have found distinct microbial communities beneath conifers and broadleaf species (Hannam et al., 2006; Prescott and Grayston, 2013; Saetre and Bååth, 2000). Why these dissimilarities are absent in this study system is unclear, but changes in soil microbial communities are shown to be strongly dependent on N availability and soil moisture (Brockett et al., 2012; Forsmark et al., 2024; Koelemeijer et al., 2025; Maaroufi et al., 2019). No plot level data on these factors were measured in this study, but they could hypothetically be responsible for the clustering present in the ordination (fig. 15), which does not align with any of other measurements present in the experiment.

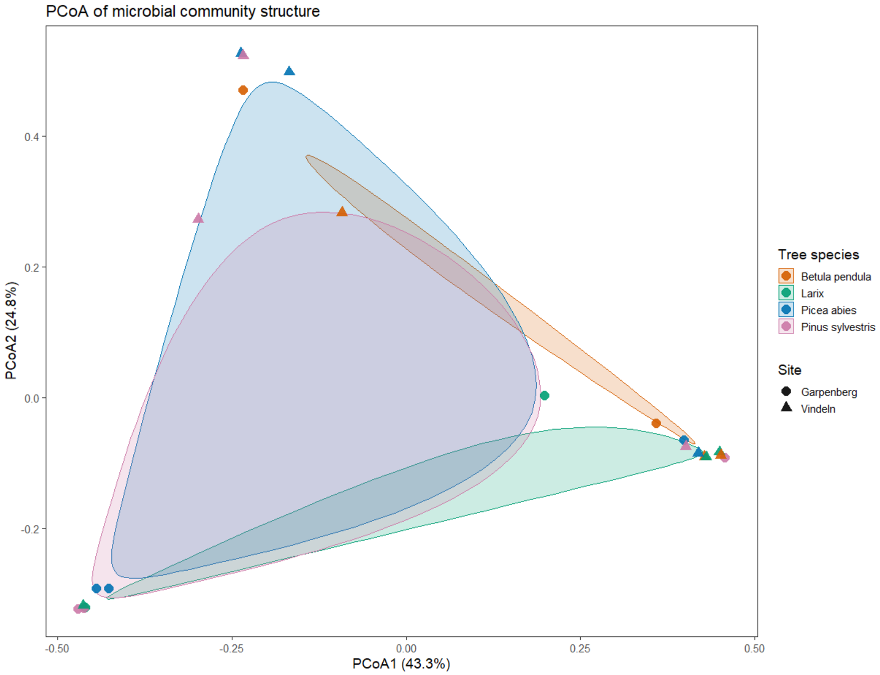


Figure 15. Principal coordinate analysis of soil microbial community structure in relation to litter origin and site (tree species) based on pooled samples from each plot (n = 22) across both sites present in the experiment.

Worth noting however is that the later stages of mass loss, represented in this study by humus substrates from associated litter origin plots, was unresponsive to any species related factors (Table 5). This result gives credence to the idea about a “maximum decomposition limit” (Berg and Ekbohm, 1993), which corresponds to the point when the litter “becomes humus” and enters its second phase of decomposition (Berg et al., 1996; Prescott et al., 2000). Long term decomposition experiments indicate that the decay rate of different types of litter (and litter from different species) may converge at this point (Prescott et al., 2004), meaning initial trait differences between species might not matter as much as quantity of litter input, or local environmental conditions for the accumulation of soil C.

4. Conclusions

In all studies, the vast majority of C changes from the tested management practices occurred in the above ground C stock (biomass of the living trees). This outcome was expected, as the primary purpose of forest management is to maximize the quality and quantity of harvestable tree biomass. Fast growing species such as *Larix spp*. and *Pinus contorta* are well-suited to further this goal, outperforming every native species in the tree species study during the timespan of the experiments (**Paper III**). Fertilization is also a common tool for increasing aboveground C stocks, and now a suggested upper time limit regarding the long-term effects of standard fertilization practices may have been established (**Paper II**). The results indicate that it can persist into the juvenile phase of the subsequent forest rotation, enabling an approximately 20% increase in tree growth before diminishing.

The organic layer is the part of the soil profile that often exhibits the strongest responses in relation to forest management (Achat et al., 2015; Gundale et al., 2024) and this largely held true for the experiments conducted in this thesis as well. Fertilization have been shown to affect both N and C dynamics in this layer, but most data is in relation to much higher fertilizer doses than what is used in operational forestry (150 kg ha^{-1}). The data from my fertilization experiment (**Paper II**) showed evidence of increased N stocks in this soil layer, indicating that it can function as a nutrient store between forest rotations. A comparable legacy effect may at one point have existed for the soil C stock as well, but no such effect was detectable at the time of the repeated measurements. Tree species choice also seems to induce small distribution changes in soil C stocks (**Paper III**). However, while many soil C inputs and outputs in both common garden experiments were tree species dependent, these differences did not translate into differences in total belowground soil C stocks. The inherent properties of different types of tree species litter (**Paper IV**) also influenced their respective initial decomposition rates to a much greater degree than the local soil environment, but chemical traits like C/N-ratio and lignin content (signal %) were not enough on their own to fully explain this process. Together these studies demonstrate that if tree species are going to be used as a tool to mitigate climate change, the measured litter decomposition differences provided by the translocation experiment are something that appear to be only initially effective since they seem to converge over time (**Paper IV**). Instead, given that the different and highly species-specific growth rates (**Paper III**) control the amount of C that accumulates in aboveground biomass as well as the quantity of litter inputs to soil, which often affects the organic layer, they may have a more important role in controlling soil C than differences in litter quality among species.

The mineral soil could be considered less responsive, resisting almost all changes brought about by all the forest management procedures used in this thesis. Older unmanaged forests have been shown to store greater amounts of C than young managed forests, both in standing biomass and soil (Luyssaert et al., 2008; Paw U et al., 2004; Zhou et al., 2006), and can also be associated with higher levels of what is considered stable mineral C (Gundale et al., 2024; Kumpu et al., 2025). Harvesting and subsequent conversion of these forests into a rotation-based forest management system (**Paper I**) is therefore the experiment which had the biggest theoretical possibility of impacting the mineral soil. However, only a non-significant 3 % of the total C stock difference between managed and unmanaged forest stands was explained by the mineral soil compartment, whereas a weak but significant decrease of about 9 % was discovered in the organic layer. This resistance to C stock changes within the mineral soil, which in turn creates slow turnover rates, indicates that long timescales are required to observe significant changes. Simulations do show that shifts in mineral soil can lag behind aboveground changes by decades or even centuries (Dean et al., 2017). Therefore, while forest management can influence certain compartments ecosystem C stock, the mineral soil C appears to be a much less responsive pool in the short to medium term.

4.1 Management implications and future research

Based on the results of this thesis my research suggests that a more comprehensive view of management effects could be used, in which aboveground and belowground C stocks are evaluated simultaneously at the ecosystem C level. Reframing the problem in this way would make it possible to incorporate important information about the relationships between these two ecosystem compartments into existing forest management practices, thus widening the range of solutions applicable to the challenge of optimizing the carbon sequestration capacity of boreal forests. For instance, the conversion of unmanaged forest into an even-aged rotational system induced a reduction in tree biomass, which may appear proportionally minor as it decreases over time as the regenerated stands mature. However, the C stock within the organic layer also exhibited a reduction, and while it is not possible to estimate the recovery time of the organic layer with the data provided by the experiment, other meta-analyses suggest the time needed is >100 years (Gundale et al., 2024; Palviainen et al., 2020). Reframing management into an ecosystem C perspective thus means that climate benefits gained from utilizing the aboveground renewable resource also need to make up for the reduction in C stock from the organic layer, which could lead to a slight rebalancing of subsequent climate benefit scenarios.

Fertilization was instead shown to induce long-term legacy effects on tree growth that do not diminish until the next forest rotation reaches its juvenile phase. This suggests that, in addition to an ecosystem perspective, a more comprehensive view of forest management could benefit from incorporating longer temporal dimensions as well. Doing so would remove the need to assess the effects of fertilization within the confines of a single forest rotation. Thereby increasing the utility of the practice, which already has been proposed as one of the only management practices that can be reliably scaled to mitigate climate change within a shorter timeframe (Bergh and Hedwall, 2013).

A more comprehensive management perspective also revealed slight differences in climate change mitigation potential among tree species, when evaluated at the ecosystem C level rather than solely on the basis of tree biomass. As a management option tree species could therefore be chosen based on their site-specific growth potential, aiming to optimize the total ecosystem C stock. On a strategic timescale this has the potential to increase the C sequestration capacity of boreal forests, but considerable time must be spent to establish enough new stands, before the cumulative effects would impact the regional scale.

Further research is needed to examine if the management practices researched in this thesis could have synergistic effect over longer timeframes. For example, increased knowledge about how different tree species and their site-specific growth potential interacts with the mechanisms responsible for retention of fertilizer N across stand rotations, and how these vary across forest types (Blaško et al., 2022), could be used to avoid applying fertilizers in areas at risk of prolonged legacy effects (**Paper II**). Thereby unwanted long-term effects on the boreal forest ecosystem could be mitigated, while at the same time maintaining and/or improving the benefits of both forest fertilization and tree species choice to increase biomass growth. Forest fertilization can also be used to increase soil C stocks and an average (based on varied data) scaling factor of 10 kg C in soil per 1 Kg of added N ha^{-1} has been suggested (Jämtgård et al., 2023). If this scaling factor would apply when converting unmanaged forests into rotation-based forest management (**Paper I**), the subsequent losses of C from the organic layer could be mitigated, shortening the otherwise relatively long (Gundale et al., 2024; Palviainen et al., 2020) recovery time.

The above also illustrates the importance of additional long-term experiments as the cold climate and nutrient poor environment make boreal forests grow slower relative to other biomes. The tree species experiments utilized in this thesis are only about 30 years old (**Papers III** and **IV**), which may be too little time to fully realize changes in total soil C stock. It is possible that such effects may develop over longer time scales in conjunction with differences in soil microbial community, which have been shown to develop between tree species over longer timescales in lower latitude forest habitat environments. Forestry decisions must also take into consideration that many other values, such as the potential for biodiversity connected to the larger volume and higher structural diversity of dead wood, are not usually present in younger managed stands (**Paper I**). These structures need time to develop, and long-term experiments would help ascertain how they interact with the range of management practices examined in this thesis. Such data would help inform discussions that seek to balance the broad array of societal values and ecosystem services that boreal forest provide.

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Popular science summary

This thesis explores the link between forest management and carbon (C) sequestration, particularly belowground. It investigates C effects of a forest management system shift, going from unmanaged to rotational forestry and two different forest management practices and their related effects on soil C stocks. The studies are based on experimental data from extensive field trials in Sweden, aiming to account for common sources of error and long-term effects. The impact on the soil C stock in older unmanaged forests in relation to even-aged management, especially on mineral soil, was examined in Paper I. The long-term legacy effects from standard forest fertilization practices on soil C stock, tree growth, nutrients and biodiversity was examined in Paper II. The potential to use different tree species to increase the soil C stock was examined in Papers III and IV. Together these two studies examine both the above and belowground C inputs, and C outputs from decomposition. The tree species effect on total ecosystem C stock was also evaluated.

All studies show that the majority of C stock changes from the tested forest management practices occurred in the biomass of the living trees, followed by lesser responses in the soil organic layer. In contrast, the mineral soil showed very limited responses to the forest management practices examined in this thesis. Overall, the results suggest a more comprehensive view of forest management could be used, in which aboveground and belowground C stocks are evaluated at the same time. This would shift the traditional focus of forest management from aboveground biomass towards total ecosystem C management. Which would make it possible to include important information about the relationships between these two ecosystem compartments into existing forest management practices. Offering a wider range solutions to the challenge of optimizing the carbon sequestration capacity of boreal forests.

Populärvetenskaplig sammanfattning

Denna avhandling utforskar sambanden mellan skogsskötsel och kolinbindning, med särskilt fokus på marken. Den undersöker ett skogsskötselssystemskifte när trakthyggesbruk används i obrukad skog samt två skogsskötselmetoder och deras effekter på markens kolförråd Studierna bygger på experimentella data från stora fältförsök inom Sverige, där målet har varit att ta hänsyn till, några i litteraturen, relativt vanliga felkällor och långtgående effekter. Effekterna på markens kolförråd, speciellt i relation till mineraljorden, när trakthyggesbruk sker i äldre obrukade skogar undersöktes i artikel I. De långsiktiga effekterna från vanlig skogsgödsling på förråden av markkol, trädtillväxt, näring och biologisk mångfald undersöktes i artikel II. Potentialen att använda trädslagsval som ett verktyg för att öka markens kolförråd undersöktes i artikel III och IV. Tillsammans hanterar dessa två studier inflöden av kol från både över och under jord, samt deras samspel med nedbrytning och markens mikrobiella sammansättning. Trädslagens effekt på ekosystemets totala kolförråd undersöktes också.

Oavsett studie skedde den övervägande delen av förändringarna i kolförrådet i trädens biomassa, följt av medelstora förändringar i markens organiska skikt. Mineraljorden uppvisade i stället mycket begränsade förändringar och stod emot den absoluta majoriteten av effekterna från de skogsskötselmetoder som undersöktes i denna avhandling. Resultaten visar dock att det är möjligt att med framgång använda en skogskötselmässig helhetssyn, där kolförrådet ovan - och under mark utvärderas samtidigt. Det skulle flytta det traditionella fokuset från trädens biomassa till en total ekosystemsförvaltning av kol. En sådan inramning skulle göra det möjligt att ta hänsyn till viktiga samband mellan dessa ekosystemkomponenter, och bygga in dessa i befintliga skogsskötselmetoder, vilket kan öppna upp för nya lösningar med syfte att ytterligare optimera kolinlagringen i boreala skogar.

Acknowledgements

This work was a collaborative effort, and I am truly grateful to everyone who made this possible.

Thank you to my supervisors Michael Gundale and Annika Nordin, who guided me through the process and helped me understand how to make all the different parts of science fit together. Building something together with you has meant a lot to me and I am deeply thankful for your support and for believing in me.

Thank you to my fiancé, Linnéa. Without you and your deep knowledge of how to break enormous tasks and abstract concepts down into smaller, practical steps of gradual improvement, this work would never have been possible. I am also so happy about our two kids, whose antics can transform even the worst day into a beautiful memory, and for the occasional chaos that can arise in a manuscript when the computer is left unattended.

Thank you to my parents, Eva and Mårten Larsson who has been supportive throughout the entire process and believed in me, even when I sometimes did not.

Thank you to all my co-authors: Michael Gundale, Annika Nordin, Jenny Dahl, Clydecia Spitzer, Tomas Lundmark, Hyungwoo Lim, Joachim Strengbom and Tinkara Bizjak-Johansson, for all your valuable input and help writing our manuscripts. Special thanks to and Benjamin Forsmark and Clydecia Spitzer who helped me navigate the pitfalls of science and for teaching me how to plan, structure and perform a science project in practice.

Thank you to Annika Nordin research group, the Carbon/Nitrogen group, to the forest ecology lab group, everyone at Svartbergets försökspark, the lab technicians at SLU and UPSC, especially Jenny Ekman, the field workers, and a special thank you to the UPSC administrative staff.

Finally, I would like to thank Stora Enso and KAW for providing the funding that made this work possible, and Eva Stattin and everyone else at Stora Enso for being extremely helpful throughout the entire process.

Many more have helped making this project a reality, in one way or the other, and I am truly happy that all of you invested your time and energy into making this possible.

Again, thank you.

