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Abstract

Scots pine (*Pinus sylvestris* L.*)* is one of the most important tree species in Europe. The first thinning fills the purpose of shaping the stand for future growth through the selection of which trees to retain. This thesis aimed to explore the mechanistic basis of thinning responses in the short-term, through the establishment of thinning experiments in central Sweden, which included biomass harvests and continuous monitoring of sap flow and stem radial change. Long-term thinning strategies were evaluated using a series of thinning experiments across Sweden. The results show that Scots pine trees were able to swiftly adjust biomass allocation strategies. Although thinning, by design, reduces leaf area index (LAI) and standing biomass, an increased growth for individual trees, on average, and for dominant trees, was immediate. After thinning, the stands presented higher water use efficiency. Indirect measurements were not able to detect substantial changes in LAI and root distribution between years. In the long-term evaluations of selective and schematic thinnings, it was observed that the amount of retained basal area is more important for tree growth and stand development than the spatial distribution of trees. With imminent changes in the climate and the possibility of increased frequency and intensity of droughts and other extreme events, it becomes important to adapt management alternatives to mitigate the negative effects of such changes. This thesis demonstrates that thinning has the potential to contribute to greater resilience of Scots pine forests in the boreal zone.

Keywords: forest management, ecophysiology, scots pine, growth, transpiration, water use efficiency, biomass quantification.

Gallringsstrategier och deras inverkan på tillväxt, allokering och vattenanvändningseffektivitet i tallbestånd

Sammanfattning

Tall (*Pinus sylvestris* L.) är en av de viktigaste trädslagen i Europa. Den första gallringen fyller ofta funktionen att forma det framtida beståndet genom valet av vilka träd som ska behållas. I den här avhandlingen utforskas mekanistiska förklaringar till gallringsrespons på kort sikt, genom etablering av gallringsförsök i Mellansverige. Långsiktiga gallringsstrategier utvärderades med hjälp av en serie gallringsexperiment över hela Sverige. Resultaten visar att tall snabbt kunde anpassa allokeringsstrategier för biomassatillväxten. Även om gallring, genom design, minskar bladareaindex (LAI) och stående biomassa, var en ökad tillväxt för enskilda träd, i genomsnitt och för dominerande träd, omedelbar. Efter gallring visade bestånden högre vattenanvändningseffektivitet. Indirekta mätningar kunde inte detektera betydande förändringar i LAI och rotfördelning mellan åren. I långtidsutvärderingarna av selektiva och schematiska gallringar observerades att mängden bibehållen grundyta är viktigare för trädtillväxt och beståndsutveckling än trädens rumsliga fördelning. Med nära förestående klimatförändringar och risk för ökad frekvens och intensitet av torka och andra extrema händelser blir det viktigt att anpassa skötselalternativ för att mildra de negativa effekterna av sådana förändringar. Denna avhandling visar att gallring har potential att bidra till ökad motståndskraft hos tallskogar i den boreala zonen.

Nyckelord: skogsskötsel, ekofysiologi, tall, tillväxt, transpiration, vattenanvändningseffektivitet, biomassa.

Estratégias de desbaste e seu impacto na dinâmica de crescimento, padrões de alocação e eficiência do uso da água em povoamentos de Pinheiro Silvestre

Resumo

O pinheiro silvestre (*Pinus sylvestris* L.) é uma das espécies de árvores mais importantes da Europa. O primeiro desbaste tem o propósito de moldar o povoamento para crescimento futuro por meio da seleção de quais árvores manter. Esta tese teve como objetivo explorar a base mecanicista da resposta ao desbaste em curto prazo, por meio do estabelecimento de experimentos de desbaste na região central da Suécia, que incluíram colheitas de biomassa e monitoramento contínuo do fluxo de seiva e da variação radial do caule. Estratégias de desbaste de longo prazo foram avaliadas usando uma série de experimentos de desbaste em toda a Suécia. Os resultados mostram que os pinheiros silvestres foram capazes de ajustar rapidamente as estratégias de alocação de biomassa. Embora o desbaste intrinsicamente reduza o índice de área foliar (IAF) e a biomassa, um aumento no crescimento de árvores individuais, em média, e de árvores dominantes, foi imediato. Após o desbaste, os povoamentos apresentaram maior eficiência no uso da água. Medições indiretas não foram capazes de detectar mudanças substanciais no IAF e na distribuição de raízes entre os anos. Nas avaliações de longo prazo de desbastes seletivos e esquemáticos, observou-se que a quantidade de área basal retida é mais importante para o crescimento das árvores e desenvolvimento do povoamento do que a distribuição espacial das árvores. Com mudanças iminentes no clima e a possibilidade de aumento da frequência e intensidade de secas e outros eventos extremos, torna-se importante adaptar alternativas de manejo para mitigar os efeitos negativos de tais mudanças. Esta tese demonstra que o desbaste tem o potencial de contribuir para uma maior resiliência das florestas de pinheiros silvestres na zona boreal.

Palavras-chave: manejo florestal, ecofisiologia, pinheiro silvestre, crescimento, transpiração, eficiência do uso da água, quantificacão de biomassa.

Dedication

To my mother, Elizabeth.

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. Segtowich, A. C.*, Langvall, O., Huuskonen, S., Fahlvik, N. and Holmström, E. Swift adjustment of biomass allocation strategies in Scots pine after thinning (submitted)

II. Segtowich, A. C.*, Langvall, O., Gutierrez Lopez, J. and Holmström, E. Water use efficiency increased after release cutting of Scots pine stands (manuscript)

III. Segtowich, A. C.*, Magh, R. K., Langvall, O., Marshall, J., Grabowska, M. and Holmström, E. Root distribution and leaf area index four years after thinning, an early case study (manuscript)

IV. Segtowich, A. C.*, Huuskonen, S., Fahlvik, N. and Holmström, E. (2023). Select or Not? Comparing the Impact of Selective and Schematic Thinning on Scots Pine Tree Growth and Stand Structure. Forests, 14 (6), pp 1194. https://doi.org/10.3390/f14061194

Paper IV is published with open access.

*Corresponding author

The contribution of Amanda de Castro Segtowich (ACS) to the papers included in this thesis was as follows:

I. ACS was part of the field work for data collection, developed the research idea, and was responsible for data analysis and manuscript writing with input from the co-authors.

II. ACS was part of the field work for data collection, developed the research idea, and was responsible for data analysis and writing of the manuscript with input from the co-authors.

III. ACS was part of the field work for data collection, was involved in developing the research idea, and was responsible for data analysis and manuscript writing with input from the co-authors.

IV. ACS was responsible for data analysis and writing of the manuscript with input from the co-authors.

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Abbreviations

A	Photosynthetic capacity
$A_L:A_S$	Leaf area-to-sapwood area ratio
ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
APAR	Absorbed photosynthetically active radiation
BAI	Basal area increment
CI	Competition index
CUE	Carbon use efficiency
CV	Coefficient of variation
DBH	Diameter at breast height
g_s	Stomatal conductance
HDR	Height-to-diameter ratio
LA	Leaf area
LAI	Leaf area index
LCR	Live crown ratio
NAcE	Nutrient acquisition efficiency
NPP	Net primary production
NUE	Nutrient use efficiency
NUtE	Nutrient utilization efficiency

QMD	Quadratic mean diameter
RCT	Root contact trees
RUE	Resource use efficiency
RWU	Root water uptake
SA	Sapwood area
SI_{100}	Site index (height in m at 100 years)
SLA	Specific leaf area
SPEI	Standardised precipitation evapotranspiration index
SUR	Seemingly unrelated regression
TR	Thinning ratio
VPD	Vapour pressure deficit
WUE	Water use efficiency
WUEi	Intrinsic water use efficiency

1. Introduction

1.1 Forests and trees in a changing climate

Historically, light and nutrient deficiency (specifically nitrogen) have been assumed to be the main factors limiting tree growth in temperate and boreal forests (Bergh *et al.* 1999; Tian *et al.* 2021). However, if climate warming is not accompanied by increased precipitation, water could become a limiting factor, primarily in cold-temperate forests like those in southern Sweden and central Europe, but also in boreal forests (Bergh *et al.* 2003). Some authors predict an increase in the frequency and intensity of water deficit periods in Europe, including Scandinavia (Spinoni *et al.* 2018). Thus, drought can also become a limiting factor in Swedish forests, as observed in the unprecedented hot and dry period in spring-summer 2018 (Schuldt *et al.* 2020), which could potentially have contributed to the recent tree growth decline in Sweden (Laudon *et al.* 2024).

Increased greenhouse gas emissions and their concentration in the atmosphere, mostly caused by anthropogenic actions, have accelerated climatic changes. They are manifested in various ways, including changes in extreme temperatures and precipitation patterns (Karl & Trenberth 2003; Lucht *et al.* 2006). Climate change is set to affect forests worldwide in different ways, not just in relation to abiotic factors like water, light and nutrients, but also biotic factors, such as herbivores and pathogens (Ayres & Lombardero 2000). Respiration is a key process in the ecosystem carbon balance, which influences the potential of forests to be sinks or sources of carbon (Valentini *et al.* 2000). Air and soil warming are predicted to lengthen the growing season in boreal forests, cause earlier snow melt, and increase fine root and nutrient turnover, evapotranspiration and water demand, as well as respiration rates (Bergh *et al.* 2003; Mellander *et al.* 2007). In boreal forests, tree growth is, therefore, predicted to increase due to longer growing seasons and warmer temperatures (Ruckstuhl *et al.* 2008). With a Nordic implementation of the process-based BIOMASS model (McMurtrie *et al.* 1990), Bergh *et al.* (2003) showed that higher temperatures would result in an earlier photosynthetic onset in the spring and a prolonged growing period through the autumn for Scots pine and Norway spruce. Both species would increase net primary production (NPP) from 24–37% in spring (+4ºC scenario). Some climate change scenarios predict that boreal trees in mid-northern latitudes may be replaced by temperate trees or grasses due to warmer winters, which favour temperate species, and hotter summers, which harm boreal trees (Joos *et al.* 2001; Lucht *et al.* 2006).