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Forest Ecology and Management 578 (2025) 122458

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Conversion of unmanaged boreal forest to even-aged management has a stronger effect on carbon stocks in the organic layer than the mineral soil

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ARTICLE INFO

Keywords:
Forest management
Soil organic carbon
Ecosystem carbon stock
Unmanaged forests
Boreal forest
Carbon sink

ABSTRACT

Forest management can impact forest carbon stocks, above- and belowground. The even-aged management practice removes the aboveground carbon stock at harvest, which is thereafter restored as the new forest stand establishes. The effects of even-aged management on forest soils in earlier unmanaged stands are however less well understood, and it has been suggested that large carbon losses may occur. In this study we use a unique paired sampling approach of stands in north inland Sweden. Half of the sampled stands had been clear cut within the previous 54 years, and half were left unmanaged. Our results show that clear-cutting harvesting and subsequent transformation of unmanaged stands into even-aged management resulted in lower aboveground carbon stock in the living trees. For the soil there was weak evidence for a loss of c. 15 % of the carbon stock in the organic layer. No evidence of an effect in the more stabilized soil organic carbon within the mineral soil layers was found.

1. Introduction

Boreal forests store about one third of the global forest C pool, and the majority of the C stock can be found in the soil (Gundale et al., 2024; Pan et al., 2011; Skogsdata, 2017). Impacts of forest management on soil C stocks thus has a huge potential to impact the net forest C balance, and boreal areas remain relatively understudied compared to other regions (James and Harrison, 2016; Luyssaert et al., 2007; Xu et al., 2014). This lack of data along with associated uncertainties has led to a controversial debate on how to best utilize (Bellassen and Luyssaert, 2014), and/or incorporate different types of boreal forests as components in policy frameworks to mitigate climate change (Lundmark et al., 2014; UNFCCC, 2016). Young, fast-growing managed stands are known to achieve higher rates of C uptake compared to older unmanaged stands, while unmanaged stands instead have been shown to store greater amounts of C (Gleixner et al., 2009; Gundale et al., 2024; Nord-Larsen et al., 2019), both in standing biomass and soil (Luyssaert et al., 2008; Paw U et al., 2004; Zhou et al., 2006). The suggestion that old unmanaged stands could be preserved to maintain large C stocks is therefore well represented among scientists (Knohl et al., 2003; Luyssaert et al., 2008; Naudts et al., 2016; Zhou et al., 2006). Long-term modelling studies support this conclusion, and for soils show a persistent decline in SOC levels after several rotation periods in managed forests (Dean et al., 2017; Harmon et al., 1990). Other studies suggest that long-term forest management improves the C balance in boreal forest due to avoided emissions and that C sinks can recover within a couple of decades (Peichl et al., 2023; Pukkala, 2017). The lack of consensus is in part because multiple factors cause substantial spatial variation in SOC (e.g., hydrology, soil clay content, etc.), making accurate estimates challenging (Gundale et al., 2024; Hoffmann et al., 2014). Further, a variety of sampling techniques are used to estimate SOC, which makes direct comparisons between studies difficult (Vanguelova et al., 2016). Relatively few studies have also simultaneously quantified soil C stock in unmanaged vs. managed stands.

When measuring SOC levels in response to harvesting, the biggest effects are often found in the organic layer, and seems to scale with intensifying harvest practices (Achat et al., 2015). The mineral soil is usually affected to a lesser degree, and while most studies on average show decreasing SOC trends in response to harvesting (Gundale et al., 2024; Nave et al., 2010), only a few studies have shown a significant loss of SOC in mineral soil layers (James and Harrison, 2016). Mechanical site preparation is also often used in conjunction with harvesting,

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https://doi.org/10.1016/j.foreco.2024.122458
Received 12 August 2024; Received in revised form 27 November 2024; Accepted 3 December 2024

especially even-aged management, to promote the establishment of the new stand. The degree to which this practice affects soil C stocks is unclear, with some studies showing that the effects are not permanent (Mjöfors et al., 2017). The C present in the mineral soil is also often regarded as most stable, potentially over millennial timescales, due to organic matter binding to mineral surfaces, fungal necromass or stabilization within soil aggregates (Adamczyk, 2021; Wiesmeier et al., 2019; Yang et al., 2020), and it is unclear to what degree even-aged management in older unmanaged forests destabilizes this pool.

In this study we utilized a unique experimental setup in the north-west of Sweden to compare the soil C stock in older unmanaged forest stands (hereafter referred to as "unmanaged stands"), paired with younger, even-aged managed forest stands (hereafter referred to as "managed stands"), allowing effective control for between-site heterogeneity. The study region is located downslope from the Swedish mountain range, and incorporates relatively large areas of unmanaged forest that have never been subjected to even-aged management (Shorohova et al., 2011). We compared C stock in soil and forest biomass from 23 stands, each with a paired unmanaged and managed stand (spanning stand ages of 106–223 years, and 14–54 years, respectively). We hypothesized that converting unmanaged forest into even-aged forests would cause a reduction of above-ground biomass and soil C stocks, in both the organic layer and the mineral soil (down to 50 cm depth). The data from this analysis could be of great utility for increasing our understanding of the boreal ecosystem C budgets, and for quantifying the eventual changes in the forest C balance when even-aged management practices are applied to previously unmanaged stands. The results could also be used to improve high resolution models relevant to silvicultural management in Sweden and other remaining areas across the boreal biome, where decisions about eventual management and/or conservation in mature forests may have important impacts on climate change mitigation.

2. Materials and methods

2.1. Study area and experimental design

The study includes 23 sites (Fig. 1) in north-west of Sweden (Västerbotten and Norrbotten County), lat. 65–66°, long. 16–20°, 200–630 m above sea level. The region is located just downslope from the Swedish mountain range and has large areas of intact unmanaged forests that have never been utilized for even-aged management. However, most of the forested area has historically been selectively cut with varying proportions of large diameter trees removed and/or been subject to stand replacing fires. Even-aged forestry in these areas became widespread after 1948, when regulations on land use (Lappmarkslagen) in the area were lifted, and there are still large continuous areas of old forests left. At each site we identified a paired managed (even-aged management initiated by clear-cutting) and unmanaged stand. Each managed stand was assumed to have been equivalent to the adjacent unmanaged stand prior to clear-cutting. The managed stands had a mean site index of 14.4 (H_{100}, m) and tree ages ranged between 14 and 54 years old (average age 27 years). The unmanaged stands showed a mean site index of 13.9 (H_{100}, m) and tree ages ranged between 106 and 223 years (average age 163 years). While it is somewhat contradictory to assign an age to an unmanaged forest containing a multilayered stand structure and an uneven age distribution, we did so using a well-accepted weighted arithmetic mean where the older trees with larger diameters contribute more to the assigned mean age of the plot (Nilsson et al., 2022). This was done to provide the reader with a more complete picture of the differences in tree ages between unmanaged and managed stands, (for information on all stands see Supplementary table 1). Nine of the managed stands were dominated by Norway spruce (*Picea abies* (L.) Karst and 14 by Scots pine (*Pinus sylvestris* L.), while 14 of the unmanaged stands were dominated by Norway spruce, and 9 by Scots pine, (data obtained by the forest company Sveaskog, personal correspondence). All selected sites were dry or mesic site types lying on moraine or river sediments, with soil textures ranging from silty to sandy. All measurements were carried out in squared-shaped plots of approximately 0.1 ha where the plot centers are situated at least 20 m from the boundary of the adjacent unmanaged or managed stand, and at least 50 m from any other adjacent stand. Within these plots, forest inventory (living and dead biomass) was performed in four circular sub-plots with a 7-meter radius and sub-plot centers situated 20 m from each other (Fig. 2) and soil sampling, including measurement of the ground vegetation and litter-layer were performed on points laid out in a grid pattern within each square-shaped plot.

Fig. 1. The distribution of sites used in the study. Each site consisted of paired unmanaged and managed forest stand. The white dot marks the town of Arvidsjaur.

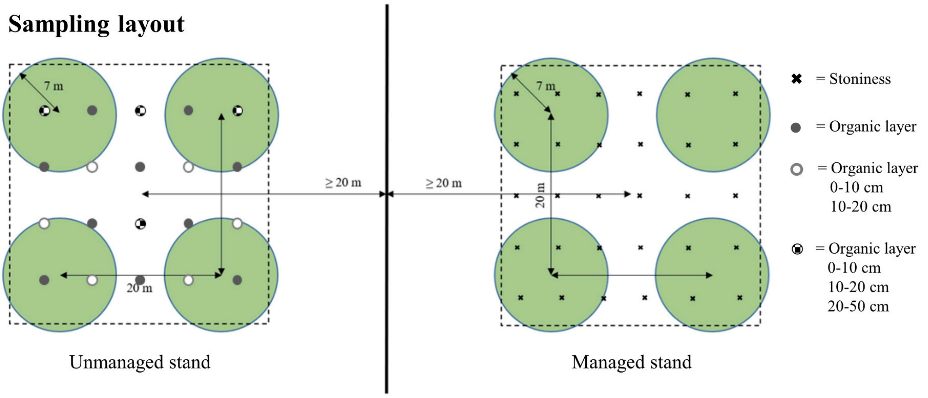

Fig. 2. A depiction of sampling at each site utilizing a paring consisting of an unmanaged stand with an adjacent managed stand. All sampling was performed within 0.1 ha plots. Living trees and dead wood were sampled within the green circular sub-plots. Stoniness, soil samples, ground vegetation and litter layer, were collected on points located on a grid within the plots marked with dashed lines. Note: Both stoniness and soil sampling were performed in all plots, the figure only depicts them separately for clarity.

2.2. *Sampling and laboratory analyses*

2.2.1. *Living and dead tree biomass*

Field measurements to assess C stocks in living and dead tree biomass were carried out between 2017 and 2019 and were estimated from four circular sample sub-plots (7-meter radius), with at least 20 m between sub-plot centers (Fig. 2). Trees with diameters > 100 mm within the 7-meter sample sub-plots and trees with a diameter of 40–99 mm within 3.5 m from the sub-plot centers were included in the study. Sample trees were used to measure both height and age (stem cores at 1.3 m). In the managed stands only the main tree layer was included when establishing stand age. Dead wood with a diameter over 100 mm and height or length of more than 1.3 m that was classified as “hard dead wood” (more than 90 % of the stem consisting of hard non-decomposed wood) according to Skogsdata (2017), was registered in each sub-plot, whereas other decay stages of dead wood were not included in our sampling. Carbon in living trees for all tree species, (*Pinus sylvestris*, *Picea abies*, *Betula spp.*, *Salix caprea* and *Populus tremula*) were then calculated using Marklunds biomass functions (Marklund, 1988). For calculations of *S. caprea* and *P. tremula* biomass, the functions for birch were used, but adjusted according to the density of the wood (Heureka SLU, 2016). Biomass of coarse roots down to 2 mm were calculated for *P. sylvestris* and *P. abies* only using allometric functions by Marklund, (1988), and adjusted by 6 % based on Petersson and Ståhl, (2006). Other tree species were assumed to be minor contributors to these pools due to their low abundance in all plots. Carbon contents were assumed to be 50 % of dry mass in all living biomass, and measured values were upscaled to Mg C ha^{-1}. Biomass of dead wood was calculated based on volume estimates according to Näslund (1941) and density of the dead wood (spruce 0.29, pine 0.31 and broadleaves 0.37 g cm^{-3}). The amount of C in dead wood was assumed to be 50 % (Russell et al., 2015) and measured values were upscaled to Mg C ha^{-1}. Each of these biomass pools measured within the plots were then added together, resulting in total Mg C ha^{-1}.

2.2.2. *Bulk density and stoniness*

Mineral soil bulk density (BD) was sampled in a sub-set of plots, including 10 in unmanaged stands and 9 in managed stands, at three depth intervals, 0–10 cm, 10–20 cm, and 20–50 cm, with five sub-samples per depth and plot. Bulk density estimations were based on the excavation method (Gatea et al., 2018) where a ca. 15 cm diameter hemispherical pit was excavated, a soft mesh cloth was inserted in the pit and then filled with 2 mm plastic granules. The volume of the granules was then determined, and the excavated soil was sieved (2 mm). If smaller stones or larger fragments with a combined volume over 20 cm^3 (approximately 5 % of the pit volume) were found, the sampling procedure was stopped, and a new excavation pit was dug in close proximity. Collected samples were transported back to the lab, dried at 70º C for 48 hours, sieved again (2 mm) and weighed. The mass of the processed samples was then divided by the volume of plastic granules used to fill the pit, yielding bulk density estimates (g cm^{-3}). Bulk density in the organic layer (humus) was estimated with the aid of bulk density functions, (equation 18, Nilsson and Lundin, 2006)

Stone and boulder content at all sites for each pair of unmanaged/managed stands was estimated using the rod penetration method, where an iron rod with a diameter of 10 mm was driven through the soil until it reached a stone or boulder (Viro, 1952). This was done at 30 points in each sampling plot. The mean penetration depth was calculated into volumetric content of stones and boulders in percent using Viro (1952) modified by Stendahl et al., (2009), regression equation SB = 82.5 – 2.75 *Si, Si being mean penetration depth of the 30 points. Based on the assumption that it should be no ecological reason for the stoniness value to differ within a pair of unmanaged and managed plots, we used an average stoniness value per paired site ((SB on unmanaged plot + SB on managed plot)/2) for all calculations.

2.2.3. *Ground vegetation and litter layer, organic and mineral soil C content*

The C content of the organic layer, mineral soil, ground vegetation and litter layer were sampled during autumn 2017 and summer 2019. The organic layer (including F and H sub-layers) was sampled with methodology similar to Maaroufi et al., (2019) in a grid-pattern in each plot using a 100 mm cylinder. Material was collected from 20 points and the thickness of the organic layer was recorded. The organic layer samples were pooled and mixed thoroughly to obtain one composite sample per plot. In 2019, at nine pairs of unmanaged and managed sample plots, the ground vegetation and litter layer on top of the samples from the organic horizon was removed and transported back to the lab for determination of C content. The ground vegetation and litter were not analyzed separately, due to difficulty in separating them. Mineral soil was collected between 2017 and 2019 from soil pits with individual non-volumetric samples from multiple depth increments (0–10, 10–20, and 20–50 cm) using similar methodology as Blaško et al., (2020) and Blasko et al., (2022). The two upper mineral soil layers (0–10 and 10–20 cm) were sampled from 10 sample points in a grid across the plot, whereas the 20–50 layer was sampled from 4 points (Fig. 2), when possible (9 out of 23 pair of plots). All subsamples from each layer were pooled plot-wise, giving one composite sample for each soil layer and plot. Ground vegetation and litter, organic and mineral soil samples were transported to the lab and dried at 70° C for 48–60 hours. The organic soil was sieved (2 mm), omitting mostly roots and some coarse fragments. Organic material removed by the sieve was weighed to account for this fraction in later analyses given that the bulk density function was based on soil specifically, rather than roots. Mineral soil was sieved at (2 mm). Samples from the organic layer were then ground in a ball mill for 60 seconds while the mineral soil samples were placed on a roller mill for 24 hours. Carbon content (%) of each soil sample was then determined using an elemental analyzer (EA-IRMS; Flash EA 2000; Thermo Fisher Scientific). The C stock (Mg ha^{-1}) in each layer of organic and mineral soil was calculated using C content (%) from the EA-IRMS analysis, bulk density of the soil, and depth of each soil layer, and then adjusted for stoniness (mineral soil) or organic coarse fragments/roots (organic layer). Carbon content in ground vegetation and litter dry mass was assumed to be 50 % and measured values were upscaled to Mg C ha^{-1}.

2.2.4. Calculations and statistical analyses

We first used a mixed effects ANOVA with random effect of site to test if soil depth, forest age, or tree species had any effect on mineral soil BD. Soil depth was the only significant factor affecting BD (p = 0.012), Therefore, for upscaling soil C stocks (described above), we applied average BD values separately to each soil layer (0.613 g/cm^3 used for 0–10 cm, 0.639 g/cm^3 for 10–20 cm and 0.787 g/cm^3 for 20–50 cm.).

To compare SOC stocks in unmanaged and managed stands, we used mixed effects ANOVAs, with forest type (unmanaged or managed) serving as a fixed factor, and site serving as a random factor. The random factor was added to control for site-to-site variation in properties such as soil texture, moisture, topography etc., and since our response variables differed in the number of sampled stands (e.g. ground vegetation + litter and 20–50 cm soil depth were only sampled at 9 out of 23 stands), we analyzed data for each ecosystem C compartment separately. All statistical analyses were performed using R studio (v. 3.5.1; Rstudio Team,2020) and normality of residuals within soil layers was confirmed through observation of residual plots.

For all statistical tests we used a significance terminology suggested in Muff et al., (2022), where different ranges of p-values are reported on a continuum from “little or no evidence” to “very strong evidence”. A p-value of 0.0001 – 0.001 subsequently equals very strong evidence, a value of 0.001 – 0.01 equals strong evidence, 0.01 – 0.05 equals moderate evidence, 0.05 – 0.1 equals week evidence and a p-value of 0.1 – 1 is considered as no evidence.

3. Results

3.1. Total ecosystem C stock

The different number of samples between the ground vegetation (and litter) and 20–50 cm mineral soil depth compared to the rest of the dataset makes statistical comparisons on total mean ecosystem C difficult. However, comparisons referring only to the means show that total mean ecosystem C was 106.8 Mg C ha^{-1} in unmanaged forest stands, and 69.5 Mg C ha^{-1} in the managed stands. The biggest difference was found in the biomass of the living trees, equivalent to 45.4 and 13.4 Mg C ha^{-1} respectively. Comparing only mean SOC (organic layer and mineral soil) the difference was 47.6 Mg C ha^{-1} in unmanaged forests and 43.4 Mg C ha^{-1} in managed forests (Table 1).

3.2. Aboveground C stock

Statistical analysis of aboveground ecosystem compartment C pools shows that there was very strong evidence for a significant difference in C pools within the living trees (*$p < 0.001$*) and deadwood (*$p < 0.001$*) compartments between unmanaged and managed stands (Fig. 3).

Table 1

Mean ± SE C pools sampled in unmanaged and managed forest types. Results are based on averaging all values for each respective layer in both forest types.

	Mg C ha^{-1}		
Compartment	Unmanaged forest	Managed forest	p-value
Living trees	45.4 ± 3.4	13.4 ± 3.3	< 0.001 * **
Ground vegetation & litter	12.4 ± 0.7	12.4 ± 2.2	0.994
Dead wood	1.4 ± 0.3	0.3 ± 0.1	< 0.001 * **
Organic horizon	21.9 ± 2.1	18.7 ± 1.5	0.054 *
Mineral soil 0–10 cm	6.5 ± 0.7	6.2 ± 0.7	0.461
Mineral soil 10–20 cm	6.4 ± 0.6	5.9 ± 0.5	0.212
Mineral soil 20–50 cm	12.8 ± 2.8	12.6 ± 3.0	0.848
Total aboveground C	59.2	26.1	Unbalanced data
Total belowground C	47.6	43.4	Unbalanced data
Total ecosystem C	106.8	69.5	Unbalanced data

Note: All compartment values are based on samples from 23 paired stands except ground vegetation & litter and mineral soil 20–50 cm, which are based on samples from 9 paired stands.

3.3. Belowground C stock

Statistical analysis of the soil organic C (SOC) ecosystem compartments shows that there was weak evidence *($p = 0.054$)* for a significant decrease of C within the organic layer when comparing unmanaged and managed stands. However, no evidence was found for differences in other measured belowground ecosystem C compartments (Fig. 4).

4. Discussion

The purpose of this study was to fill an existing knowledge gap by providing robust data on C stocks in unmanaged and managed boreal forest stands. Such data will help provide solutions to model errors and thereby get closer to a more data driven approach in discussions about boreal forest management and its effects on SOC. Any life-cycle assessment of the goods produced, and related discussions about substitution effects are however beyond the scope of this study. Our results show that the average aboveground C stock was 33.1 Mg C ha^{-1} lower in managed vs. unmanaged stands. The substantial difference in aboveground C stock is expected and in line with our hypothesis but none-the-less represents a major shift in ecosystem C stocks, as the transition from unmanaged to even-aged management transforms a large forest C stock acting as a relatively slow sink (C uptake ha^{-1} y^{-1}), into a smaller forest C stock, that acts as a relatively large sink (Coursolle et al., 2012; Gundale et al., 2024; Peichl et al., 2023). We also hypothesized that converting unmanaged forest into even-aged forests would cause a reduction in soil C stocks, in both the organic layer and the mineral soil (down to 50 cm depth). This prediction was based on expectations that clear-cutting may increase decomposition rates via altered soil surface temperature or by reduced carbon inputs from above- and belowground litter inputs (Gundale et al., 2024). In line with this assumption, we found weak evidence of a 3.2 Mg C ha^{-1} reduction in the organic horizon at an average of 27 years after clear-cutting. However, in contrast to our hypothesis, we found no evidence that management caused a decrease in mineral soil C. Adding together C in all mineral soil layers (0–10, 10–20 and 20–50 cm) resulted in a non-significant loss of 1.0 Mg C ha^{-1} C in managed versus unmanaged forest stands. Hence, only ca. 3 % of the total C stock difference between managed and unmanaged forest stands was explained by the mineral soil compartment. This result corresponds

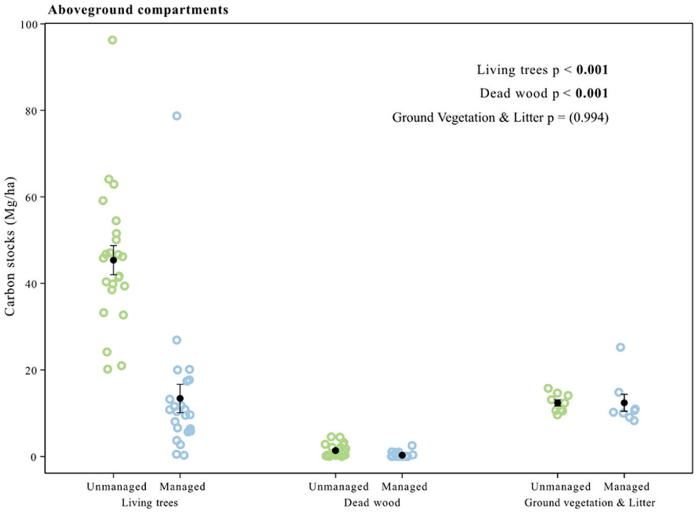

Fig. 3. Visualization of aboveground ecosystem compartments based on pooled measurements from all sites included in the study. Mean ± SE is indicated by black points and arrows while the colored circles showing the full range the measurements. P-values in bold indicating very strong evidence based on comparisons between the two forest types for each measured compartment.

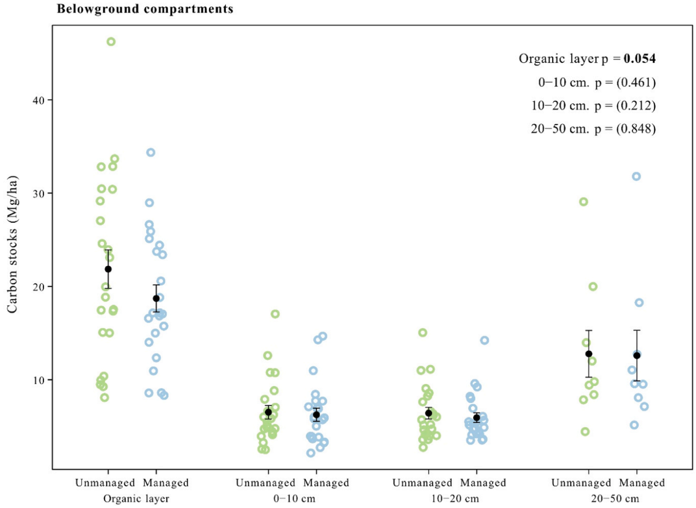

Fig. 4. Visualization of SOC ecosystem compartments based on pooled measurements from all sites included in the study. Mean ± SE is indicated by black points and arrows while the colored circles showing the full range the measurements. P-values in bold indicating weak evidence based on comparisons between the two forest types for each measured compartment.

well to other studies where mineral soil C is often less affected by harvest than the organic horizon or "humus-layer" (Achat et al., 2015; James and Harrison, 2016; Nave et al., 2010). Frequent explanations given for this greater stability of C in mineral soil are stabilizing interactions between organic matter and mineral particles within soil aggregates (Mikutta et al., 2006; Torn et al., 1997), or incorporation of C in root-derived compounds and fungal necromass (Adamczyk, 2021; Adamczyk et al., 2019). While it is not possible to estimate the recovery time of the organic layer with the data provided by our measurements, other meta-analyses suggest the time needed is > 100 years (Gundale et al., 2024; Palviainen et al., 2020). Both SOC stocks and their rate of change are however known to decrease with latitude (Olsson et al., 2009). Small changes over time might therefore be difficult to observe in high latitudes compared to the southern boreal region (Ågren et al., 2007), thus care should be taken when scaling the results of this study to other parts of the boreal region. Our study also does not allow for a complete analysis of soil C differences across a full stand rotation cycle, and it is feasible the C inputs during later stages of stand development will compensate from the losses we show occur at a relatively young stand age.

While the C stock in the living trees expectedly decreased due to clear cut-harvesting, the C stock in the ground vegetation and litter did not show any evidence of a decrease. While it is possible that the harvest of the unmanaged stands did effect this ecosystem compartment, other studies show a rapid establishment of a productive understory layer only years after harvest (Peichl et al., 2023). No effect might therefore still be visible at the time of our measurements.

The reduction in dead wood C stock between unmanaged and managed stands was 1.1 Mg C ha^{-1}. From a pure CO_2 standpoint, even though statistically significant and amounting to a loss of 80 %, this pool is of minor importance compared to other pools measured in our study. The substrate however serves as the host to a substantial number of saproxylic beetle and fungal species, including many red-listed species (Birkemoe et al., 2018; Gao et al., 2015). Therefore, while the decrease in dead wood does not contribute much to the total C balance of the studied forests, it could still have substantial negative impacts on biodiversity as it represents a major habitat loss. Assessing the climate benefits of forest management in potentially dead wood rich stands, such as the unmanaged stands in our study, thus needs to take this into account. Furthermore, the dead wood inventoried in our study only includes the most recent decay class, "hard dead wood" (more than 90 % of the stem consisting of undecomposed wood) with a diameter over 100 mm and height or length of more than 1.3 m. While legislation, policy and to some extent its low commercial value normally exclude dead wood in Swedish forests from harvest (Nilsson et al., 2020), some loss of the substrate due to forest management still occurs (e.g., exposed logs in advanced stages of decay outside retention groups are easily destroyed by machines etc., Siitonen, 2001). The inputs of new dead wood is also greatly reduced in young stands (Nilsson et al., 2020). For this reason, "hard dead wood", which represents the most recent dead wood input, would be most likely to differ between unmanaged and managed stands. However, we note that measurement of all decomposition stages may have revealed differences in other decay classes as well (Skogsdata, 2017). Although, divergence in dead wood mass for the more advanced decay stages would likely take more time to develop in the managed stands than we considered in our study (average stand age 27 years), given that it has been estimated that total dead wood decomposition has been estimated to take 200 years or longer (Hofgaard, 1993).

Our study provides a snapshot picture of the ecosystem C stocks at the time of the measurements; and further, it utilized a paired comparison and sampling approach that is not well represented in the literature, which helped to control for landscape heterogeneity that is often problematic when making forest C stock comparisons (Ortiz et al., 2013; Vanguelova et al., 2016). While this study was focused only on the forest C balance, other types of data are also relevant for understanding the climate impacts of forests. For example, boreal forests can serve as sources or sinks for other greenhouse gasses (N_2O and methane; Vestin et al., 2020). Further, boreal forests are known to impact the Earth's energy balance via their generally low surface albedo (Betts, 2000), which management may also affect. Future measurements of these other climate drivers, as well as life cycle accounting of harvested products, or consideration of the fact that these areas are often subject to other economic interests such as reindeer herding and or recreation (Margaryan and Fredman, 2017; Zhou and Gong, 2005), needs to be taken into account to provide a full picture regarding the climate and societal impacts of the forest types compared in our study.

5. Conclusion

This study presented data on how forestry can affect forest C balances from a unique experimental design where unmanaged stands could be compared to stands managed with even-aged management, established by clear-cut harvesting 14–54 years before present. From a C balance perspective the transformation of previously unmanaged stands into even-aged managed stands brought about an aboveground C stock loss of 33.1 Mg C ha^{-1}. We also found weak evidence of a decrease in C stocks in the organic layer of 15 % (3.2 Mg C ha^{-1}), but no evidence of a decrease in the more stabilized SOC present in the mineral soil was found. Our result thus supports previous research demonstrating that clear-cut harvesting can decrease soil C stocks in the organic horizon. Although the C stock difference between unmanaged stands and stands turned into even-aged management may appear proportionally minor as it decreases over time as the regenerated stands mature, forestry decisions must take into consideration that the previously unmanaged stands may contain many other values usually not present in managed stands, such as the potential for biodiversity connected to the larger volume and structural diversity of dead wood. Data on the response of the forest C balance to forestry will thus help inform discussions that seek to balance the broad array of societal values and ecosystem services forests in these remote northern regions provide.

Funding

This work was supported by Future forests, Stora Enso AB and Knut and Alice Wallenberg foundation [no. 2018.0259].

CRediT authorship contribution statement

Hyungwoo Lim: Writing – review & editing, Methodology, Conceptualization. **Michael J Gundale:** Writing – review & editing, Supervision, Methodology, Data curation. **Annika Nordin:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Data curation, Conceptualization. **Jenny Dahl:** Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Marcus Larsson:** Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Tomas Lundmark:** Writing – review & editing, Resources, Methodology, Funding acquisition, Data curation, Conceptualization.

Declaration of Competing Interest

The funders had no role in the design of the study; the collection, analysis, or interpretation of data; writing of the manuscript; or in the decision to publish the results. The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: A.N. reports a relationship with Stora Enso AB that includes employment. A.N. reports a previous relationship (2016–2020) with Sveaskog AB that included: Board membership. M.L reports a relationship with Stora Enso that includes Funding. J.D., M.J. G. H.L. and T.L. declares no conflicts of interest and has no affiliation with any commercial entities.

Acknowledgments

M.L. acknowledges Jenny Ekman for performing the lab-analysis. A. N. acknowledge Stora Enso AB for permitting her leave of absence from her current position with the company to take part in the reported research and supervision. We also want to acknowledge the current landowner Sveaskog for letting us conduct the study on their land.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122458.

Data Availability

Data will be made available on request.

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Forest Ecology and Management 563 (2024) 121967

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Diminishing legacy effects from forest fertilization on stand structure, vegetation community, and soil function

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ARTICLE INFO

Keywords:
Forest fertilization
Forest growth
Vegetation community composition
Mineralization
Soil organic carbon
Ion-exchange resin

ABSTRACT

While there is consensus that fertilization with nitrogen (N) is a cost-effective way of increasing both forest biomass yield and timber harvest profitability, the strength and longevity of legacy effects are debated. To quantify legacy effects of past fertilization, we analysed 21 mixed *Pinus sylvesteris* and *Picea abies* stands. The stands, on average 23 years old at the time of this study, were either unfertilized (n=7), fertilized with 150 kg N ha^{-1} once 36 years ago (n=7), or twice, 45 and 36 years ago, respectively (n=7), during the previous stand rotation. We performed measurements on soil N mineralisation and N availability, forest growth, ground vegetation community composition, soil and vegetation C/N ratios and soil C and N stocks, many of which responded to legacy N fertilization earlier in stand development. Our results show that the legacy effects of fertilization during the previous stand rotation have diminished through time, indicating an eventual convergence of stand properties. Specifically, all significant effects present in the previous measurement period (over a decade ago), were weaker or completely absent in the current study (i.e. 36 years after fertilization and 23 years after initiation of the new stands). None-the-less, this indicates a longer legacy effect of N fertilization than what is normally considered and suggests that care should be taken to mitigate unwanted, long-term effects when utilizing N addition to promote tree growth in boreal forests.