1.2 Characteristics of Scots pine

Scots pine (*Pinus sylvestris* L.) is a light-demanding species suited to well-drained soils (Carlisle & Brown 1968). It is one of the most important tree species in Northern Europe (Forest Europe 2020), and in Sweden it makes up approximately 40% of the total standing volume in forests (Swedish Forest Agency 2020). It is mainly used for timber, pulp and paper production (Krakau *et al.* 2013; Burawska-Kupniewska *et al.* 2020; Gülsoy 2023). The bark of this species is flaky, scaly on the upper trunk, and thicker at the bottom, which protects against fire (Krakau *et al.* 2013). This species can vary in physiological characteristics, such as the timing of bud flushing, leaf retention and tolerance of extreme soil and climate conditions (Carlisle & Brown 1968). Since it is mostly an inland species, its stomatal conductance is less sensitive to water stress; stomata will not readily close in lower water availability scenarios (Whitehead *et al.* 1984). Its needles contain a thick epidermis with a protective wax coating, which limits water loss (Krakau *et al.* 2013). The maximum age for Scots pine needles can vary between 4 – 6 years (Niinemets & Lukjanova 2003; Muukkonen 2005), with the first and second-year old needles generally presenting higher photosynthetic capacity (Muukkonen 2005). Where nutrient deficiency is more prominent, Scots pine displays highly competitive behaviour (Carlisle & Brown 1968). In a study on Baltic provenances of Scots pine, Matisons *et al.* (2019) found that this species presents high phenotypic plasticity in wood anatomy, being able to adjust traits such as tracheid lumen size and cell wall thickness. Moreover, its leaf area to sapwood area ratios (A_L:A_S) are highly plastic (Delucia *et al.* 2000), allowing it to quickly adjust how much it invests in leaf area relative to sapwood production for water supply. This ratio decreases in lower water availability environments due to a higher investment in sapwood (Delucia *et al.* 2000) and it increases when water is more available by increasing leaf area (Giuggiola *et al.* 2013). Additionally, Scots pine has a comprehensive root system, with deep taproots and coarse roots, which can reach 6 m in depth (Krakau *et al.* 2013) and horizontal roots that can reach over 10 m from the stem (Henriksson *et al.* 2021). Ding *et al.* (2020) found that Scots pine root growth was mainly influenced by temperature, and that pioneer roots were more resilient to adverse conditions, such as low temperatures and drought, than fibrous roots.

1.3 Tree growth and ecophysiology

Growth, by definition, is "the increment in dry mass, volume, length, or area that results from the division, expansion, and differentiation of cells" (Lambers & Oliveira 2019). Tree growth is influenced by a variety of factors, such as climate, light, water and nutrient availability. Diameter and height growth involve the activity of meristematic tissues, which are a very small portion of the total mass (Kramer & Kozlowski 1979). Moreover, trees can adjust different types of growth independently (Lambers & Oliveira 2019).

Sap flow is an important ecophysiological process for understanding plant water relations (Cohen *et al.* 1981). Regardless of whether one measures sap flow using the heat pulse method (Burgess *et al.* 2001; Lopez *et al.* 2021) or the heat dissipation method (Granier 1985; Granier 1987), sap flow sensors ultimately measure changes in temperature along the stem after heat has been applied. These methods' principle is that the rate of applied heat transport is positively correlated to the sap flow rate (Granier 1985; Burgess *et al.* 2001; Dodd *et al.* 2023). There is a trade-off between tree growth and water loss, since stomata need to be open in daylight for as much time as feasible to maximize photosynthesis, which, in turn, will maximize transpiration (Dodd *et al.* 2023). Transpiration depends, among other factors, on evaporative demand, which increases throughout the morning, causing transpiration rates to increase and cell water potentials to decrease due to water loss (Dodd *et* *al.* 2023). When water becomes a limiting factor, stomata will close, causing transpiration rates to decline (Jarvis & McNaughton 1986). This has been demonstrated in Scots pine; low volumetric water content in topsoils causes stomatal closure, followed by reduced transpiration rates (Irvine *et al.* 1998). In central Sweden, Lagergren and Lindroth (2002) found that stomatal conductance started to decrease, on average, after 80% of the soil water available for plants was depleted.

Leaf area index (LAI) is the amount of leaf area (m^2) per unit ground area (m^2) (Watson 1947). As described by Bréda (2003), it greatly informs the forest microclimate by directly influencing rainfall and radiation interception, as well as via water and carbon exchange. Thus, it is an important ecophysiological variable that is directly linked to forest productivity and important for process-based models (Gower *et al.* 1999; Bréda 2003). LAI can be measured directly, through destructive harvesting of foliage and the application of allometric equations, or indirectly, using methods such as the LAI-2200C and hemispherical photography (Gower *et al.* 1999; Bréda 2003; Goude *et al.* 2019). According to Bréda *et al.* (1995), in stands with a higher leaf area index (LAI), such as unthinned ones, transpiration is mainly influenced by LAI and thus competition, whilst for thinned stands, other factors such as vapour pressure deficit (VPD), net radiation and wind can have a bigger influence on how much a tree transpires. If LAI is less than 4 m^2 m^{-2}, then we can generally conclude that the light availability and photosynthetic capacity for individual trees is high, but productivity tends to be reduced in more open stands (Kramer & Kozlowski 1979), e.g. after thinning. Delucia *et al.* (2000) argue that a simultaneous increase in sapwood mass and a decrease in leaf mass will result in trees allocating more resources (photosynthates) to structural mass, while having less total leaf area.

Root water uptake (RWU) is a process that is mainly driven by transpiration, which results from a water potential gradient between the soil and root interface and the xylem vessels (Javaux *et al.* 2013; Couvreur *et al.* 2014; Rothfuss & Javaux 2017). This process is also influenced by other factors like stomatal opening and atmospheric evaporative demand (Tardieu & Simonneau 1998; Couvreur *et al.* 2014; Huber *et al.* 2015).

1.4 Thinning in forest management

As the demand for products and services from forests increases, it becomes increasingly important to understand how different silvicultural and management practices influence the ecological processes within a forest (Powers *et al.* 2010). Forest management usually involves mid-rotation measures, such as thinning, after canopy closure (Whitehead *et al.* 1984). Historically, the higher-intensity thinnings in the 1960s in the Nordic countries were a result of the demand for increased productivity from mechanized forest operations (Mäkinen *et al.* 2005b).

Different thinning strategies can influence the adaptability of forest stands (Linder 2000) and alter productivity (Nilsson *et al.* 2010), mortality (Powers *et al.* 2010), biodiversity (Neill & Puettmann 2013) and responses to drought (Sohn *et al.* 2016a; Sohn *et al.* 2016b) and other extreme events, as well as potentially change the hydraulic resistance between soil and canopy (Whitehead *et al.* 1984).

Thinning can be done in different ways. Schematic thinning is spatially based, regardless of tree size; an example is cutting corridors (Mäkinen *et al.* 2005b; Bergström 2009; Karlsson *et al.* 2013; Witzell *et al.* 2019). Selective thinning removes trees based on their size. Thinning from below refers to when the smallest (suppressed and/or damaged) trees are removed, whereas in thinning from above, the largest trees (dominant and/or co-dominant) are removed (Mäkinen & Isomäki 2004a; Mäkinen & Isomäki 2004b; Nilsson *et al.* 2010). The choice of thinning form will impact diameter distributions of the remaining trees. A key measure of thinning is the thinning ratio (TR), which is the ratio of mean diameter of harvested trees and retained trees (Nilsson *et al.* 2010). For thinning from below, TR < 1.0 and for thinning from above, TR > 1.0, whereas for schematic thinning or in strip roads, the ratio should be 1 (or close to 1), since trees are harvested regardless of size.

Thinning can minimize tree mortality by reducing individual competition and maintaining relative densities below the zone where competition mortality begins (Powers *et al.* 2010; Xie *et al.* 2020). When the forest canopy closes and one or more resources are limiting for the stand, competition between trees becomes a key factor in the self-thinning process (Drew & Flewelling 1977; Franklin *et al.* 1987; del Río *et al.* 2001). Thinning intrinsically leads to increased resource availability (water, light and nutrients) to the remaining trees, either instantaneously (light, for example) or slowly (nutrients) (Franklin *et al.* 1987).

In addition to density-induced mortality, climate change is also set to affect the function and structure of forests, but management practices may help mitigate this (Xie *et al.* 2020). Drought-induced mortality can play out via two main pathways McDowell *et al.* (2008); McDowell (2011): carbon starvation, when carbon uptake through photosynthesis is lower than carbon use by respiration, growth and defence, and hydraulic failure, when cavitation disrupts water transport from the soil to the leaves. Both of these pathways make trees more prone to biotic damage from pests and pathogens (McDowell *et al.* 2008). Therefore, techniques to minimize water stress in established stands that are well into their rotation period are necessary (Steckel *et al.* 2020). Thinning can be particularly important in drought-susceptible sites as it increases water availability, at least in the short term, and reduces the severity of climate-sensitive disturbances, such as insects and fire (Elkin *et al.* 2015). Steckel *et al.* (2020) found, for example, that Scots pine drought recovery and resilience were better on sites with more water availability. Sohn *et al.* (2016a) found that Scots pine post-drought recovery was higher in heavily thinned stands than in an unthinned treatment. These strategies can be implemented either immediately after climatic disturbances or before they take place, which Elkin *et al.* (2015) call reactive and preemptive strategies, respectively. Laurent *et al.* (2003) found that, in the 6 years after treatment, heavy thinning made Norway spruce trees more resistant to drought stress, which shows that thinning can alter the relationship between climate and radial growth while improving physiological processes as a response to water stress. Thinning effects may change over time and vary depending on species composition, soil and climate conditions and stand age. Molina *et al.* (2021) reported that heavily thinning Aleppo pine stands increased understory growth and sapling density 10 years after thinning, affecting tree water use and growth.

1.5 Growth and yield thinning responses in Scots pine

Understanding and quantifying the short- and long-term effects of thinning on the growth and yield of Scots pine has historically been a major focus of research in Europe (del Río *et al.* 2017). On a long-term experiment in Sweden, with 35 Scots pine sites spread across the country, Nilsson *et al.* (2010) found that, despite a significantly higher individual tree basal-area-weighted mean diameter at breast height (DBH) for the thinned treatments, the total gross stem volume production was significantly reduced for all thinning treatments, compared to the unthinned control. Similarly, long-term experiments in Finland show individual tree basal area growth increased with thinning intensity (Mäkinen & Isomäki 2004c). On a shorter term, 8-10 years after thinning, Mäkinen *et al.* (2005a) found an increase of mean diameter for the remaining trees with decreasing stem density, with thinning increasing stem taper and decreasing the slenderness of the trees. Moreover, there was a decrease in annual volume production of approximately 34% for the intensive thinning (Mäkinen *et al.* 2005a). Likewise, Bianchi *et al.* (2024) found that volume increment declined significantly in the 15 years after moderate and heavy thinnings, with the unthinned treatment showing the highest growth in that timespan. Similar results were found on long-term experiments in Spain, with more intense thinning increasing quadratic mean diameters (QMD) (del Río *et al.* 2008). Overall, the total volume in the heavy and moderate thinnings was less than in the control (del Río *et al.* 2008).

A study comparing different selective, half-systematic and systematic thinning techniques and an unthinned control found that the control had significantly lower mean DBH, while the thinning treatments did not differ from each other Mäkinen *et al.* (2005b). However, the authors mention that, on average, mean DBH was higher for selective thinning, followed by half-systematic and systematic thinning.

1.6 Resource use efficiency

Ecophysiology studies are important to better understand species responses to climatic changes and management practices, improve future forest productivity and achieve efficient and sustainable use of resources like carbon, water, light and nutrients (Rubilar *et al.* 2024). Trees uptake resources, which they can store for future use or allocate toward biomass in roots, stem wood, bark, branches and needles (Bloom *et al.* 1985). Two processes primarily regulate the net exchange of carbon dioxide (CO_2) between terrestrial ecosystems and the atmosphere: net primary production through photosynthesis and heterotrophic respiration (Gower *et al.* 2001), which will determine whether forests are sinks or sources of carbon (Gower *et al.* 1994). Tree biomass quantification enables estimations of how much carbon has been stored in trees, above or below ground, and provides allometric equations which upscale physiological variables, helping to understand water relations and contribute to process-based models (Urban *et al.* 2015).

Resource use efficiency (RUE) can be generally referred as the amount of biomass produced per unit of a supplied resource (Hodapp *et al.* 2019). Water use efficiency (WUE) is the ratio between carbon assimilated by (or stored in) plants, and the amount of water released to the atmosphere by transpiration (Fatichi *et al.* 2023). It can also be expressed as intrinsic water use efficiency (WUEi), which is calculated from a leaf perspective, and refers to the ratio between photosynthetic carbon acquisition (photosynthetic rate) and water loss through stomata (Ren *et al.* 2024). Carbon use efficiency (CUE), which is an essential variable in carbon cycling models (Hagenbo *et al.* 2019), is the ratio of net to gross primary productivity, representing the fraction of carbon taken up by plants that was incorporated into tissues and not respired (Collalti *et al.* 2018). Light use efficiency is the above-ground biomass or stem wood biomass increment per unit of absorbed photosynthetically active radiation (APAR) (Forrester *et al.* 2013). Nutrient use efficiency (NUE), according to Reich *et al.* (2014), has two main components: nutrient acquisition efficiency (NAcE) - how effectively plants uptake nutrients from the soil and nutrient utilization efficiency (NUtE) - how effectively they use nutrients to produce biomass.

Thinning may influence RUE in different species. Several pine species show an increase in basal area increment (BAI) in thinned stands, such as Scots pine (Sohn *et al.* 2016a), ponderosa pine (McDowell *et al.* 2003), Aleppo pine (del Campo *et al.* 2014; Manrique-Alba *et al.* 2020) and black pine (Manrique-Alba *et al.* 2021). However, this increase does not always translate into an increase in WUEi. Manrique-Alba *et al.* (2020) found an increase in BAI and a decrease in WUEi, which the authors suggest could be due to a proportionally greater increase in stomatal conductance (g_s) than photosynthetic capacity (A). When working with lodgepole pine, Wang *et al.* (2020) found no thinning impact on stand-level WUE when water was not limiting, and otherwise similar control and thinned treatments. However, under drought conditions, the thinning treatments significantly increased stand WUE, in comparison to the unthinned treatment. Fernandes *et al.* (2016) found that tree level WUE was higher in thinned Aleppo pine stands. Wang *et al.* (2019) observed reduced stand transpiration after thinning, but there was no significant difference between the drought and non-drought years for the control and one of the thinning treatments. These results suggest the importance of thinning in promoting forest resilience, especially under water stress conditions (Sohn *et al.* 2016b; Wang *et al.* 2019; Wang *et al.* 2020).

CUE is expected to decrease as forests age (Collalti *et al.* 2018; Hagenbo *et al.* 2019). In their simulations, Collalti *et al.* (2018) found that CUE decreased faster in the unthinned forest, and suggest that thinning could mitigate this decrease and reduce mortality risks derived from physiological and climatic interactions. Thinning was also found to increase CUE in ponderosa pines stands, compared to an unthinned control (Doughty *et al.* 2021). When working with Scots pine on two sites in the Mediterranean, Blanco *et al.* (2009) observed that, in the more nutrient-limited site, thinning did not affect NUE. They suggest that thinning from below might not be the best alternative to increase nutrient availability for the retained trees, as it mostly removes suppressed, smaller and damaged trees which have lower nutritive demands. Furthermore, they suggest higher-intensity thinning from below (over 30% of basal area removal), thinning from above or fertilization as alternative management options (Blanco *et al.* 2009). In a study with Norway spruce, individual tree LUE was higher in the unthinned treatment than the thinned one for trees of similar sizes, although this was not the case in the mature forest (Gspaltl *et al.* 2013). At a stand level, the thinning treatment showed higher LUE, due to the higher number of large trees, for two of the forest types (including the mature forest). However, this pattern was not observed in the immature forest, in which LUE was higher for the unthinned treatment (Gspaltl *et al.* 2013). Binkley *et al.* (2013) argue that dominant trees' higher LUE and total forest growth are largely influenced by the combined effects of increased light interception and higher LUE by larger trees. They suggest thinning from below would be more beneficial for increasing LUE, as it mostly keeps co-dominant and dominant trees in the stand (Binkley *et al.* 2013).

2. Thesis aims

This thesis builds on extensive research on thinning in boreal forests by providing insights into the mechanistic basis of short-term thinning responses in boreal Scots pine forests. Such studies are still underrepresented in the boreal zone (Sohn *et al.* 2016b). For this, two thinning forms (thinning from above and from below) and two intensities (moderately and heavily thinned) were used, in addition to an unthinned control (Papers I, II and III). It also tackles the impact of selective and schematic thinning on stand structure and total long-term volume production across Sweden, using different strategies (thinning once or more than once; Paper IV).

The general aim of the thesis is to increase short- and long-term understanding of different thinning strategies and intensities in Scots pine forests. A variety of topics is considered, including: changes in above-ground biomass allocation (**Papers I, III**), response to drought and water use efficiency (**Paper II**), root distribution (**Paper III**) and long-term stand structure (**Paper IV**). The specific objectives were:

I. To assess potential changes in above-ground biomass allocation patterns three years after thinning (Paper I)
II. To evaluate if thinning can improve short-term water use efficiency (WUE) (Paper II)
III. To investigate if there has been a change in root distribution and leaf area index (LAI) four years after thinning (Paper III)
IV. To compare different thinning designs (selective and schematic thinning) and strategies (thinning once or more than once), using long-term experiments on Scots pine stands throughout Sweden (Paper IV)

V. To evaluate management implications of the different thinning forms (selective thinning from below and above, and schematic thinning) and different intensities (moderate or heavy thinning; Papers I, II, III and IV)

3. Material and methods

The data presented in this thesis were obtained from a newly established thinning experiment in central Sweden, providing short-term thinning results (**Papers I**, **II** and **III**), and from a long-term experiment spread across the country (**Paper IV**) (Figure 1).

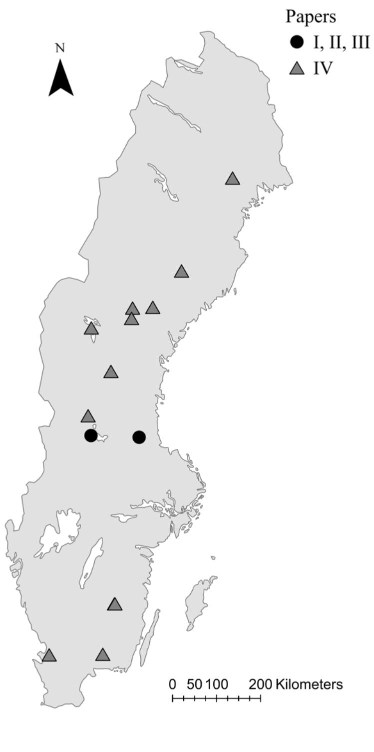

Figure 1. Map of the study sites in Sweden for Papers I, II, III and IV.

3.1 Experimental design and study description for Papers I, II and III

The research for **Papers I**, **II** and **III** was done in two Scots pine (*Pinus sylvestris* L.) forest experimental sites: Siljansfors and Jädraås (Figure 1), in which many different variables were analysed (Figure 2). Site index, based on dominant height at base age 100 years (SI_{100}) (Hägglund 1977) is 25-27 m at Siljanfors and 28-29 m at Jädraås. When the experiment was established in 2020, the stand was 40 years old in Siljansfors and 37 in Jädraås. In both sites, the soil rooting depth is more than 30 cm and the soils are classified as sandy-till moraine soils.