1. Introduction

Plant growth in northern boreal forest ecosystems is generally limited by low availability of N (Binkley and Högberg, 2016). This makes fertilization with N an attractive way of increasing forest biomass yield (Nohrstedt, 2001), which can increase timber harvest profitability by up to 15 % (Jacobson and Pettersson, 2010). About 40 000 ha of Swedish forest is fertilized annually ("measures in forestry", 2023) and while this area only represents a small part of the available productive forest land (> 20 million ha) in Sweden, there is potential for a more widespread and/or intensive use of forest fertilization (Bergh and Hedwall, 2013). The standard fertilization dose utilized in Nordic forestry is 150 kg N ha^{-1}, added once or twice late in the forest rotation, which often results in an approximately 30 % increase in biomass growth, increased N concentrations in needles, and potential effects on N leaching, changes in understory diversity, and alterations to soil C cycling processes (Mayer et al., 2020; Nohrstedt, 2001). While the impacts from standard doses normally are considered to last no more than 10 years, long term changes (i.e. > 10 years) usually only occur under more intensive fertilization (Nohrstedt, 2001). However, a few studies have reported that even standard forest fertilization practices can have legacy effects that impact the forest ecosystem properties and processes at the start of the next rotation. For example From et al., (2015) showed increased growth of young trees in stands fertilized with standard N doses during the previous forest generation, as well as changes in the species composition of the ground vegetation (Strengbom and Nordin, 2012, 2008). Furthermore, extractable soil ammonium (NH_4-N) and nitrate (NO_3-N) were found to be higher in previously fertilized stands, indicating higher rates of N mineralization and mobile soil NH_4-N and NO_3-N, than in stands that were not previously fertilized (From et al., 2015). Hence, these studies suggested that standard fertilizer additions in boreal forests may induce legacy effects on vegetation growth and N cycling.

While the potential to increase forest growth is attractive, N addition also has the potential to induce vegetation changes that negatively affect biodiversity (Bobbink et al., 2010, 1998; Midolo et al., 2019). The N

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https://doi.org/10.1016/j.foreco.2024.121967
Received 9 February 2024; Received in revised form 3 April 2024; Accepted 2 May 2024

enrichment levels which an ecosystem can tolerate without suffering significant harmful effects according to present knowledge (i.e. the N critical load; Nilsson and Grennfelt, 1988) is suggested to occur in boreal forest understory vegetation at levels as low as 6 kg N ha^{-1} yr^{-1} (Nordin et al., 2005) and the effects often intensify with increasing N loads (Midolo et al., 2019). Rare species (Suding et al., 2005) such as orchids, (e.g., *Calypso bulbosa*), or areas with low background N deposition are also often impacted to a larger degree than common species or areas exposed to comparatively higher rates of background N deposition (Hedwall et al., 2013). Changes in species composition could also arise through indirect N addition-effects such as changes in the light environment (Strengbom et al., 2004), or altered susceptibilities to natural enemies such as pathogenic fungi (Nordin et al., 2006; Strengbom et al., 2002).

The increase in forest productivity following fertilizer additions can also lead to increased soil carbon accumulation, beneficial for the mitigation of atmospheric CO_2 (Friedlingstein et al., 2020; Hyvönen et al., 2008; Johnson and Curtis, 2001; Jörgensen et al., 2021). This effect is mainly due to the increased production of above and belowground plant litter, and shifts in the soil microbial community, hampering soil organic matter decomposition (Forsmark et al., 2021; Haas et al., 2018; Jörgensen et al., 2022; Maaroufi et al., 2019, 2015). However, the majority of results demonstrating impacts of N additions on soil carbon accumulation in boreal forests stem from experiments using either large doses of N applied a single time, or small doses added repeatedly during long periods of time (Forsmark et al., 2020; Huang et al., 2011; Hyvönen et al., 2008; Maaroufi et al., 2015; Olsson et al., 2005). It remains unclear whether standard forest fertilization regimes used by the forest industry, (i.e., one or two “standard” dose applications during late rotation) result in long-term increases in soil carbon storage. Therefore, to make informed decisions regarding fertilization practices, there is a need for improved understanding of the strength and longevity of any unintended legacy effects that may arise from it.

In this study we utilize a study system situated in the boreal forest of mid-Sweden, designed to represent standard fertilization practices in accordance with the guidelines recommended by the Swedish Forest Agency (“measures in forestry” 2023). We evaluated whether a one or two-time application of 150 kg N ha^{-1} at the end of the previous stand rotation resulted in long term legacy effects on both above and belowground forest properties 36 years since fertilization and 23 years into the current forest rotation. Legacy effects in this study system were initially reported by Strengbom and Nordin, (2012, 2008), and (From et al., 2015), approximately 10 years after the new stands were initiated. At c. 23 years of age, the stands have now reached canopy closure, which may have consequences for how forest properties and processes are affected by legacy N. In addition to follow up measurements of tree growth, N mineralization and extractable soil N, and ground vegetation species composition, effects on soil carbon were also examined.

We tested the following hypotheses:

That fertilization would have a legacy effect on:

1. soil N cycling process, such that previously fertilized stands would exhibit higher net mineralization rates and higher amounts of mobile soil NH_4-N and NO_3-N. We expected this because a previous study from the same experimental system showed nearly four times higher soil N mineralization rates on fertilized sites compared to the control (From et al., 2015).
2. tree growth during the current stand rotation, where fertilized stands would exhibit larger basal area, height growth, and volume. We expected this because a previous study from the same experimental system showed on average 25 % higher trees on fertilized sites compared to the controls (From et al., 2015).
3. understory plant community composition and foliar N content, such that previously fertilized stands would show greater abundance of nitrophilic species (e.g., graminoids), and higher foliar N contents. We expected this because a previous study from the same experimental system showed that species composition and foliar N content of stands that had been fertilized were separated from the controls (Strengbom and Nordin, 2008).
4. soil C and N, such that previously fertilized stands would exhibit larger soil C and N stocks.

Testing these hypotheses in combination will provide valuable information regarding the persistence of legacy effects stemming from standard N fertilization practises in boreal forests, which may help optimise future forest management practises to maximise biomass growth, while simultaneously avoiding unwanted side-effects.

2. Materials and method

2.1. Study area

Data used in this analysis was gathered from 21 forest stands, each sized between 4.7 and 22.4 ha spread out over an 8500 ha forest land area in the middle boreal zone (Ahti et al., 1968) in central Sweden (62°58 "N, 16°40"E). The studied stands either had, or had not, been subjected to N fertilization before harvest and regeneration. Control (C) stands ($n = 7$) were never fertilized, N1 stands ($n = 7$) were fertilized with 150 kg N ha^{-1} once in 1985, and N2 stands ($n = 7$) were repeatedly fertilized with 150 kg N ha^{-1} in 1977 and 1985; thus, our study included 7 stands for each treatment (Table 1). Fertilizer N was added as granules of ammonium nitrate (NH_4NO_3) spread by tractor or aircraft. The forest land, currently owned by the forest company SCA (*Svenska Cellulosa Aktiebolaget*) was at the time of stand selection owned by the Swedish state-owned company, Sveaskog. The initial stand selection done in 2008, see From et al., (2015) was based on information describing the stands before clear-cut, originating from Sveaskoǵs forest inventory. Care was taken to select the stands with similar initial productivity indices, elevation, temperature sum (growing degree days; Womach, 2005), slope (forest floor incline from 1 (<10 % inclination) to 5 (>50 %), tree species composition, soil conditions and stand age at the time of site selection. Further details of the study system are found in (From et al., 2015; Strengbom and Nordin, 2008).

The annual precipitation in the area is between 500 and 600 mm per year, and the atmospheric background N deposition ranges from 1.6 to 2.4 kg ha^{-1} $year^{-1}$ (Karlsson and Hellsten, 2022). All stands used in the study had mesic site conditions with Udic moisture regime and soil were Typic Haplocryods developed on glacial till with an organic surface

Table 1
Number of stands per treatment, site index (SI), elevation (above sea level, a.s.l.), temperature sum (GDD) and forest floor slope. The stands were fertilized once in 1985 (N1) with 150 kg N Ha-1, twice (N2), both in 1977 and 1985 with 150 kg N Ha-1 or never fertilized (C).

Stands (n)	Control 7	N1 7	N2 7	*F*-value	*p*-value
Site index (H100), m)	20.6 ± 0.2	19.7 ± 0.3	20.4 ± 0.3	3.00	0.08
Elevation a.s.l (m)	334 ± 21	358 ± 20	334 ± 17	0.54	0.59
Temperature sum (GDD)	937 ± 6	900 ± 22	923 ± 11	1.59	0.23
Slope (1−5)	2.00 ± 0.22	1.86 ± 0.26	1.72 ± 0.18	0.41	0.67

Note. Table adapted from (From et al., 2015).

layer (O-horizon), sometimes also referred to as plant litter layer, where the upper part is relatively undecomposed and the lower parts were strongly humified (Driessen, 2001; From et al., 2015; Strengbom and Nordin, 2008). The relative abundance of the two dominant species (*Pinus sylvesteris and Picea abies*) prior to clear-felling ranged from 25 % to 75 % with no difference between fertilized and unfertilized stands (Mann–Whitney U-test: $U = 83.5$, $p = 0.348$) (From et al., 2015), and the forest field layer was dominated by dwarf shrubs such as *Vaccinium myrtillus* and *Vaccinium vitis-idaea.,* i.e., all stands were classified as spruce forest of bilberry type (Påhlsson, 1995). All stands were harvested by clear-felling between 1997 and 2000, subjected to soil scarification, and then planted with identical seedling stock of either *Pinus sylvestris* or *Picea abies* at a density of 2200–2300 seedlings ha^{-1}. Today the majority of stands contain a combination of both species and a mix of planted and naturally regenerated trees. Some areas have also been pre-commercially thinned, removing mainly spontaneously regenerated birches that have mixed into the planted conifer seedlings.

2.2. Buried bags and ion capsules

The buried bag technique (Eno, 1960; Gundale et al., 2011) was used to investigate N mineralization in all stands. Between June 15–18, 2021, seven samples from the entire O-horizon in each replicate stand (i.e. 147 samples in total) were collected with a cylindrical (diameter 10 cm) soil corer along 45 m transects passing through the centre of each stand. The depth of the O-horizon (ca. 5–15 cm) made sampling of the entire horizon possible for all 49 samples. After gently removing large roots and the top layer of easily identifiable plant material, half of each sample was put in a plastic bag, put into a cooler and transported back to the lab for analysis. The other half was put into another plastic bag and buried in the organic horizon *in situ*. The buried cores were then collected 85 days later (14–15 of September), transported them to the lab in a cooler, and processed them for analysis. All samples were sieved (2 mm mesh) and then extracted in 1 mol KCL and analysed for NH_4 and NO_3 using an Auto Analyzer 3 spectrophotometer (OmniProcess, Solna, Sweden). Net mineralization was calculated as the difference in NH_4-N and NO_3-N (mg g^{-1} dry weight [DW] soil) between the June and September sample times. Any damaged bags were excluded before estimating mineralization, and before statistical analyses, sub-replicate samples of NH_4-N and NO_3-N from the same stands were pooled to obtain one single value of mineralization per stand, with these stand level values serving as true replicates.

Resin ion-exchange capsules (PST-1, Universal Bioavailability Environment/Soil Test, MT, USA) were used to estimate the amount of soil mobile NH_4-N and NO_3-N (mg/capsule) in all stands. Between the 15–18 of June 2021, six capsules were buried just beneath the bottom of the organic horizon along a transect through each stand center. Later the same year, between the 14–15 of September, all capsules were retrieved, put in plastic bags, and transported to the lab for analysis. In the lab, the ion-exchange capsules were brushed off to get them as clean as possible, and then placed in 50 ml Falcon tubes. Ten ml of 1 mol KCl was then pipetted into the tubes, followed by 30 min agitation. This process was repeated 3 times, resulting in a total of 30 ml sample extracts. The NH_4-N and NO_3-N concentration on these extracts were analysed using an Auto Analyzer 3 spectrophotometer (OmniProcess, Solna, Sweden). Before statistical analysis sub-replicate samples from the same stands were pooled to obtain one single value per stand.

2.3. Tree growth

Data on tree species composition and tree growth were gathered in June 2022. The stands were inventoried by using a square grid randomly positioned over the entire 8500 ha forest area on the map. Each grid cell was 100 × 100 m in size and all grid cell intersections contained within each of the 21 stands on the map were inventoried using circular ($r = 5.64$ m) plots, located during the inventory process with GPS. If a plot randomly landed on a nature conservation set-aside patch originating from the previous stand, it was excluded from sampling. After the removal of these specific sub-plots, a total of 253 sub-plots were inventoried across the whole experiment, divided among the different stands. Each stand was thus inventoried using the same "resolution" but the number of inventoried plots per stand varied depending on the size of the stand (4 plots in the 2.34 ha smallest stand, and 25 plots in the 26.4 ha biggest stand). In every plot, tree species and diameter at breast height (1.3 m.) was measured for all trees taller than 1.3 m. We also measured the height of the tree closest to the plot centre, and one tree in every cardinal direction closest to half the radius of the plots, i.e., 5 samples trees in total within each plot (Gundale et al., 2014). If two trees were equally close to the cardinal points, the clockwise positioned trees were used. As the stands used in this study are actively managed forests, pre-commercial thinning's had been performed in some of the stands since the last measurement in 2010. Pre-commercial thinning is a regular part of the forest management regime in Sweden, performed when the stand height is about 2–6 m (Pettersson et al., 2012) and involves removing selected, mainly young trees that have spontaneously regenerated and serve as competition for the planted cohort. This is done with a handheld motorized brush cutter to allow more development space for the remaining trees. The practice is not to be confused with commercial thinning, which is performed much later in stand development with the aid of a harvester and forwarder-group, and removes a substantial portion of stand basal area. At the time of our measurements, 5 stands in the C-treatment, 4 stands in the N1-treatment, and 3 stands in the N2-treatment had been subjected to pre-commercial thinning, while the rest remained un-thinned. For all variables, sub-replicate values from the same stands were pooled to obtain one true replicate value of average DBH and height per stand. Thus, for all statistical analysis, the stand was considered the unit of replication.

2.4. Ground vegetation and plant foliar chemistry

In July 2021 the vegetation was scored using a modified version of the point intercept method (Jonasson, 1988). We analysed the ground vegetation (vascular plants, bryophytes and lichens) at 200 random points along a 45 m transect through the centre of each stand. At each point we placed a stick (4 mm in diameter) and counted the number of contacts each species made with the stick. In addition, fresh foliage material from 4 different plant species, *Vaccinium myrtillus*, *Picea abies*, *Deschampsia flexuosa* and *Pleurozium scheberi* were also collected along the transects. These four species are common and represent four different groups of plants, i.e., dwarf shrubs, trees, grasses and mosses. For *Vaccinium myrtillus*, *Deschampsia flexuosa*, and *Pleurozium scheberi* fresh foliage material (leaves) were collected from seven random places along each transect while current year shoots from *Picea abies* were gathered from five different trees on or close to the transects. The material was immediately dried in paper bags in room temperature and then dried at 40 C° for 48 h in the lab. The material was then milled and analysed for total N and C concentrations (g/g dry mass) using a Isotope ratio mass spectrometer (DeltaV,Thermo Fisher Scientific, Bremen, Germany) and an Elemental analyser (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). Three samples of *Vaccinium myrtillus* were not included in the final analysis due to processing errors. Before statistical analyses, replicate samples from the same stands and species were pooled to obtain one value of foliar N content per stand and species.

2.5. Soil C and N

The soil C and N content (g g^{-1} dry mass) was sampled in each stand between the 15–18 of June 2021 at seven regular intervals along the same transects used to sample the ground vegetation. The organic horizon was sampled with a cylindrical (diameter 10 cm) soil corer, and the top 10 and 20 cm layers of the mineral soil was collected with a

Table 2

The means (±1 SE, N=7) for total soil N mineralization rates (NH4-N and NO3-N mg g−1 DW soil), total capture of N on ion capsules (NH4-N and NO3-N), tree diameter (cm) at breast height (DBH), and tree height (m), for each treatment. Results for p-values are based on a mixed-effects model ANOVA with treatment used as fixed factor and pre-commercial thinning as a random effects factor.