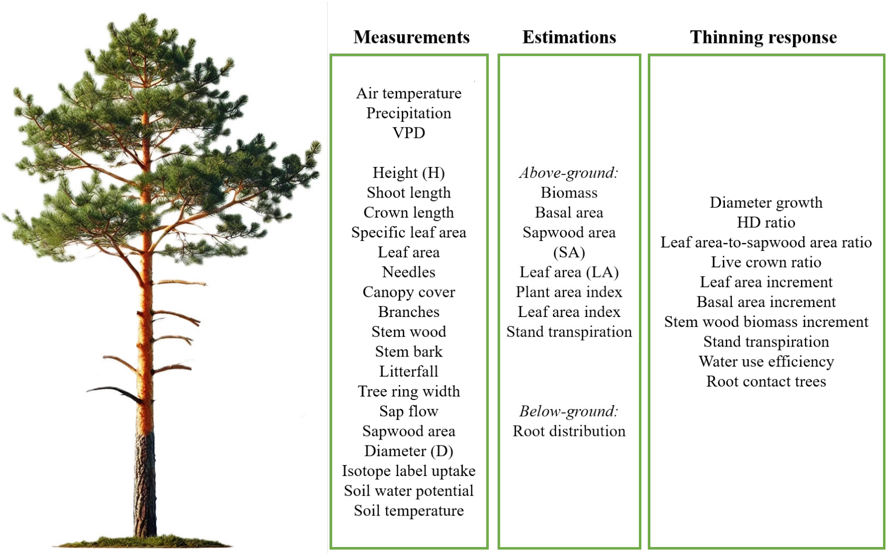

Figure 2. Variables used in Papers I, II and III on tree and stand level. This Scots pine tree has been generated with AI (DALL·E).

The experiment had four treatments: moderate thinning from above and moderate thinning from below, both with approximately 35% of basal area removed, one heavy thinning from below with 67% of basal area removed, and one unthinned control. All treatments were randomized within two blocks at each site. The removal in the thinning treatments included the establishment of strip roads. Each plot had an area of 0.1 ha. The stands started from the same baseline before thinning (Table 1), and the plots within each block had a maximum coefficient of variation of 9% in basal area before thinning.

Table 1. Mean plot attributes (N=4) in 2020, before first thinning.

Treatment	Stem density (trees ha^{-1})	Basal area (m^2 ha^{-1})	Quadratic mean diameter (QMD, cm)
control	1813	28.2	14.1
above	1830	27.9	14.0
below	1798	28.9	14.3
heavy	1743	27.5	14.2

3.1.1 Measurements (Paper I and Paper II)

The sites were measured for the first time before thinning. Measurements in Siljansfors took place in spring 2020 and in Jädraås in autumn 2020. Diameter at breast height (DBH) was measured in two directions on every tree in each plot. Tree height, height to the lowest living branch and bark thickness were measured on 20 sample trees per plot, which the five biggest DBH trees and 15 other randomly chosen trees. A second measurement was performed in autumn 2023, three years after thinning. Most sample trees were present in both measurements. However, sample trees removed during thinning were replaced in the second measurement using the same procedure from the first selection, applied to the remaining trees. A third measurement in the autumn of 2024 was done only in one of the blocks in Siljansfors, in which only DBH of all trees was measured. In Paper I, the 300 largest trees ha^{-1} were classified as the dominant trees.

3.1.2 Above-ground biomass quantification (Paper I)

Two destructive samplings were performed: one in autumn 2020, before thinning, and the other in autumn 2023, three years after thinning to quantify the above-ground biomass of tree compartments (stem wood, stem bark, living branches, dead branches and needles). In the first assessment (2020), 16 trees were sampled in total across all blocks and treatments, one tree in each plot, taking into consideration the diameter range of the sites. In 2023, 38 trees were sampled, ten of which were in the control, ten each in the moderate thinnings from above and from below, and eight in the heavy thinning from below. Trees were selected based on their initial DBH in 2020 and the quantiles in the first measurement, before thinning, and classified as big, intermediate and small trees. Big trees had a DBH above the 75% quantile (17 cm), intermediate trees had DBH between the 25% and 75% quantiles (11-17 cm), and the 25% quantile (11 cm) was the upper limit for small trees. Trees were equally sampled across the four treatments for the intermediate and big size classes (four trees in each class, per treatment). In the small size class, only six trees in total were sampled in the control and moderately thinned plots. No small-size tree in the heavy thinning from below treatment was sampled since not enough trees in this diameter class (< 11 cm) remained after thinning.

The samples' fresh weights were measured in the field, and dry weights later determined during the lab processing. Two systems of equations were built for each assessment year (2020 and 2023) using a statistical technique known as seemingly unrelated regression (SUR) with DBH as an independent variable and each biomass compartment (stem wood, stem bark, living and dead branches, and needles) as the response variable. This method was chosen since the biomass compartments within the same unit (a tree, in this case) are not independent from each other (Zhao *et al.* 2015; Siddique *et al.* 2021; Trautenmüller *et al.* 2021). This makes it is possible to calculate the model estimates simultaneously, while ensuring additivity and accounting for potential correlations between the error terms (Trautenmüller *et al.* 2021). In the case of the functions that were linearized by log transforming the response variables and later used for predictions, the correction factor proposed by Baskerville (1972) was used to avoid systematic bias.

3.1.3 Climate data (Paper II)

Long-term climate data on precipitation and air temperature were obtained from the Swedish Meteorological and Hydrological Institute (SMHI), using the closest possible station to the two sites Siljansfors and Jädraås. In both cases, the closest weather station was approximately 20 km away. For Siljansfors, the nearest station was in Mora, with data available from 1941. For Jädraås, the closest station was in Åmot, with data starting in 1996. These datasets were used to calculate the standardised precipitation evapotranspiration index (SPEI) to detect drought conditions, especially after thinning. Since the measurements in this study occurred within a short period after thinning (four years), a one-month scale was used to calculate SPEI. We used the SPEI classification suggested by Li *et al.* (2015).

3.1.4 Growth, sap flow and environmental monitoring (Paper II)

Manual dendrometers were installed in every plot, ensuring a proper replication across blocks and treatments. In total, ten trees per plot were equipped. Annual basal area growth was calculated for every treatment in each measurement year after thinning (2021-2024). Block 1 in Siljansfors was a highly equipped block with different environmental, growth and ecophysiology monitoring sensors. In this block, high-resolution dendrometers were installed on five trees of each treatment. Similarly, eight sap flow sensors were installed per treatment (one per tree). Moreover, soil water potential and soil temperature sensors (four sensors per plot) and air temperature were installed in each treatment, in the same block, which allowed for the comparison of growth data with other variables, particularly during drier periods. Furthermore, individual tree sap flow was later extrapolated to the whole stand using a standard method, which takes into account the sum of sap flow and basal area of trees being monitored with sap flow sensors and the total basal area for each plot (m^2 ha^{-1}).

3.1.5 Water use efficiency (WUE) (Paper II)

The SUR model created for Paper I in 2023 (See Topic 3.1.2) was used to estimate the stem wood dry biomass for each measurement year (2021-2024) and subsequently calculate the increments between years in Paper II. Stand transpiration was summarised per year. Annual stand-level water use efficiency (kg mm^{-1} ha^{-1} $year^{-1}$) was calculated as the sum of change in stem wood biomass increment between years divided by how much the stand transpired within each year.

3.1.6 Root distribution and leaf area index (Paper III)

To evaluate root distribution in the different treatments, deuterium-enriched water (^2H_2O) was applied in a 1 m^2 application zone in the two blocks in Siljansfors, in 2021, the first growing season after thinning, and 2024, four years after thinning. This method has been previously tested in Scots pine stands (Henriksson *et al.* 2021; Lutter *et al.* 2021), but not in a thinning experiment. The application occurred in mid-June after snowmelt. Before the application, all aboveground vegetation was removed. The applied solution was 15 litres of tapwater mixed with 500 ml of the isotopically labelled water. Watering cans and a circular frame to mark the application zone were used to enable a better and more uniform distribution of the labelled water.

After watering, the application zones were covered by plastic for four days to prevent evaporation.

Toward the end of the growing season, around mid-September, four wood cores were sampled from each tree present within a 6 m radius from the centre of the application zone, using an 8-mm diameter hole punch. For trees < 11.5 cm in DBH, only three samples were collected. The current year's (outer) annual ring was separated in the lab. Then, all separated ring samples from the same tree were pooled together. They were then dried and milled. From the milled wood samples, 0.35 mg was analysed with isotope ratio mass spectrometry (EA-IRMS, Flash EA 2000 and DeltaV, Bremen, Germany) at the Stable Isotope Laboratory at the Swedish University of Agricultural Sciences in Umeå.

From the spectrometry, the mass fraction of hydrogen (ωH) in g H / g dry mass, the ratio of deuterium (δ^2H) to the naturally abundant ^1H isotope were calculated for each tree, expressed on the VSMOW-SLAP scale in ‰ (Nelson 2000). The fraction present of the deuterium isotope (F_H), expressed in atom%, was calculated from δ^2H and a reference for the ratio (IAEA-TECDOC-825, 1995, Reference and intercomparison materials for stable isotopes of light elements). Since deuterium is naturally present in the environment, a threshold was established based on data from the Grimsö precipitation station. Thus, trees with atom% > 0.0145 and δ^2H > -70 were considered to have taken up the applied ^2H_2O, while values below this threshold were considered to indicate normal abundances in nature. Through the identification of the labelled trees, it was possible to determine how many trees overlap their root systems (root contact trees, RCT) in the 1 m^2 application zone.

Leaf area index (LAI) was indirectly measured with a LI-COR LAI-2200C Plant Canopy Analyzer (Goude *et al.* 2019). The measurements were done in two diagonals on the plots, always pointing north, three times every year (spring: early May, summer: mid-July and autumn: usually late September to early October), using a 90º view cap. The first measurement occurred in the autumn of 2020, before thinning, and continued during four years after thinning, until autumn 2024. Since indirect LAI estimation also captures branches and stems, specific functions need to be used to convert values obtained with the LAI-2200C into LAI. This study used the function of Goude *et al.* (2019).

3.2 Experimental design and study description for Paper IV

The data for **Paper IV** were obtained from a long-term thinning experiment in Sweden (Karlsson *et al.* 2013). Initially, two treatments were established: a selective thinning from below and a schematic thinning, based on a spatial selection of trees (two rows were harvested and two rows were left), both of which had 50% basal area removal. The treatments were randomized within blocks and, in total, 16 blocks were included in the study, from eight regions in Sweden. For most of the sites, there was only one block, except in three sites, which contained two blocks in each. The stands included in the study were planted between 1949 and 1958 as a provenance trial, and the thinning experiment was established between 1974 and 1981, when they were on average 25 years old.

Considering the planting design, coordinate systems were created for each treatment plot with the spatial location of each tree. The trees were spaced at 1.5 × 1.5 m (Figure 3). The area of the plots ranged from 0.05 to 0.2 ha. Since the trees present in the buffer zone were not measured, the net plots were reduced by trimming at least 3 m off the plot edges, so that all neighbouring trees within at least 3 m had a known size and distance. Through the years, the blocks were managed with different strategies. Ten blocks maintained the initial treatments, with no other thinnings in the management plan, while the other six blocks were thinned more than once (thinning was performed as selective thinning from below with 25% basal area removal for both treatments), which led to two different experiments. The plots were remeasured from 3-7 times.

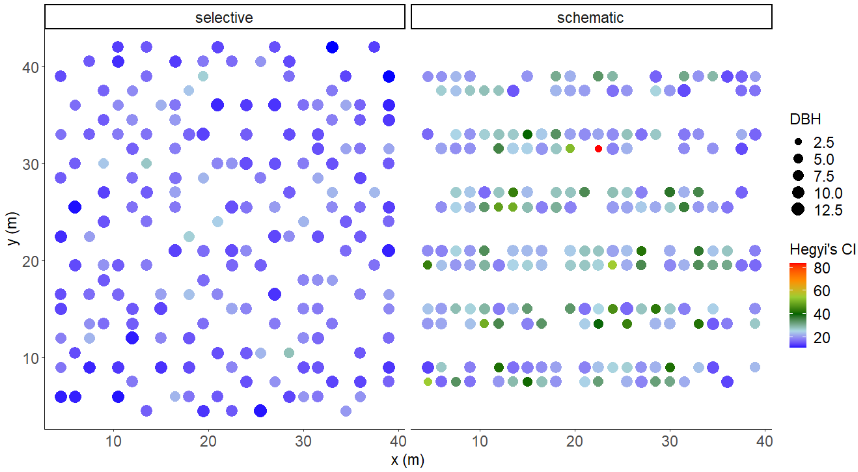

Figure 3. Representation of the spatial location of the trees for one of the sites after selective or schematic thinning treatment establishment. The size of the points is proportional diameter at breast height (DBH). The point colours indicate competition based on Hegyi's distance-dependent competition index. Higher CIs show that the tree is subject to more competition.

3.2.1 Growth predictions with and without competition indices

The growth between measurements 1 and 2 was used to develop five-year interval growth functions, both with and without competition indices (CIs). Three individual tree models were used for predicting diameter growth: one without a CI (BA-base), one with a distance-dependent CI (BA-DDCI), and one with a distance-independent CI (BA-DICI). These predictions were then used to estimate basal area at the stand level, allowing comparison of model performance against observed stand-level data (BA-stand). Plots within sites were used as random effects. Treatment (selective and schematic thinning) was initially tested, but it was not significant and so was removed from the final model.

Two distance-dependent and three distance-independent CIs were calculated and included in the base growth model. Competitor trees were selected irrespective of their distance from the subject tree. Thus, all trees in the entire plot other than the subject tree were considered as competitors. For the distance-dependent CIs, the spatial distances between trees were explicitly included in the calculations.

3.2.2 Comparison of thinning design and thinning strategies (Paper IV)

The periodic annual increment (PAI) of stem volume (m^3 ha^{-1}) between the first two measurements following thinning was compared between treatments (selective or schematic). Standing and total volumes were compared between treatments and thinning strategies (thinned once or thinned more than once). To test the heterogeneity of stand structure, the Gini coefficient was calculated (Bourdier *et al.* 2016; Pretzsch *et al.* 2022).

3.2.3 Analysis

The data for all four papers were processed in R, version 4.3.0 (R Core Team 2023). To test differences between the treatments, when suitable, an analysis of variance or covariance (ANOVA or ANCOVA) and pairwise comparisons were made. The Tukey test with 95% level of confidence was used in the *emmeans* package in R (Lenth 2023). The Shapiro-Wilk test was used, in addition to visual inspection, to test the normality of the residuals. If residuals were not normal, log, square root or inverse transformations were used. In the case of log transformations of response variables for functions that were later used for stand level estimation, the correction factor of Baskerville (1972) was used when back-transforming the values. When treatment comparisons were made using the sample trees i.e. analysis of height-to-diameter ratio (HDR) and live crown ratio (LCR), only sample trees present in both measurements were tested (Paper I).

For analyses made on one or two blocks e.g. WUE on tree and stand level from only block 1 in Siljansfors (Paper II) and analysis of root distribution made in two blocks (Paper III), only descriptive statistics were used (mean and standard error), due to a low number of replicates. Moreover, the Pearson correlation (r) was used to evaluate the relationship between stand WUE and SPEI for the different thinning treatments (Paper II). Due to a system malfunction in the moderate thinning from above treatment in 2023 and 2024, no transpiration or WUE values were calculated for this treatment in those years (Paper II).

4. Main results and discussion

4.1 Treatment effect on allocation patterns and above-ground biomass (Paper I)

Thinning significantly reduced the total above-ground biomass (Figure 4), with the unthinned control having higher total standing biomass than the thinned treatments up to three years after thinning (Figure 4b). The dominant trees in the heavy thinning from below had an increased mean annual stem wood dry weight increment and differed significantly from the control and moderate thinning from above ($p < 0.005$), but not moderate thinning from below ($p = 0.053$). Similarly, the heavy thinning from below had the highest mean increment in individual tree leaf area for the dominant trees, followed by the moderate thinnings from above and below, which did not differ from each other, but differed from the control (Figure 5). Total standing biomass decreased significantly in the short-term and may also be reduced in the long-term, as has been shown by other studies in Sweden and Finland (Nilsson *et al.* 2010; Bianchi *et al.* 2024), and is one of the major disadvantages of heavier thinnings.

A thinning response was also detected in height-to-diameter ratio (HDR), live crown ratio (LCR) and leaf area-to-sapwood-area ratio (A_L:A_S) three years after thinning. The heavy thinning from below caused a significantly lower HDR three years after thinning, which has been found in other studies (Naidu *et al.* 1998; Mäkinen & Isomäki 2004c; Deng *et al.* 2019). Moderate thinning from below and heavy thinning from below had a significantly higher LCR than the control, and they did not differ from moderate thinning from above. Hynynen (1995) found a significant thinning response in LCR five years after thinning in Scots pine stands, while such a response was detected within three years in this study. Furthermore, there was an increase in A_L:A_S for the thinned treatments in comparison to the control, especially in the heavy thinning from below, which showed the highest mean ratio. Giuggiola *et al.* (2013) suggest this is likely due to an increased water availability in the thinned stands, or more resources in general (light, water and nutrients).

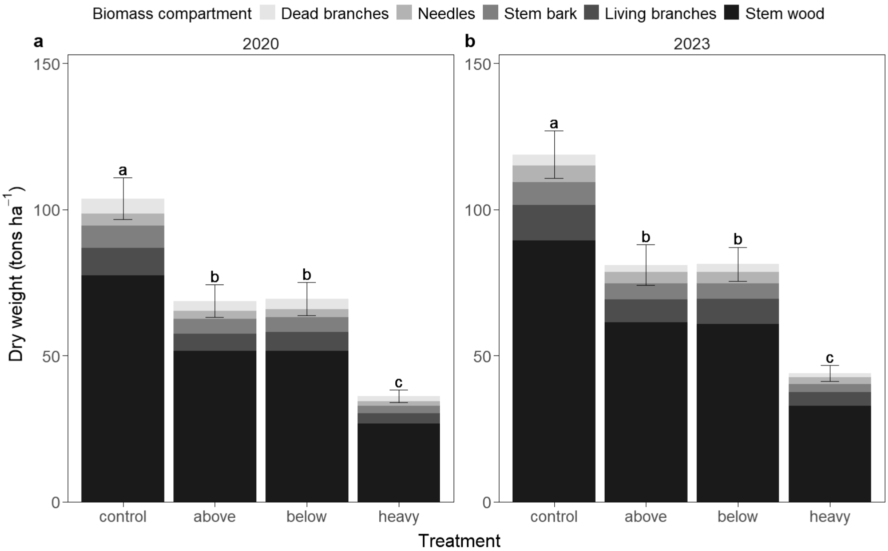

Figure 4. Biomass partitioning among the different above-ground compartments (dead branches, needles, stem bark, living branches and stem wood) for all retained trees after thinning, in 2020 (a), and three years after thinning, in 2023 (b). Error bars show the standard error of the total biomass across the four blocks. Bars that have letters in common within the same year do not differ from each other ($p > 0.05$).