Treatment	Total mineralization *(N mg g^{-1} DW soil)*	Total soil mobile N *(N mg capsule^{-1})*	DBH *(cm)*	Tree height *(m)*
C	0.188 ± 0.037	0.109 ± 0.009	5.11 ± 0.592	4.41 ± 0.362
N1	0.170 ± 0.030	0.111 ± 0.008	5.71 ± 0.320	5.30 ± 0.259
N2	0.220 ± 0.060	0.133 ± 0.015	5.18 ± 0.511	5.57 ± 0.370
p-value	0.747	0.356	0.386	0.095

metal core sampler (diameter 1.59 cm). The material was put in paper bags and after transport to the lab sieved (2 mm mesh) and then dried at 70 C° for at least 36 h, then stored in room temperature awaiting analyses. The samples where later milled, and total C and N concentration analysed using an Isotope ratio mass spectrometer (DeltaV,Thermo Fisher Scientific, Bremen, Germany) and an Elemental analyser (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). Before statistical analysis, replicate samples of C and N were pooled to obtain one value of concentration per element and stand. We upscaled C and N stocks only for the soil organic layer because many previous studies have shown that mineral soil C and N stocks are unresponsive to N fertilization (Blasko et al., 2022; Forsmark et al., 2020; Maaroufi et al., 2015; Xu et al., 2021). Carbon and N stocks in the organic layer were thus calculated by multiplying the C and N concentrations with the combined dry weight of the pooled samples from each stand, and then upscaled to Mg ha^{-1} using the combined cross-sectional area of the subsamples in each stand. For mineral soils we only analysed C:N ratios.

2.6. Experimental design and statistical analysis

For all statistical analyses the experiment is regarded as a completely randomized design, with each stand serving as the unit of replication. To test for difference in total net mineralization rates (ammonification plus nitrification, N mg g^{-1} DW soil), total soil exchangeable N (NH_4-N + NO_3-N, mg per ion capsule), tree diameter (cm), tree height (m), vegetation C and N status (g g^{-1} dry mass), soil C/N concentrations (g g^{-1} dry mass), and soil C and N stock (Mg/ha) analyses with a linear mixed-effects model ANOVA were performed. Using the fertilization treatments as a fixed factor and the pre-commercial thinning as a random effect accounted for any variation this activity may have caused. If the analysis of variance showed any significant (α=0.05) main effects from the fertilization treatments, Tukey's post hoc test for pairwise comparison was used to further the analysis. Response variables were checked for normality and homoscedasticity with the aid of residual plots, no data transformations were necessary. The analysis of variance (ANOVA) was preformed using the R. lme4-package (Bates et al., 2015).

To describe the differences in ground vegetation community structure between the different fertilization regiments, we used non-metric multidimensional scaling based on Bray-Curtis dissimilarities, using the R-vegan-package (Oksanen et al., 2022) with k=3 and no data transformations. The NMDS was followed by a PERMANOVA based on 9999 permutations using the fertilization treatments as factors. R-studio (version 1.3.1093) software was used for all statistical analyses (R Core Team, 2020).

For all statistical tests we used a terminology suggested in Muff et al., (2022), where different ranges of p-values are reported on a continuum from "little or no evidence" to "very strong evidence". A p-value of 0.0001–0.001 subsequently was interpreted as very strong evidence, a value of 0.001–0.01 as strong evidence, 0.01–0.05 as moderate evidence, 0.05–0.1 as weak evidence, and p-values > 0.1 as no evidence.

3. Results

3.1. Soil nitrogen and forest growth

Our results showed no evidence of any significant legacy effect from the previous forest fertilization on the soil N mineralization rates or mobile N. However, the trees in stands exposed to fertilization twice (N2) during the preceding stand rotation (150 kg N ha $^{-1}$ in 1977 and 1985) were on average 20 % higher than trees in the control stands, suggesting weak evidence of a legacy effect of past N fertilization on tree growth > 35 years after the last fertilization event *($p = 0.095$*; Table 2).

3.2. Ground vegetation

Our results showed no evidence, with one exception of weak evidence, that the ground vegetation was still affected by the previous fertilization(s). The NMDS showed considerable species community overlap between treatments (Fig. 1a), and a related PERMANOVA also provided no evidence ($p=0.636$) that vegetation composition differed between the fertilizer treatments. A complete species inventory list is provided in supplementary Table 1. We did, however, find weak evidence of a difference in foliar N values in dwarf shrubs ($p = 0.09$), but no evidence that the foliar N values in the three other functional groups of plants differed, including trees ($p = 0.32$), grasses ($p = 0.42$), and mosses ($p = 0.55$), (Fig. 1b).

3.3. Soil metrics

We found strong evidence ($p=0.008$) that soil C stocks differed in the organic layer, with lower C stock in the N1 treatment compared to the control and N2-treatment (Fig. 2a). However, no evidence of this effect was found comparing the control and N2-treatment. We also found strong evidence ($p=0.006$) that soil N stocks differed in the organic layer (Fig. 2b). With lower N stock in the N1 treatment compared to the control and higher N stock in the N2 treatment compared to both the N1 treatment and the control stands. Comparison of the soils' C/N-ratios, which was measured at three different depths (organic, 0–10 cm, and 10–20 cm depth; Fig. 2c), indicated no evidence of any effect between treatments.

4. Discussion

The purpose of this study was to assess legacy effects from forest fertilization in rotational forestry. Particularly the focus was to determine whether fertilizer induced effects on some key variables relating to forests productivity and understory species composition persisted following harvest of the fertilized forest stands, i.e. c. 23 years into the new forest rotation. Our data together with the existence of older measurements has given us the opportunity to follow the effects from the original fertilization event in 1977 and 1985 through the forest rotation boundary, and into the canopy closure of the new stand. Previous studies in the same study system had revealed that legacy effects from forest fertilization were present c. 10 years into the new stand rotation.

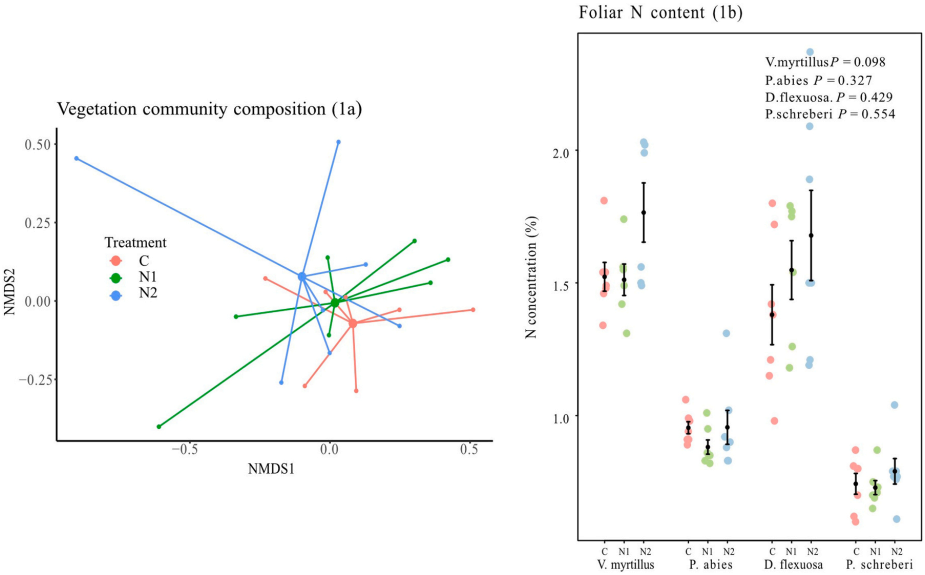

Fig. 1. Left (graph 1a.): Visualization of the NMDS ordination for the ground vegetation community composition among the different treatments. Each coloured "spider" represents a treatment (red = control, green = single nitrogen application, and blue = two nitrogen applications). Data were analysed using PERMANOVA based on 9999 permutations, where no evidence of any effect were present from the fertilization treatments (*p=0.636*). Right *(graph 1b.)* Foliar N content in four different functional groups of plants, bars represent the mean (±1 SE, N=7) for each treatment.

Specifically, the ground vegetation species composition differed due to the fertilization (Strengbom and Nordin, 2008 and 2012), and trees in the fertilized stands had grown higher than those in stands not fertilized (From et al. 2015). Here we revisited the same forest stands > 35 years after the last application of fertilizer, and well into the next forest generation as the trees had become c. 23 years old. We measured the same variables as in previous studies, as well as the carbon and nitrogen stock in the organic soil horizon, which was not measured previously. The combined body of data suggests that subsequent legacy effects from standard forest fertilization both have the potential to last much longer than originally assumed, and also confirms that legacy can persist (> 10 years), but that they appear to diminish over time.

In contrast to our first hypothesis, we detected no differences in mineralization rate between fertilized stands and non-fertilized stands (Table 1). This lack of difference diverges from measurements made earlier in the stand rotation, where mineralization was nearly four times higher in the N2 treatment compared to the control (From et al., 2015). Other long-term studies have also shown a significant decrease in gross N mineralization rate over time, but under much higher N application rates compared to our experiment (Högberg et al., 2014).

In partial support of our second hypothesis, we found weak evidence, but a relatively large effect size (20 % increase), of a legacy effect from N addition on tree height between the control and N2 stands. In the previous study using the same sites, N fertilization showed a similar average effect size of ca. 20 % in tree height between the control and N2-stands, but as the variation among sites then was much smaller, the effect of past fertilization also ended up as statistically significant ($p = 0.026$; From et al., 2015). However, in accordance with the earlier study there was no effect on tree diameter (DBH). Few other studies have evaluated legacy effects of past N addition using N doses that are comparable to the ones used in operational forest fertilization, and to our knowledge, no other study in the northern boreal zone has evaluated the growth response of trees this far in time from the fertilization event. Pettersson and Högbom, (2004) reported an overall (although non-significant) tendency of increased residual tree growth from standard fertilization application rates (150 kg N ha^{-1}), 14–28 years after the last fertilization event but within the same forest generation. Other studies have in contrast reported decreased growth approximately 20 years after cessation of N fertilization compared to controls (Högberg et al., 2014, 2006), however it is worth noting that these results were based on a more intensive fertilization regimen (1350–2160 kg N ha^{-1}) than the standard application rates used in this study. While many factors may help explain the persistent effect of the N2-treatment on growth, and increased foliar N content in dwarf shrubs present, one such factor could be that fertilization offsets the immobilization of N that is often caused by the mycelial biomass and necromass production in N poor soils (Näsholm et al., 2013). This phenomenon has the potential to open up the N cycle to plants (Högberg et al., 2017) and could therefore serve as an explanation for both the still measurable tree growth and the absence of detectable N relative to the control stands in many other measurements. There is however also a possibility that the "excess" N is lost from the system or present in an ecosystem compartment we have not measured.

In contrast to our third hypothesis, we found no difference in ground vegetation community structure or foliar N content, with the exception of weak evidence for a difference in foliar N content in *Vaccinium myrtillus*. Our NMDS showed a considerable overlap in the species composition of the ground vegetation between the treatments (Fig. 1a), and the following PERMANOVA indicated no significant effect. This result contrasts Strengbom and Nordin, (2008) who found a clear distinction in ground vegetation community composition between fertilized and non-fertilized stands in the same study system, as they noted a higher abundance of more N-demanding species on fertilized stands nine years after clear-felling. The following analysis of foliar N content in four functional groups of plants i.e., dwarf shrubs, trees, grasses, and mosses indicated a trend where stands exposed to fertilization showed a higher N content in plant foliage compared to the plants present in the control stands for all functional groups except trees. However, we found no

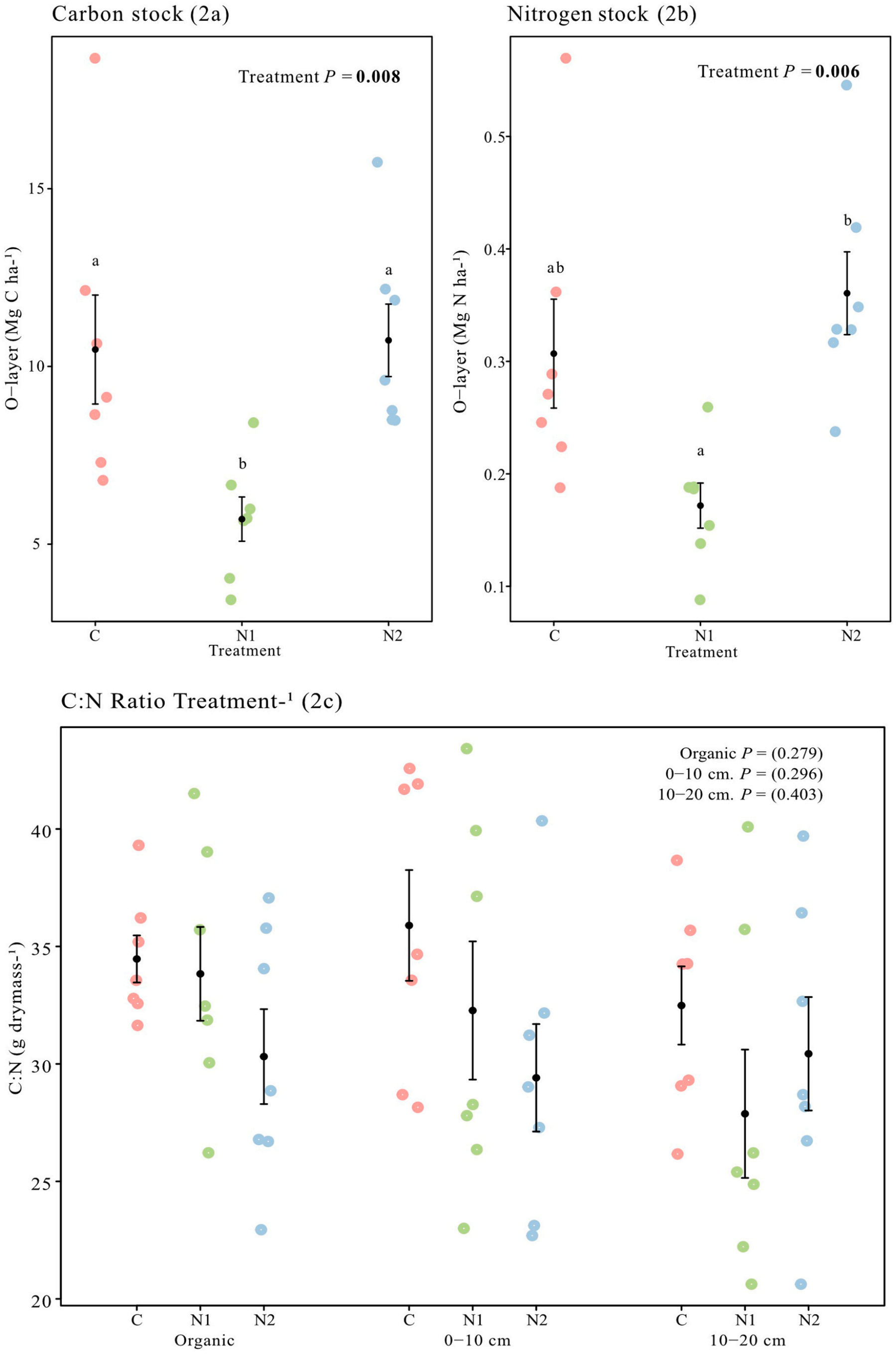

Fig. 2. The left *(graph 2a.)* shows the C stock within the organic layer. The right, *(graph 2b.)* shows the N stock within the organic layer. The bottom figure *(graph 2c)* shows C/N-ratios in three different soil layers for each treatment (organic, 0–10 cm mineral soil depth and 10–20 cm mineral soil depth. Bars represent the different means (±1 SE, N=7).

significant differences, with the exception of weak tendency for a higher foliar N content of the dwarf shrubs. This result differs compared to the analysis made on plant material collected in 2007 (approximately 10 years after clear-felling and 22 and/or 30 years after last fertilization event) where differences in foliar content between treatments could be detected in gathered plant material from all functional groups except mosses (Strengbom and Nordin, 2008). While there is a substantial body of evidence indicating that N enrichment effects terrestrial plant diversity (Bobbink et al., 2010; Sullivan and Sullivan, 2018), long term legacy measurements such as we provide are very rare. A result similar to our study was found by Jacobson, Högbom and Ring, (2020), who reported no effects of fertilizers on ground vegetation diversity 10–34 years after application, although significant differences in ground cover were detected. However their study did not measure legacy effects between subsequent forest rotations, such as we did in our study. The disappearance of a measurable legacy effect could also be due to the ongoing canopy closure. Even if N is the overall growth-limiting nutrient, the decrease in light availability might make the aboveground competition more important than any persisting legacy effect stemming from the N fertilization treatments (Strengbom et al., 2004).