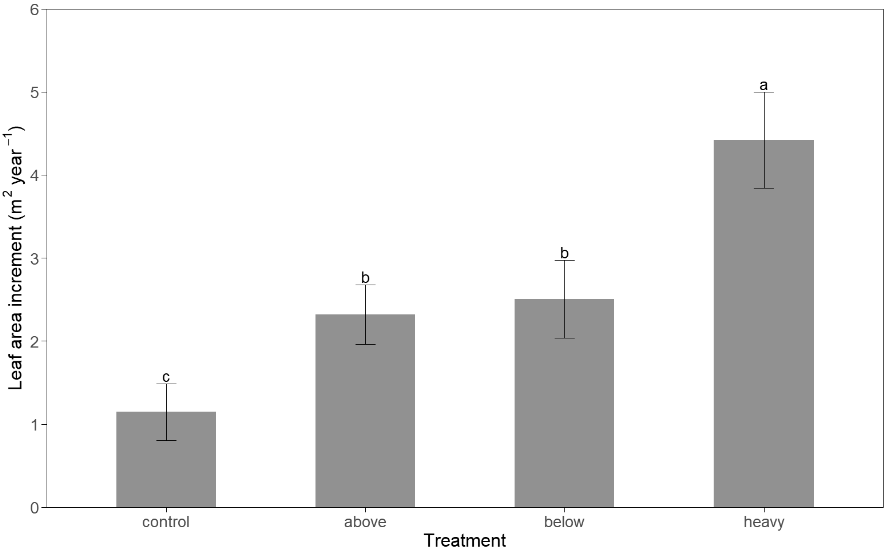

Figure 5. Mean annual leaf area increment of the dominant trees (300 largest trees ha^{-1}) three years after thinning. Error bars represent the standard error across the four blocks. Bars that have letters in common do not differ from each other ($p > 0.05$).

4.2 Effect of thinning on growth, stand transpiration and water use efficiency (Paper II)

No significant thinning response was detected in the first year after the thinning for individual tree annual basal area increment (BAI) at breast height (1.30 m) calculated from tree ring measurements ($p = 0.179$; Figures 6 and 7). However, a positive response was already detected for the heavy thinning from below in the second year after thinning. It showed a significantly higher basal area increment (11.9 cm^2 year^{-1}) than the control (7.5 cm^2 year^{-1}, $p = 0.004$) and moderate thinning from below (7.9 cm^2 year^{-1}, $p = 0.007$), but not moderate thinning from above (8.9 cm^2 year^{-1}, $p = 0.083$). The other treatments were not significantly different from each other. From the third year after thinning (2023), basal area growth was significantly higher for the heavily thinned treatment (12.8 cm^2 year^{-1}, $p < 0.006$) in comparison to all other treatments. From 2013, trees began a downward trend in BAI (Figure 7). Since the thinning intervention, the trees in the heavily and moderately thinned treatments have reversed the recent declining trend in BAI, while the control trees have not. Other studies have also found a significant increase in individual tree BAI in Scots pine stands for thinning treatments in comparison to unthinned controls (Sohn *et al.* 2016a; Candel-Pérez *et al.* 2018; Navarro-Cerrillo *et al.* 2019).

Basal area increment, measured with manual dendrometers, increased significantly under heavy thinning in comparison to the control, from the first year after thinning. The moderate thinning treatments from below and from above started to differ from the control in the third and fourth years after thinning, respectively.

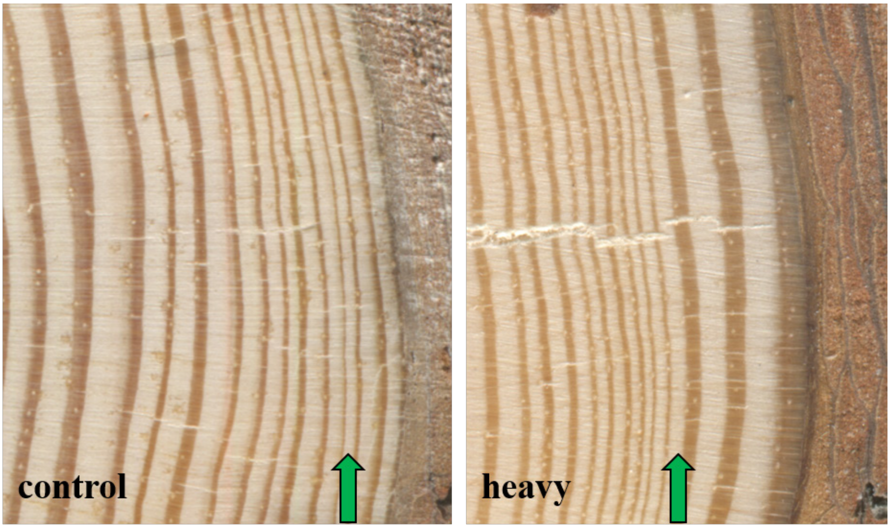

Figure 6. Tree rings at breast height (1.3 m) for the unthinned control and heavy thinning from below treatments. The arrow indicates 2021, first year after the thinning. The photos are examples taken from the analysed discs during the biomass harvest.

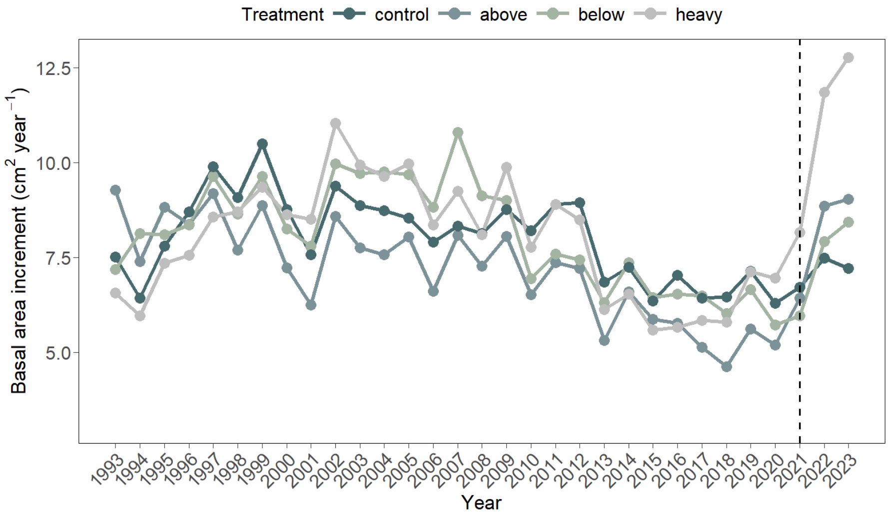

Figure 7. Mean annual basal area increment (cm^2 year^{-1}) for the four treatments at breast height. The dashed line indicates the first year after thinning.

Stand transpiration was higher in the control than in any thinned treatment, in all measurement years (2021-2024). In the first year after thinning (2021), there was a reduction of 36% and 40% in stand transpiration for the moderate thinnings from above and from below, respectively, and 65% in the heavy thinning from below, compared to the control. A decrease in stand-level transpiration after thinning has also been seen in other species, including lodgepole pine (Wang *et al.* 2019), Aleppo pine (del Campo *et al.* 2014), Norway spruce (Gebhardt *et al.* 2014; Zavadilová *et al.* 2023) and *Eucalyptus nitens* (Forrester *et al.* 2012). A study of a mixed Scots pine and Norway spruce forest in central Sweden initially detected a decrease in stand transpiration immediately after removal of 24% of basal area (Lagergren *et al.* 2008). However, within the first growing season after thinning, the thinned plot started to transpire more than the control, which continued through the second post-thinning year (Lagergren *et al.* 2008), which was not the case in this study for any of the four assessment years.

Total annual stem wood biomass production (kg ha^{-1} year^{-1}) was higher for the moderate thinning from above in three of the four assessment years. The exception was 2022, when the control produced more. The heavily thinned treatment produced the least total stem wood biomass, except in 2024 when the unthinned treatment produced less.

The heavy thinning showed a continuous increase in both tree- and stand-level water use efficiency (WUE) over the years (Figure 8). The control had the lowest stand WUE in all assessment years. Furthermore, a negative correlation between WUE and SPEI_min was detected for all treatments (Figure 9), with the strongest (but not significant) correlation being found for the heavily thinned treatment ($r = -0.81$, $p = 0.187$). The correlation between WUE and SPEI_mean was significant for the heavy thinning from below ($r = -0.98$, $p = 0.015$, Figure 10). Although this study's duration is limited, with four years of assessment, we detected a negative correlation of stand-level WUE and SPEI and a higher efficiency in the heavy thinning treatment.

This trend, along with other findings in this study, suggests that trees in the thinning treatments, especially the high intensity thinning, adapt their WUE more easily to water availability, displaying higher efficiency in drier periods. During severe dry periods, Sohn *et al.* (2016a) suggest thinning will not prevent growth losses, but found recovery after drought to be higher for the heavy thinning treatment, in comparison to the control. Thinning increased both tree- and stand-level WUE for a Norway spruce monoculture from the first year after thinning (Gebhardt *et al.* 2014). Wang *et al.* (2020) found that thinning in mountain pine had no impact on stand-level WUE when there was no water stress and did not differ from the unthinned treatment, but thinning significantly increased stand WUE in drought conditions (Wang *et al.* 2020). Trees had higher WUE on thinned plots, when to compared to the control in a study with Aleppo pine (Fernandes *et al.* 2016).

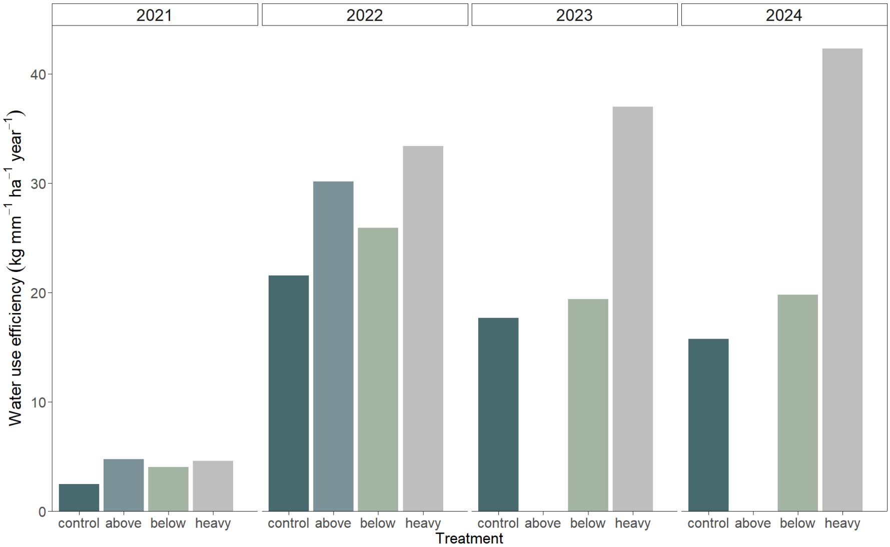

Figure 8. Stand water use efficiency (WUE) for the treatments during the four years after thinning (2021-2024).