For our last hypothesis, we expected that fertilization would have a legacy effect on soil C and N stocks, with greater stocks occurring in previously fertilized stands. We unexpectedly found evidence of both lower C and N stocks in the organic horizon present in N1 stands (fertilized in 1985) compared to the control and N2-stands, but no difference between N2 stands (fertilized in 1977 and 1985) and the controls for C stocks. When measuring N stocks however the N2-stands showed higher stocks than both the control and N1 treatments, in line with our hypothesis. The reason for this variation in results is not clear but Hasselquist et al., (2012) suggested that responses in boreal forest to added N is not always linear, and that some initial level of N addition could stimulate microbial activity, whereas higher levels may suppress it. Comparing instead the C/N-ratios in three different soil layers (Fig. 2c) resulted in a similar pattern as the foliar N content with lower C/N in previously fertilized stands for all but the deepest soil layer, but despite these apparent trends, no evidence of significant differences was detected. While the soil C and N stock variables do not have an analogous set of older measurements present on the same stands to which we can compare, we note that other studies have shown that anthropogenic N enrichment can increase soil C stocks (Forsmark et al., 2021; Jörgensen et al., 2022; Mäkipää, 1995; Ring et al., 2011) and that higher N input rates appear to increase this effect (Forsmark et al., 2021, 2020; Ring et al., 2011). Studies from more southern latitudes that do report legacy effects between forest rotations also suggests that the forest floor and ground vegetation could act as a nutrient sink for added fertilizer, realising nutrients in subsequent forest rotation and thus increasing forest growth (Subedi et al., 2014). Destruction of the soil organic material instead appear to leave a legacy effect of declining productivity (O'Hehir and Nambiar, 2010). The same type of nutrient sink have been shown to occur in boreal areas (Gundale et al., 2014), and seems to subsists between forest rotations, as illustrated by the slightly higher N stock in the O-horizon in N2 stands present in our experiment. Our study thus addresses a key knowledge gap regarding N fertilization and soil C in northern boreal forests, where studies analysing long-term legacy effects from standard fertilizer application rates are very rare.

5. Conclusion

Based on the results in this study, and in comparison to previous inventories in the same study system (Strengbom and Nordin, 2008, 2012; From, Strengbom and Nordin, 2015), our results indicate that standard N fertilization application rates in boreal forests have the potential to persist much longer than previously reported (i.e., 10 years), but that these effects clearly diminish through time. Sponseller et al., (2016) noted that a disconnect remains between basic research focused on understanding N dynamics and balances in boreal forests, and the applied knowledge needed to sustainably manage these ecosystems. Our study contributes to this important knowledge gap regarding the timespans over which N fertilization affects boreal forests and suggests that care should be taken when employing N fertilization, given that effects appear to be longer lasting than previously thought. Further research is needed to fully understand what mechanisms are responsible for retention of fertilizer N across stand rotations, and how these vary across forest types (Blasko et al., 2022). Such additional knowledge could be used to avoid applying fertilizers in areas at risk of prolonged legacy effects, and thereby mitigate unwanted long-term effects on the boreal forest ecosystem, while at the same time maintaining the benefits of forest fertilization for increasing biomass growth.

Funding

This work was supported by: Stora Enso AB and Knut and Alice Wallenberg foundation [no.2018.0259].

CRediT authorship contribution statement

Joachim Strengbom: Writing – review & editing, Resources, Methodology, Data curation, Conceptualization. **Marcus Larsson:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Annika Nordin:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Data curation, Conceptualization. **Michael J. Gundale:** Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Marcus Larsson reports financial support was provided by Stora Enso AB. Annika Nordin reports a relationship with Stora Enso AB that includes: employment. Co-author reports a previous relationship (2016–2020) with Sveaskog AB that included: board membership (A. N.).

Co-author declare no conflicts of interest, and do not have any commercial affiliations (M.J.G. and J.S.).

Data Availability

Data will be made available on request.

Acknowledgments

M.L. acknowledge Adam Björklund and Adreas Edholm for making the field measurements and lab-work possible, along with Jenny Ekman for making the lab-analysis. A.N. acknowledge Stora Enso AB for permitting her leave of absence from her current position with the company to take part in the reported research and supervision. We also want to acknowledge past and current landowners for letting us conduct the study on their land.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121967.

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Forest Ecology and Management 596 (2025) 123060

Contents lists available at ScienceDirect

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

Boreal tree species selection enhances forest carbon stocks through above- rather than below-ground changes

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ARTICLE INFO

Keywords:
Boreal tree species
Soil organic carbon
Forest growth
Boreal forest
Litter input
Root production

ABSTRACT

Forest management has the potential to impact the net forest carbon (C) balance, and a better understanding of how tree species influence soil C provides a potential tool to promote higher C uptake and storage in forests. In this study, we utilized two common garden experiments located in northern and central Sweden to compare soil organic C stocks associated with six different boreal tree species (*Betula pendula*, *Larix sp.*, *Picea abies*, *Picea glauca*, *Pinus contorta* and *Pinus sylvestris*), approximately 30 years after planting. We measured both above- and below-ground C inputs and C outputs via decomposition and analyzed how these factors influenced soil C stocks. Our results showed that the vertical distribution of SOC differed between the species, and furthermore, many of the SOC input and output processes measured were species-dependent. Despite this, we found no differences in total belowground soil C stock between the species. The aboveground biomass C stocks, in contrast, were highly species-specific, with the rank order of species differing between the two sites. As such, our study indicates that tree species choice may serve as a tool to promote ecosystem C stocks, and in turn enhance the climate change mitigation potential of forests.

1. Introduction

Boreal forests store about one third of the global forest carbon (C) pool, and the majority of this C stock can be found in the soil (Pan et al., 2011; Skogsdata, 2017). Forest management has the potential to impact the net forest C balance (the sum of all C inputs and outputs), and a better understanding of how tree species selection influences soil organic carbon (SOC) dynamics could provide yet another tool for enhancing boreal forests' climate change mitigation potential. However, despite decades of research (Mayer et al., 2020; Prescott and Vesterdal, 2013), the mechanism by which different tree species accumulate soil organic carbon (SOC) remains difficult to disentangle from site-specific factors (Mayer et al., 2020). Interactions between tree species and other factors such as soil properties, soil biota, and local climate can all serve as influential controls on SOC (Augusto and Boča, 2022; Prescott and Vesterdal, 2013; Verstraeten et al., 2018).

It is recognized that the variability in the quality and quantity of above-ground litter inputs of different species can alter soil processes, which in turn can increase or decrease soil C (Xu et al., 2013). However, many studies have found little or no difference in aboveground litterfall C between different tree species when compared in common garden or paired stand studies (Vesterdal et al., 2013). Some evidence suggests that conifers and deciduous species can have different effects on the vertical distribution of soil C and organic horizon C stocks, which may be due to differences in litterfall C inputs and rooting activity (Hansson et al., 2013a; Vesterdal et al., 2013). Deciduous trees, have been found to promote SOC in the mineral soil; however, in boreal forests effects are often found to be small and inconsistent (Gundale et al., 2024; Prescott and Vesterdal, 2013). Interactions with environmental factors further complicate these relationships, and the quantities of above ground litter inputs are also shown to be dependent on site fertility and associated tree biomass production (Hansen et al., 2009; Matala et al., 2008). In contrast, much less is known about belowground litter C inputs, in large part due to the difficulty of quantifying these fluxes. Fine root turnover rates are likely affected by local climate and site factors, and appear to increase with increasing mean annual temperature and precipitation (Yuan and Chen, 2010), and differs among tree species (Hansson et al., 2013b). Evidence also suggests that fine root turnover may be a similar or larger C input to soil than aboveground litter (Gundale et al., 2024), with this input being concentrated mainly in the mineral soil (Kleja

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https://doi.org/10.1016/j.foreco.2025.123060
Received 30 April 2025; Received in revised form 30 July 2025; Accepted 1 August 2025

et al., 2008). Other studies have found higher root production by broadleaf species than by conifers (Oostra et al., 2006; Withington et al., 2006), which may also contribute to differences in the vertical distribution of soil C between species.

Different tree species also have different resource acquisition strategies, associated with their functional traits, referred to as the "plant economics spectrum" (Reich et al., 1997). Plant traits can be defined on a spectrum from "acquisitive" to "conservative," indicating high resource capture that supports rapid growth (e.g. high specific leaf area and/or high leaf nutrient content) or resource conservation strategies that correspond with slow growth rates (e.g. high levels of structural defence, low specific leaf area and/or high lignin content), respectively (Díaz et al., 2016). The former traits are typically found in early-successional tree species such as *Betula pendula* or *Pinus sylvestris,* whereas the latter are generally found in late-successional species, such as *Picea abies*. Trait coordination is also speculated to be analogous across the whole plant, indicating that both above and belowground litter inputs would exhibit similar "qualities" (Spitzer et al., 2025; Weigelt et al., 2021). These trade-offs in "acquisitive" or "conservative" plant function should translate into different rates of decomposition, where increasing rates often are associated with higher litter nitrogen (N) content, and decreasing rates instead generally occur under higher litter lignin content (Gundale et al., 2024; Liski et al., 2003; Prescott, 2010; Zhang et al., 2008). However the "early" stages of quality-dependent decay may not necessarily predict soil organic C accumulation, and a "maximum decomposition limit" has been suggested (Berg and Ekbohm, 1993), which corresponds to the point when the litter "becomes" humus and enters its second phase of decomposition (Berg et al., 1996; Prescott et al., 2000). Long term results indicate that the decay rate of different types of litter (and litter from different species) may converge at this point (Prescott et al., 2004), meaning trait differences between species might not matter as much as quantity of litter input, or local environmental conditions.

In this study, we utilized two common garden experiments located in northern and central Sweden to compare soil organic C stocks associated with six different boreal tree species, approximately 30 years after planting. We further explored the role of above and belowground C inputs, and C outputs via decomposition, and how these factors influenced soil C stocks. We tested the following hypotheses:

1. Tree species will differ in their soil C stocks and soil C vertical distribution (organic versus mineral horizons).
2. The species differences in soil C stocks will be linked to their differences in litter production and decomposition rates.
3. Species-specific growth responses to local and regional climate variability will serve as an important control on soil C stocks.

2. Materials and methods

2.1. Site description and sampling design

Two common garden experiments were utilized in this study, one located in northern Sweden and one located in central Sweden. The northern site, Svartberget (64°15′N 19°47′E), was established in 1992 and consisted of 10 tree species, divided over 30 plots and 3 blocks. The central site, Garpenberg (60°18′N 16°17′E), was established in 1995 and consisted of 8 tree species, divided over 20 plots and 3 blocks. All species present on both sites are common in the boreal region, including four species native to Sweden, *Betula pendula, Pinus sylvestris, Larix sukaczewii* and *Picea abies.* The remaining species are considered exotic species in Sweden, (*Abies lasiocarpa, Abies sibirica, Picea glauca, Picea mariana, Pinus banksiana, Pinus contorta* and *Pseudotsuga menziesii*). There were three replicate plots for each species at Svartberget, (i.e., a complete block design), whereas at Garpenberg *Betula pendula* and *Larix sp.* were only present in two blocks (i.e., an incomplete block design; Fig. 1). At Garpenberg there were also two species of *Larix* present, one plot of *Larix sibirica* (*sukaczewii)* and two plots of *Larix marschlinsii.* Due to the low replication of each of these species at this site, we treat *Larix* at the genus level, i.e., *Larix* sp. to enable statistical analysis. In total 6 species (*Betula pendula, Larix* sp.*, Picea abies, Picea glauca, Pinus contorta and Pinus sylvestris*) were common between the two common garden experiments. At establishment all plots were scarified and planted using a

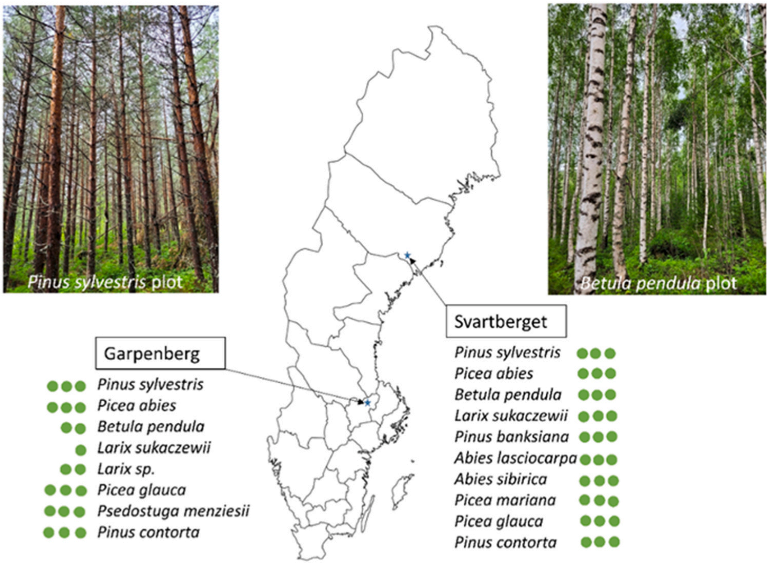

Fig. 1. Map showing the locations of the two field sites in Sweden. Tree species monocultures present at each site are listed and the number of green dots indicate the number of replicate plots of each species found at the site. Photos are of one replicate plot of two species, source: (Spitzer et al., 2025).

seedling spacing of 2 m, resulting in 289 seedlings per plot.

Both sites had a similar site index (SI), defined as the average height that the dominant trees of a particular species will attain at a specific reference age. Svartberget had an SI value of 22 (H100) and Garpenberg had an SI value of 23 (H100). The average growing season temperature during 2018–2022 was 13.3°C at Svartberget and 15.9°C at Garpenberg (Swedish Meteorological and Hydrological Institute, "SMHI", 2025). Both sites at the time of establishment were classified as spruce forest of bilberry type (Påhlsson, 1995), however with mixed occurrences of *Pinus sylvestris*. The soil is a relatively shallow podzol developed on glacial till (moraine). For more information about the site properties, see Table 1.

2.2. Tree growth and above ground biomass

Forest inventory at both sites was performed during 2022 by randomly selecting 20 trees in each plot and measuring tree height and diameter. Stems per hectare were calculated by total count of trees in each plot and scaling this value to the hectare level. The aboveground biomass was then calculated using the data from the forest inventory and the appropriate biomass equation. For tree species native to Sweden, except *Larix sp.*, we used Marklund's biomass functions to convert stem volume to biomass (Marklund, 1988). For *Larix sp.*, equation 136 in Zianis et al., (2005) was utilized. For all other tree species, the biomass equation from Jenkins et al., (2003) was utilized, with different constants used for each species (supplemental 2). Only functions constructed for total aboveground biomass were considered and selected for the calculations. Any ground vegetation present in the measured plots was not inventoried due to its very minor contribution to the aboveground C stock, and therefore was not included in our calculations.