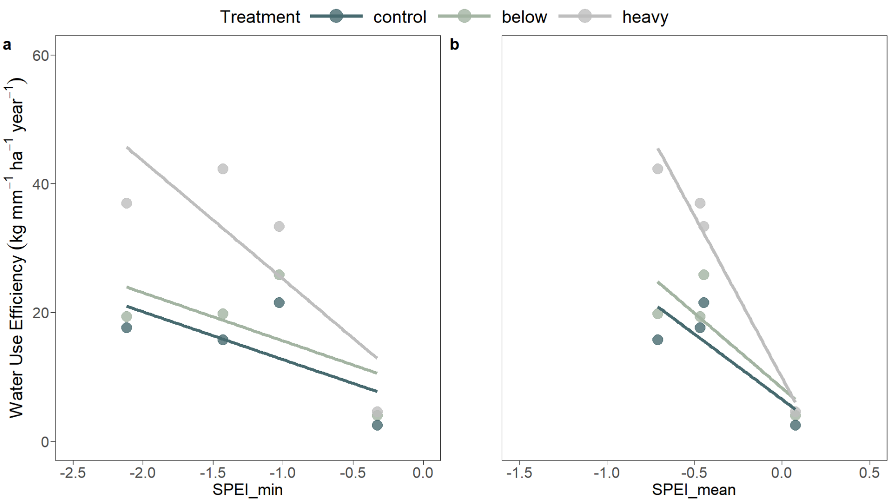

Figure 9. Annual stand-level water use efficiency (kg mm^{-1} ha^{-1} year^{-1}) in relation to the standardised precipitation evapotranspiration index (SPEI), which here is divided into SPEI_min (a), which includes the lowest SPEI values from the beginning of the growing season (May, June or July), and SPEI_mean (b), which considers the average SPEI values over the growing season (May-October).

4.3 Root distribution and leaf area index (Paper III)

Thinning, by design, reduced the density of trees within a 6-m radius from the centre of the application zone, with the control presenting the highest stem density. The number of labelled trees showing enriched deuterium content in the application zone varied between 1 and 7, across all blocks and treatments (Table 2). On average, the number of root contact trees (RCT) was higher in the control and moderate thinnings than in the heavy thinning from below treatment (Table 2). The furthest distances of a ^{2}H labelled tree were 4.5 m in 2021 and 3.2 m in 2024, both of which were found in the control treatment (Figure 10).

On average, across all blocks and treatments in this study, the number of RCT was 4 per m^2. Earlier studies with Scots pine in Sweden (Henriksson *et al.* 2021; Lutter *et al.* 2021) found, on average, 8 and 4 RCTs, respectively.

Table 2. The number of ^{2}H labelled trees sampled within a 6-m radius of the centre of the application zone (a 1 m^2 circle), referred to as root contact trees (RCT), per m^2.

Treatment	**Root contact trees per m^2**				
	2021		**2024**		**Mean**
	Block 1	**Block 2**	**Block 1**	**Block 2**	
control	3	4	7	1	3.8
above	5	5	5	5	5.0
below	5	4	4	1	3.5
heavy	3	2	3	2	2.5

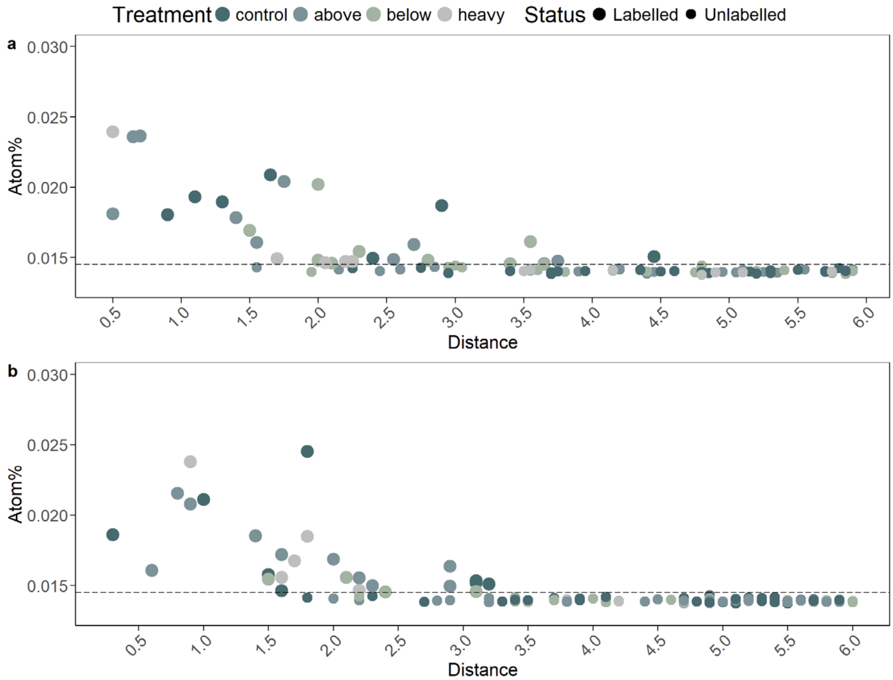

Figure 10. The proportion of ^{2}H (Atom%) and the distance for trees analysed within 6 m of the centre of the application zone in each treatment.

The treatments started from the same baseline before thinning, showing an average LAI of 2.0 m^2 m^{-1} (Figure 11). After thinning, LAI was reduced to 1.3 m^2 m^{-2} in the moderate thinnings and 1.0 m^2 m^{-2} in the heavy thinning. Although there was an increase in LAI for all treatments between years through direct measurements (Paper I), such increase was not detected with indirect measurements of LAI. The seasonal variation was consistent, with the peak in LAI usually being observed in the autumn (Figure 11). Other studies have found a seasonal peak in LAI for Scots pine in August (Beadle *et al.* 1982; Stenberg *et al.* 1994).

Indirect measurements of LAI with LAI-2200c may be affected by environmental conditions, such as solar elevation angle, which is lower during late autumn (Heiskanen *et al.* 2012), and the functionality of the equipment itself (Stenberg *et al.* 1994). Nonetheless, it can be a useful tool to detect stressful periods. In this study, unlike in the other measurement years, no “autumn peak” was observed in 2023. More summer needle fall, compared to summer and autumn combined, was detected in 2023 (21%)

than in 2021 (9%) and 2022 (12%). This pattern was consistent for all treatments, including the control. The earlier and higher senescence of needles, along with the absence of a peak in LAI in autumn 2023, coincided with the extreme dry period calculated with the SPEI. In June 2023, SPEI was -2.12 (Paper II). Trees were possibly shedding older needles slightly earlier in the season to adapt to water deficit.

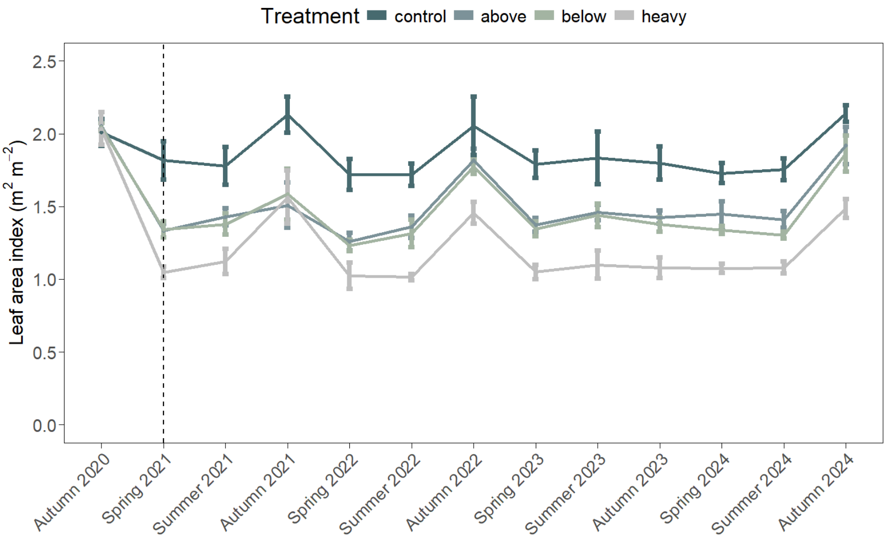

Figure 11. Leaf area index (LAI), indirectly measured with the LICOR-2200 for the four treatments, from the autumn of 2020 (before thinning) until autumn 2024. The error bars represent the standard error of the mean for the four blocks. The vertical dashed line in the spring of 2021 indicates the first measurement after thinning.

4.4 Stand development and structure (Paper IV)

Basal area (m^2 ha^{-1}) did not differ among treatments (selective and schematic thinnings) in the short-term, on average, 6 years after thinning ($p = 0.214$) or in the long-term, on average, 35 years after first thinning, for stands that were thinned once ($p = 0.092$) or more than once ($p = 0.736$). There were no significant differences between treatments for PAI for volume (m^3 ha^{-1}) between the first two measurements ($p = 0.850$) or for standing volume at the second measurement ($p = 0.768$). When comparing the total volume in the last measurement, no difference was found between treatments in blocks that were thinned more than once ($p = 0.673$; Figure 12a). Likewise, there were no significant differences in total volume for blocks that were thinned only once ($p = 0.060$; Figure 12b). Standing volume also did not differ significantly among treatments at the last measurement.