2.3. Litter fall

Between August 2021 and August 2022 aboveground litter was collected using circular (48 cm in diameter) litter traps with a mesh bottom. Three traps per plot were installed and emptied twice: once after snowmelt and again in late summer. The traps were placed ≥ 1 m from the nearest tree, at a maximum distance of 10 m from the plot center, and at least 10 m from the nearest adjacent trap. This approach was used to effectively sample the center of each plot, while avoiding edge effects and litter inputs from adjacent plots. The collected litter was pooled at the plot level, transported to the lab, and dried at 70° C for at least 48 h. The litter was then sorted into leaves or other detritus (e.g. twigs), saving only leaves or needles from the tree species native to the plot. The samples were then weighed, and a subsample was milled and analyzed for total N and C concentrations (g/g dry mass) using an isotope ratio mass spectrometer (DeltaV,Thermo Fisher Scientific, Bremen, Germany) and an elemental analyzer (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). After analysis, the C and N concentrations were multiplied with the combined dry weight of the pooled samples from each plot, and then upscaled to Mg ha^{-1} using the combined area of the litter traps used in each plot. Coarse and woody debris (sticks, branches, bark cones etc.,) from each species was collected between 2022 and 2023. A 2 × 2 m square in the center of each plot was cleared of any debris, then marked and left for one year. After this period, any new material entering the plot was collected, dried at 70 °C for 48 h, and then weighed. The weight of the samples was then upscaled to Mg ha^{-1} using the plot area. For upscaling, the C content of the coarse and woody debris biomass was assumed to be 50 %.

Table 1
Site description of the two common garden experiments utilized in this study. The soil properties are mean values calculated across all plots.

Site properties	Svartberget	Garpenberg
Site index (H100)	22	23
Elevation a.s.l.	300	195
Slope (%)	> 15	< 5
GDD, (base +5°C) *	792	950
Moisture regime	Mesic	Mesic
number of plots	30	20
Size of plots (m^2)	1156	1156
Seedling spacing (m) *	2 × 2	2 × 2
Trees * plot^{-1}*	289	289
Soil type	Podzol	Podzol
Parent material	Moraine	Moraine
Soil texture	Sandy silt	Coarse silt
pH (Humus)	4.25	3.98
pH (Mineral soil 0–20 cm)	5.30	4.78
C/N (Humus)	33.8	25.6
C/N (Mineral soil 0–20 cm)	30.5	26.7

Note: *Growing degree days (GDD), seedling spacing and number of trees per plot are given at the time of site establishment.

2.4. Fine root production

To measure fine root production, we used ingrowth cores, a method extensively used in ecosystem studies (Brunner et al., 2013), which we adapted from (Forsmark et al., 2021). The cores were made from nylon mesh (Sintab Product, AB Sweden) with 2 mm mesh openings and in early summer 2021, fine-root ingrowth cores (5 cm wide and 20 cm long) were installed vertically at the centre of each of the four sides in every plot, at a minimum distance of 3 m from the plot edge and at least 70 cm away from the closest tree. Each core was filled with sieved (2 mm) mineral soil from a pit at the center of the same plot where it was installed (which was packed in the cylinder to approximately the same bulk density as the surrounding soil), and then buried within the mineral soil to a depth of 20 cm. The removed organic layer was placed back on top of the cylinder which was then left to incubate. Two years after installation (with an incubation time of 24 months), the root-ingrowth cores were collected. The incubation time of 24 months was chosen to allow for two full growing seasons, which both minimized the initial disturbance effect and root biomass turnover during the measurement period (Brunner et al., 2013; Finér et al., 2011). After collection, the root-ingrowth cores were transported to the lab, the soil was removed, and the root biomass from individual ingrowth cores was pooled at the plot level. The pooled root biomass was then dried at 70°C for at least 48 h and sorted, removing everything except fine roots from the tree species native to each individual plot. The remaining biomass was weighed and then upscaled to Mg ha^{-1} y^{-1} using the combined volume of the root ingrowth cores installed in each plot. The C content of the fine root biomass was assumed to be 50 % (Nilsson et al., 2008; Spitzer et al., 2025), and the values were adjusted for stoniness of each plot (described below).

2.5. Decomposition rate

To measure decomposition rate for each tree species, we used litter bags made from a nylon mesh with 100 µm openings (Sintab Product, AB Sweden). The mesh size was chosen to allow for microbial processes and fungal ingrowth, but to exclude soil macrofauna. In total 600 bags were used in the experiment, with half of them filled with tree species litter gathered from litter traps the year before, and half filled with material from the organic layer (i.e. "humus-layer"). At the beginning of autumn 2022 all bags were filled with 3 g of dry mass and were then gently put back in the field just beneath the organic layer, at the intersection with the mineral soil, and in the same plot as their respective litter origin. Consequently, we placed 6 litter bags and 6 humus bags in each plot. A year later all bags were collected and brought back to the lab, dried in 70° C for at least 48 h, and weighed to allow calculation of mass loss. Values from individual bags were pooled at the plot level before statistical analysis.

2.6. Soil sampling

In the summer of 2021, the organic horizon and mineral soil were systematically sampled in a grid pattern at 10 locations in each plot (i.e. sub-samples). For the organic horizon we used a PVC tube (Ø10 cm) fitted with a serrated blade and the top 0–10 and 10–20 cm layers of the mineral soil were collected with a metal core sampler (diameter 1.59 cm). Sampling was limited to 20 cm depth to avoid inconsistency caused by reaching the parent material in some locations across both sites. The collected material was pooled at the plot level, sieved (2 mm mesh) and then dried at 70 C° for at least 48 h, and later stored at room temperature until analysis. The samples were later milled, and total C and N concentrations were analyzed using an isotope ratio mass spectrometer (DeltaV,Thermo Fisher Scientific, Bremen, Germany) and an elemental analyzer (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). Soil pH was measured in all plots using dried samples from all soil layers by mixing 10 ml of soil and 10 ml of deionized water.

Stone and boulder content (SB) at both sites was estimated using the rod penetration method, where an iron rod with a diameter of 10 mm was driven through the soil until it reached a stone or boulder (Viro, P.J., 1952). This was done at 60 points in a grid pattern at each site. The mean penetration depth was calculated as volumetric content of stones and boulders in percent using Viro (1952) modified by Stendahl et al., (2009), using the regression equation $SB = 82.5 - 2.75*Si$, where Si is the mean penetration depth of the 60 sample points.

Carbon stocks in the organic layer were calculated by multiplying the C concentration with the combined dry weight of the pooled samples from each plot, and then upscaled to Mg ha^{-1} using the combined cross-sectional area of the subsamples in each plot. The C stocks in mineral soil were calculated using bulk density functions, equation 31 from Nilsson and Lundin, (2006). The C concentrations obtained in the previous analysis were thus multiplied with the value of the calculated bulk density and the total volume of each mineral soil layer, yielding an upscaled value of Mg ha^{-1} for all plots.

2.7. Calculations and statistical analyses

All statistical analyses were carried out using R 4.2.1 (R Core Team, 2024) and we considered individual plots as the unit of replication. While we gathered data from all 50 plots present in our experiment, our analysis only focused on the six tree species present on both sites (*Betula pendula, Larix sp., Picea abies, Picea glauca, Pinus contorta and Pinus sylvestris*). This resulted in 35 plots in total divided over 2 sites and 6 blocks (3 blocks per site, except for *Betula pendula* and *Larix sp.* which were only present in 2 blocks at Garpenberg, *Larix sp.* was however instead present two times within one block due to different planted species, Fig. 1). Information including all species present at both sites can be found in appendix Fig. 1. For all analyses, except when testing tree species and site interaction, we used a mixed model (Bates et al., 2003) ANOVA type III with fixed effect of tree species, and a random effect of site. Our somewhat limited dataset prohibited more complex mixed models where the blocking factor was nested under site, however, model testing based on the AIC criterion showed that models with random effects of site generally outperformed models with a random effect of block. When testing tree species and site interaction block was instead included as a random factor.

We first analysed only the tree species effect on ecosystem C, tree biomass and soil C (in all soil layers), after which we tested each of our measured variables (above ground biomass, root growth, litterfall, coarse and woody debris, decomposition rate in litter and humus and soil pH) against tree species to ascertain which of these were species dependent. Finally, all variables were tested together (without interactions) against each soil layer and total soil C. If any variable shown to be species dependent in the preceding statistical test also showed evidence of effecting soil C, this was taken as confirmation that tree species were able to affect soil C stock in our experiment. To avoid problems with multicollinearity, tree species was excluded from our statistical model in the final step due to being used in the previous model, along with tree biomass, since the variable was highly correlated with other model variables (variance inflation factor ~ 3 or higher). Lastly, we used a linear model to test tree species and site interaction against ecosystem C, tree biomass and soil C to ascertain if different tree species were affecting C stock differently depending on environmental factors. Post hoc analysis, when performed, was based on estimated marginal means and Tukey's adjustment (Lenth et al., 2025). Model responses were checked for normality and homoscedasticity with the aid of residual plots, which resulted in a log transformation (natural logarithm) of all variables, except soil pH.

For all statistical tests, we used the terminology suggested in Muff et al., (2022), where different ranges of p-values are reported on a continuum from "little or no evidence" to "very strong evidence". A p-value of 0.0001–0.001 subsequently was interpreted as very strong evidence, a value of 0.001–0.01 as strong evidence, 0.01–0.05 as moderate evidence, 0.05–0.1 as weak evidence, and p-values > 0.1 as no evidence.

3. Results

Our results show that the largest average SOC stock across the two sites was found for *Pinus contorta,* and while *Pinus contorta* also ranked among the top species in measured above ground tree biomass, the highest above ground C stock was found in *Larix* sp., which also consequently ranked the highest in total ecosystem C stock (Fig. 2). When testing total ecosystem C and above ground biomass C between the tree species, we found very strong evidence for differences ($p < 0.001$). However, we found no evidence of a total SOC stock difference between the species (Fig. 2). The analysis of tree species effects on soil C distribution however showed strong evidence ($p = 0.005$) of a difference in SOC between species within the deepest mineral soil layer (10–20 cm; Table 2a). The species with the highest SOC stock in this mineral soil layer, *Pinus contorta*, had c. 40 % more C than the species with the lowest C stock in this soil layer, *Larix* sp. (Fig. 2). For the organic layer or the upper mineral soil layer (0 – 10 cm) there was no significant effect of tree species on the C stock (Fig. 2, Table 2).

Our analysis showed very strong evidence ($p < 0.001$) for an effect of tree species on tree biomass, amount of coarse woody debris, amount of litterfall, rate of litter mass loss and rate of root growth (Table 2b). We found no significant tree species effect on humus mass loss and soil pH (Table 2b). The tree species differences between these variables did not in general translate into differences in soil C, except for the amount of litterfall, for which we found moderate evidence for an effect on C in the deepest layer of the mineral soil (Table 2c). For soil pH we found strong evidence for an effect on the overall soil C stock ($p < 0.001$), moderate evidence of an effect in the 0–10 cm mineral soil layer ($p = 0.028$) and strong evidence ($p = 0.003$) of an effect on the deepest 10–20 cm mineral soil layer (Table 2c).

We also tested the effect of site on forest ecosystem C stock, tree biomass and total soil C stock (Table 3). We found that the interaction between species and site showed very strong evidence ($p < 0.001$) for affecting tree biomass C. Furthermore, ecosystem C stock also displayed an interaction effect between species and site, the evidence was however weak ($p = 0.064$), indicating that the strong influence of the tree species on the ecosystem C stock is only weakly related to the site. In contrast, total soil C stock showed very strong evidence ($p < 0.001$) of being affected only by site.

The results also show that despite the fact that the two experimental sites were established at the same time, tree biomass for most species tended to be higher at the northern compared to the site in central Sweden. This was particularly noticeable for the broadleaved species, *Betula pendula*, and for *Picea abies* (Fig. 3). In contrast, SOC was generally lower in the northern site than in the central, which was also displayed by the strong evidence (< 0.001) for an effect of site on total soil C stock

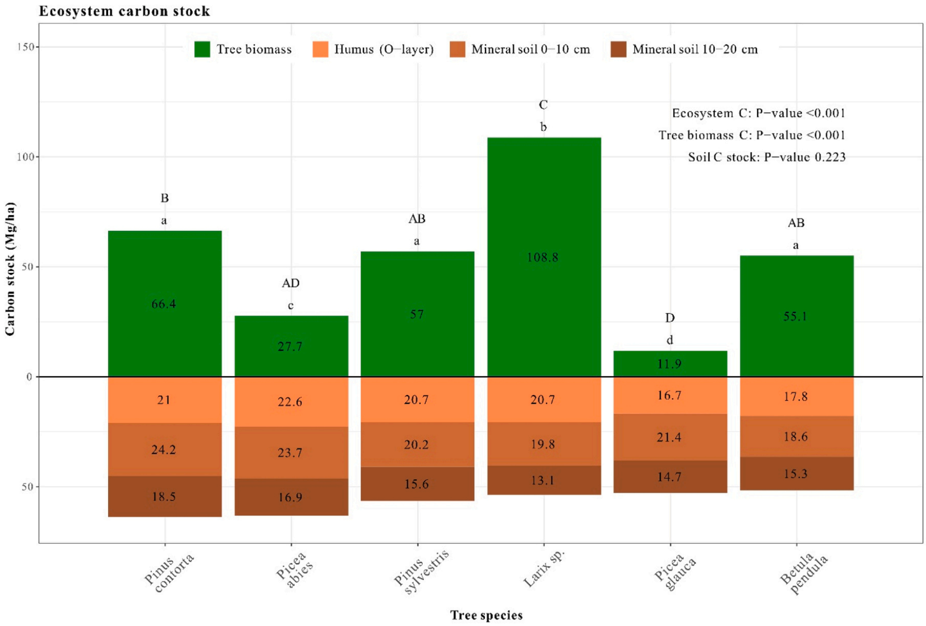

Fig. 2. The average amount of C stock in different ecosystem compartments for different tree species at both sites (n = 6 species^{-1}, except *Betula pendula* where n = 5). The species are organized in descending order, starting with the highest belowground C stock. Letters above or below bars indicate significant differences between species. Top capital letters = post hoc test of ecosystem C and bottom letters = post hoc test of tree biomass C. Additional information can be found in supplemental table 3.

with no significant interaction effect of species (Table 3).

4. Discussion

The purpose of this study was to assess whether tree species selection could serve as a management tool to increase below-ground SOC stocks. Further, we aimed to determine if some key variables related to soil C input and output could be used to explain eventual differences between the tree species in our experiment after approximately 30 years. Some previous studies have shown that while different tree species can affect SOC accumulation within different soil layers, the total C stock are not always affected (Mayer et al., 2020); and there is some evidence of differences in SOC distribution between conifer and broadleaves species (Mayer et al., 2020). Our results largely agree with these results and indicate that tree species can at least partially affect soil C distribution, as the SOC in the deepest mineral soil layer showed strong evidence ($p = 0.005$) of a species response (Table 2a). However, the differences in our study were not shown to be between conifers and broadleaves, but between *Pinus contorta* and *Larix* sp., which showed the highest and lowest C stock of all species within the deepest soil layer, respectively. Our analysis also indicated that belowground soil C stock is more dependent on site factors than tree species, as the total soil C stock showed very strong evidence ($p < 0.001$) of being site dependent (Table 3). In contrast, tree biomass, and in turn ecosystem C stocks, showed weak evidence ($p = 0.064$) for an interaction between tree species and site (Table 3).

For our first and second hypotheses, we predicted that total soil C stocks and soil C vertical distribution would differ between tree species, and that these differences would be due to species-specific differences in litter production and decomposition rate. We found little evidence to support these predictions, which could be due to strong legacy effects of the relatively large soil C stocks that had accumulated prior to the establishment of the experiment. Nonetheless, we did find some evidence that tree species affected soil C in the deepest (10–20 cm) mineral soil layer over the duration of our experiment, where *Larix* sp. and *Pinus contorta* differed both from each other, and all other tree species (*Pinus contorta* showed the highest C stock of all species and *Larix sp.* the lowest). Further, we found that litterfall showed a significant positive relationship with soil C stock in the deepest mineral soil layer. While not explicitly measured in this study, these results may reflect differences in dissolved organic carbon (DOC) dynamics. Other studies have shown that DOC degradability and fluxes can vary due to tree species (Kiikkilä et al., 2006; Merilä et al., 2024), potentially leading to differences in vertical stratification of soil C within different mineral layers over time. We also found that many of our other measured C input and output variables showed evidence of differences among tree species, although we did not find evidence that these differences translated into differences in soil C stocks. For instance we found that aboveground litter production varied significantly between species, whereas similar experiments report little variation between species, linking differences instead to local site fertility (Augusto et al., 2015; Hansen et al., 2009). In comparison to aboveground litter production, data on fine root production are much more scarce (Mayer et al., 2020) and there is no clear pattern of how fine root production rates differ between boreal tree species, or contribute to soil C stocks (Augusto et al., 2015). Our data showed that fine root production differed strongly among species ($p < 0.001$), but these differences did not translate into differences in soil C stocks.

Focusing on our decomposition measurements, the analyses revealed that litter mass loss, which represents the early stages of decomposition, showed very strong evidence ($p < 0.001$) to differ between species, where *Picea glauca* and *Pinus sylvestris* exhibited the lowest (18 %) and highest (26 %) rate of mass loss, respectively (table S1). Humus mass loss on the other hand did not differ between the species ($p = 0.205$).

Table 2
Visible at the top (a) are the results of testing SOC in different ecosystem compartments and soil layers (distribution) against tree species. The middle part (b) of the table shows the respective p-values of our measured variables when tested against tree species. The bottom part (c) of the table displays measured variables that show weak evidence or higher when tested against SOC in different soil layers. Each result is presented with their respective Chisq (X^2) and p-values.

(a) SOC stocks & distribution

Ecosystem compartment	Model variables	X^2-value	p-value
Ecosystem C stock	Species	117.57	**< 0.001**
Tree biomass	Species	425.19	**< 0.001**
Total soil C stock	Species	6.960	0.223
Humus C stock	Species	7.905	0.161
Mineral soil 0–10 cm	Species	5.627	0.344
Mineral soil 10–20 cm	Species	16.879	**0.005**

(b) Soil properties and C fluxes

Measured variables	Model variables	X^2-value	p-value
pH Humus	Species	4.972	0.419
pH mineral soil 0–10 cm	Species	4.912	0.426
pH mineral soil 10–20 cm	Species	1.360	0.928
Average pH (all soil layers)	Species	4.930	0.424
Tree Biomass	Species	425.19	**< 0.001**
Woody coarse debris	Species	139.473	**< 0.001**
Litterfall	Species	29.757	**< 0.001**
Root growth	Species	29.465	**< 0.001**
Litter mass loss	Species	23.109	**< 0.001**
Humus mass loss	Species	7.204	0.205

(c) Variables affecting SOC

Soil layer	Model variables	X^2-value	p-value
Total soil horizon	pH	13.889	**< 0.001**
O-Layer (Humus)	-	-	-
Mineral soil 0–10 cm	pH	4.869	**0.028**
Mineral soil 10–20 cm	pH	7.210	**0.003**
	Litterfall	3.589	**0.045**

Note: To avoid problems with multicollinearity, tree species was excluded from our statistical model in the final step when comparing all variables together against soil C (bottom part of table, c) due to being used in the previous test, along with tree biomass since the variable being highly correlated with other model variables (variance inflation factor ~ 3 or higher).

Table 3
Results of testing SOC in different ecosystem compartments against tree species and site interaction. Each result is presented with their respective Chisq (X^2) and p-values.

Species & Site interaction

Ecosystem compartment	Model variables	X^2-value	p-value
Ecosystem C stock	Species	26.182	**< 0.001**
	Site	0.990	0.423
	Species:Site	1.668	**0.064**
Tree biomass	Species	172.440	**< 0.001**
	Site	87.161	**< 0.001**
	Species:Site	6.786	**< 0.001**
Total soil C stock	Species	1.382	0.227
	Site	19.024	**< 0.001**
	Species:Site	1.450	0.202

This result supports the idea that decay rate differences across species may converge at a “maximum decomposition limit” (Berg and Ekbohm, 1993; Prescott et al., 2004), corresponding to the point when litter “becomes” humus (Berg et al., 1996; Prescott et al., 2000). At this later stage of decomposition, local environmental site factors (temperature, moisture etc.) might play a larger role in controlling decomposition processes than the initial litter quality differences between the species (Prescott et al., 2000).

Soil pH was the only variable we measured that served as a strong significant predictor for soil C (Table 2c). This effect was independent of tree species identity in our dataset, i.e. soil pH did not significantly differ between the tree species. Plant growth can indeed acidify the rhizosphere through the uptake of cations in biomass, which over time can lead to a buildup of hydrogen ion concentration in the soil solution. Many studies do show that differences in tree species characteristics can affect this process so that e.g. conifer species acidify the soil more than broadleaved species (Augusto et al., 2015; Kjønaas et al., 2021; Mareschal et al., 2010; Oostra et al., 2006). The differences in soil acidity between conifer and broadleaved species has however been shown to be minor, i.e. a few tenths of a pH unit (Augusto et al., 2015). The relatively young age of our experiment and/or the fact that all but one species *(Betula pendula)* in our experiment were conifers may also have affected our results. Further, legacy effects may have been stronger than the effect of the current stand, and could have obscured any species effects on soil pH, which instead may manifest over longer time scales.

For our third hypothesis we expected that tree species-specific growth responses to local and regional climate variability (represented by our different sites, Table 1) would serve as an important control on SOC stocks. In contrast to our prediction, we found no evidence for an interaction effect between tree species and site ($p = 0.202$) on SOC stocks (Table 3). We did however find weak evidence ($p = 0.064$) that total ecosystem C stocks were influenced by an interaction between tree species and site, which was mainly driven by strong evidence ($p < 0.001$) for species-specific differences in aboveground tree biomass C (Table 3). On both experimental sites, tree species with “acquisitive” traits (*Betula pendula, Larix* sp*., Pinus contorta* and *Pinus sylvestris*) that usually dominate early in forest succession were shown to exhibit higher levels of tree biomass C than “conservative” trait species (*Picea abies* and *Picea glauca*) that usually dominate later in forest succession (Gundale et al., 2024). This is expected as the experiments are still quite young in relation to the length of a normal forest rotation of 60–100 years in boreal managed forests, and the much longer successional dynamics in unmanaged forest (Nilsson et al., 2022). In addition, the rank order between species in relation to their above ground tree biomass C stock differed between sites, mainly in that *Betula pendula* and *Pinus sylvestris* had a similar aboveground biomass when present on the northern site; while, in the central site *Betula pendula* biomass and annual growth was smaller than those of *Pinus sylvestris*, and more equaled *Picea abies* (Fig. 3). This suggests that there is a potential for managers to optimally match species with site characteristics to maximize ecosystem C stocks (Augusto et al., 2025). For instance, in our northern site, a hypothetical mixture of *Larix sp.* with *Pinus contorta* and/or *Betula pendula* could potentially enhance above- as well as belowground C stock, whereas in the central site a hypothetical mixture of *Larix sp.* and *Picea abies* could potentially achieve the best effect.

The explanation for the rank order differences in ecosystem C observed in our study requires more data than what we have available, but an important difference between our sites, except their geographical distance, is the slope (Table1). Svartberget is located at the lower part of a hillside, creating a natural drainage, while Garpenberg is situated on flat terrain. This means that the Garpenberg site generally has longer periods when the soil is fully saturated with water i.e. after heavy rains or snowmelt, which likely slows down decomposition (Prescott, 2010) and promotes accumulation of soil organic matter, irrespective of the tree species present (Fig. 3). Further research should explore a mechanistic basis underpinning these species by site interactions, and additional pathways through which they influence soil C stocks.

5. Conclusion

This study presented data on tree species effects on soil C stocks based on measurements from two common garden experiments. Our results show that while many soil C inputs and outputs are species dependent, these differences did not translate into differences in total belowground soil C stocks over a 30 year-long time period. However, we found a species effect on C in the deepest mineral soil layer. Our results also point toward the idea that abiotic site factors such as climate and

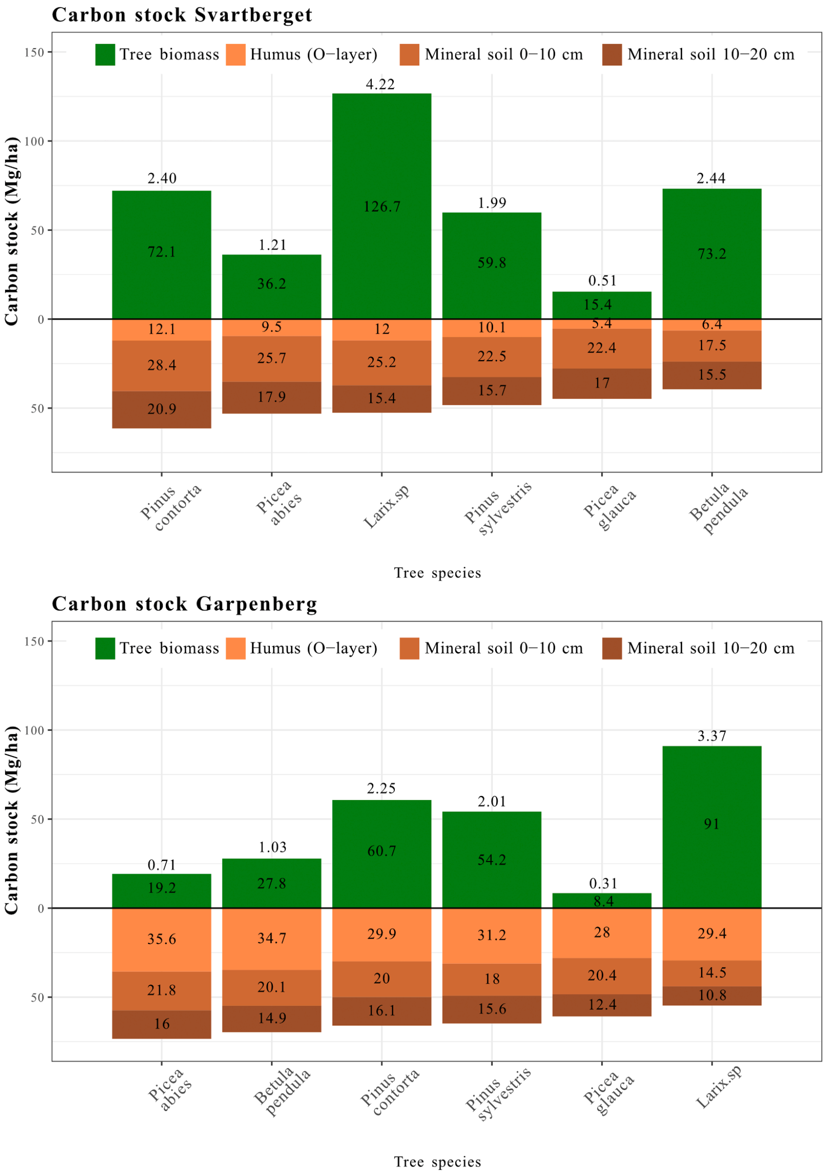

Fig. 3. The average amount of C stock in different ecosystem compartments for different tree species at Svartberget (n = 3 species^{-1}) and Garpenberg (n = 3 species^{-1}, except *Betula pendula* where n = 2). The species are organized in descending order, starting with the highest belowground C stock, numbers above bars show the average annual growth in above ground biomass C (Mg C ha^{-1} y^{-1}) since establishment, Svartberget is the most productive site for all tree species except *Pinus sylvestris*.

slope may be more important than tree species for the accumulation of total soil C. Despite these results, there is still an argument to be made that tree species choice can be beneficial as a tool to mitigate climate change. The aboveground biomass C stocks we observed were highly species specific and translated into significant differences in total ecosystem C stocks, which may in the long term also translate into more pronounced tree species effects on soil C. Our results are also in line with larger meta-analysis studies indicating that tree species could be chosen based on their site-specific growth potential, which can serve to maximize ecosystem carbon stocks, and in turn the climate mitigation potential of boreal forests.

CRediT authorship contribution statement

Marcus Larsson: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Clydecia M. Spitzer:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Michael J. Gundale:** Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization. **Annika Nordin:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Data curation, Conceptualization.

Funding

This work was supported by: Stora Enso AB, Knut and Alice Wallenberg foundation [no. 2018.0259].

Declaration of Competing Interest

Marcus Larsson reports financial support was provided by Stora Enso AB. Annika Nordin reports a relationship with Stora Enso AB that includes: employment. Co-author reports a previous relationship (2016–2020) with Sveaskog AB that included: board membership (A. N.). Co-author declare no conflicts of interest, and do not have any commercial affiliations (M.J.G. and C.M.S).

Appendix

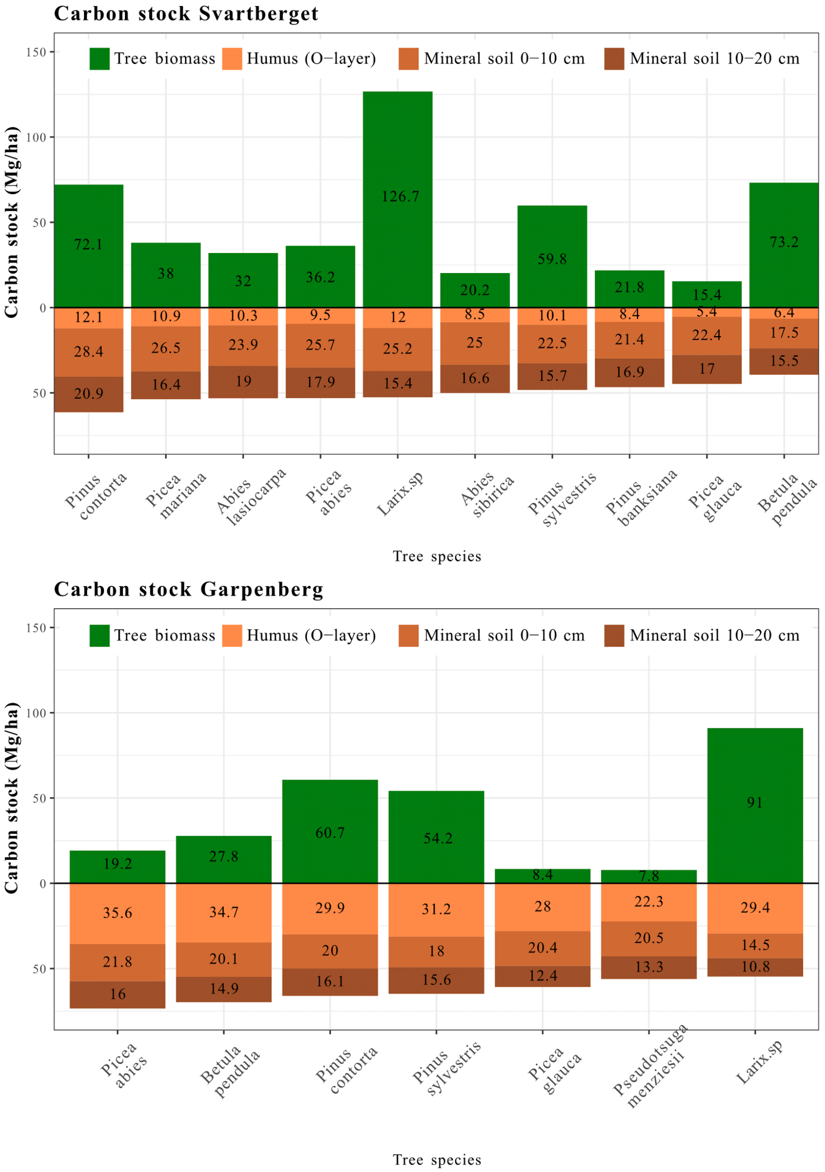

Fig. appendix 1. The average amount of C stock (Mg C ha) in different ecosystem compartments for all different tree species at Svartberget (n = 3 species^{-1}) and Garpenberg (n = 3 species^{-1}, except *Betula pendula* where n = 2). The species are organized in descending order, starting with the highest belowground C stock

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123060.

Data availability

Data will be made available on request.

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