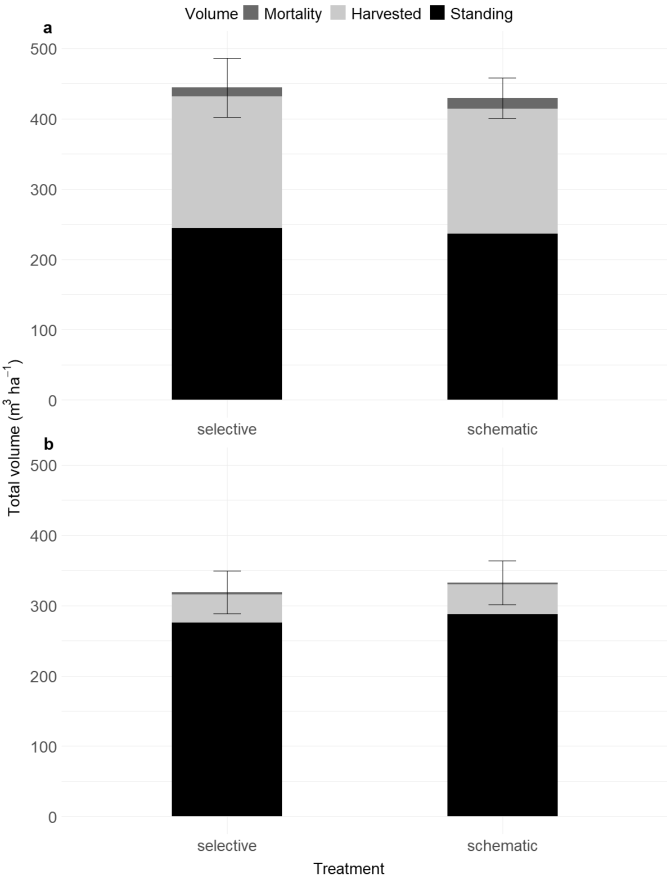

Figure 12. Total volume production (m^3 ha^{-1}) of the blocks thinned more than once (a) and only once (b), subdivided into mortality, harvested, and standing volumes. The error bars represent the standard error of the total volume within the thinning treatments. The site index ranged from 23 to 29 for blocks that were thinned once and from 24 to 32 for blocks that were thinned more.

For sites that have had only one thinning, the selective thinning treatment showed a significantly higher mean annual DBH growth (0.32 cm $year^{-1}$) than the schematic thinning (0.29 cm $year^{-1}$). Whereas that difference was not significant in sites that have had more than one thinning. Mean annual DBH growth was 0.42 cm $year^{-1}$ for both treatments. Similarly, McCreary and Perry (1983) found that selective thinning showed a significantly higher mean DBH increment than strip thinning. Despite a higher mean increment in DBH for the selective thinning treatment, Mäkinen *et al.* (2005b) did not find a significant difference among the treatments (selective, half-systematic and systematic). However, the authors argue that a higher mean diameter increment for selective thinning based on basal area removal would make sense, since the growing space for the retained trees, enabled through competition release, is more evenly distributed.

Thinning forms and strategies may result in different stand structure and resource distribution in the short-term, and potentially also in the long-term (Sprugel *et al.* 2009). In this study, stand structure was more heterogeneous in sites that received only one thinning for the schematic thinning treatment, since there were generally more smaller trees, and a higher stem density. This is seen in the higher Gini coefficient and coefficient of variation (CV; Table 3). Consequently, mean DBH was mostly concentrated in smaller diameter classes for the schematic thinning, in comparison to the selective thinning. In sites that were thinned more than once, the original trend started to diminish, and differences in heterogeneity among treatments were no longer significant (Table 3).

The schematic thinning treatment has a higher stem density and more smaller trees, making these stands more heterogeneous, whereas the selective thinning stands have a more homogenous structure. Other studies have shown that schematic thinning treatments lead to a more heterogeneous forest (Ahnlund Ulvcrona *et al.* 2017; Nuutinen *et al.* 2021; Kankare *et al.* 2022; Ronoud *et al.* 2022). When comparing the predicted basal area (m^2 ha^{-1}) at 5, 10, and 35 years after thinning, no significant differences were found among the tested models, regardless of whether competition indices (CIs) were included. This indicates that the trees' spatial distribution does not drive tree growth and stand development, but rather retained basal area and size distribution. Furthermore, Sprugel *et al.* (2009) argue that light distribution might not vary so much among different stand structures, which could also explain why no significant short- or long-term differences in standing volume or basal area were detected in the different thinning treatments.

Table 3. Coefficients of variation and Gini coefficients in the first and last measurements. N is the number of blocks, and sd is standard deviation.

Treatment	Thinning strategy	First measurement			Last measurement		
		N	CV% ± sd	Gini ± sd	N	CV% ± sd	Gini ± sd
Selective	Thinned once	10	18.17±1.78	0.10±0.010	10	17.47±3.12	0.10±0.018
Schematic	Thinned once	10	29.59±4.65	0.16±0.025	10	23.98±1.89	0.13±0.010
Selective	Thinned more	6	16.54±1.47	0.09±0.009	6	13.16±1.42	0.07±0.008
Schematic	Thinned more	6	28.11±3.13	0.16±0.018	6	15.27±3.46	0.08±0.019

4.5 Management implications (Papers I, II, III and IV)

The choice of thinning form (selective thinning from below, selective thinning from above and schematic thinning) and strategy (intensity and frequency of thinning) will depend on management goals. Thinning significantly reduced standing biomass in the short term for the thinning treatments, especially in the heavy thinning from below, and these effects could potentially prevail in the long term (Nilsson *et al.* 2010; Bianchi *et al.* 2024), which is a shortcoming of high-intensity thinnings. However, two of the short-term studies have shown that trees, especially in the heavy thinning from below treatment, but also in the moderately thinned ones, have quickly adapted their allocation strategies by increasing stem wood biomass production and stand WUE, in comparison to the unthinned control, especially in drier conditions. These results highlight that thinning and, particularly heavier thinning, could be a useful strategy for mitigating water stress in Scots pine forests that are still far from their harvest age, at least in the short term. Since moderate thinning from below and above performed similarly in the first four years, due to the same basal area removal, intensity of thinning rather than thinning form drove the responses. Advantages derived from thinning, however, may not hold in the long term. If the aim is to mitigate drought, Sohn *et al.* (2016a) recommend shorter thinning intervals. Furthermore, the responses may depend on site-specific conditions. In southern Sweden, where maximum summer temperatures tend to be the highest, drought damage risk is considered to be higher (Aldea *et al.* 2024; Ogana *et al.* 2024) than in central (sites for Papers I, II, III) and northern Sweden. Therefore, water stress mitigation by thinning may be even more apparent in sites with higher susceptibility to drought stress (Sohn *et al.* 2016b).

Similarly to the comparison between selective thinning from below and above, selective thinning from below and schematic thinning did not differ significantly in total and standing volumes in the last measurement. This is due to them having the same basal area removal at the time of thinning. Thinning from above and schematic thinning resulted in different thinning ratios, but they still show similarities. For example, both provide economic advantages from the first commercial thinning when larger trees are cut (Nilsson *et al.* 2010; Witzell *et al.* 2019). Schematic thinning requires less fuel consumption, with cost and emissions benefits, due to increased harvester productivity (de la Fuente *et al.* 2022). Thinning from above and schematic thinning would also lead to longer rotations if the aim were to reach a target diameter. From an ecological perspective, longer rotations benefit biodiversity like lichens and ectomycorrhizal mushrooms (Roberge *et al.* 2016; Petersson *et al.* 2023) as well as promoting deadwood through natural mortality and increasing the size of retention trees in final fellings (Koskela *et al.* 2007). Schematic thinning could also benefit biodiversity by creating a more heterogeneous stand structure (Ahnlund Ulvcrona *et al.* 2017; Witzell *et al.* 2019).

If the management goal is to mitigate short-term drought impacts on tree growth, especially in severely dry sites, heavy thinning from below has shown the most promise. If the goal is to reduce water stress while maintaining higher standing biomass and income at final felling, shorter rotations with moderate thinning from below seem to be more suitable. If the priority is to gain more income from first thinning, and potentially higher biodiversity benefits, moderate thinning from above and schematic thinning would be more appropriate, despite longer rotations.

Increased frequency and intensity of droughts may make thinnings preferable to clearcuts, particularly in drier areas. Thus, a more flexible thinning plan would be beneficial for climate change mitigation. Larger forest holders usually keep a prioritized list of stands to thin. The measures are executed in a set order depending on density and dominant height. In the future, such planning systems might benefit from including a drought risk variable, with more dynamic options for thinning intensity and thinning intervals.

The long-term experiment comparing selective and schematic thinning showed that the exact spatial pattern of tree retention does not matter for basal area (m^2 ha^{-1}) and total volume (m^3 ha^{-1}). Likewise, in the short-term, moderate thinnings from above and below have performed quite similarly so far. This indicates that the amount of basal area retained after thinning, its size distribution, and overall competition are more important influences on tree growth and stand development than the spatial distribution of trees. Thus, when it comes to tree selection in thinning operations, it is more important to focus on vitality, size and quality rather than even spacing.

5. Conclusions

Above-ground biomass allocation: A swift change in allocation strategies was observed within three years after thinning. This change primarily occurred in terms of a significant increase in dbh and stem wood biomass increment for the dominant trees in the heavy thinning from below, as well as an increased individual tree leaf area and leaf area-to-sapwood-area ratio for all the thinned treatments, when compared to the control, for the same set of trees.

These findings show a swift adaptation of the trees in the thinned treatment and, especially in the heavily thinned treatment, suggesting that Scots pine is able to quickly adapt to greater resource availability enabled by competition release.

Water use efficiency: Stand transpiration was higher in the control compared to the thinned treatments. Individual tree basal increment area increased significantly for trees in the thinning treatments compared to control. The heavily thinned treatment, in particular, presented an increased WUE, on tree level and on stand level, especially in drier periods (lower SPEI values). Moderate thinnings also increased stand WUE, in comparison to the control.

These findings indicate that the heavy thinning from below and, to a lesser extent moderate thinning, have the potential to mitigate drought stress for Scots pine trees, at least in the short term.

Leaf area index and root distribution: Mapping root distribution and root uptake of isotopically labelled water indicated that Scots pine trees in a midrotation forest, in general, take up little water more than 3-4 m from the stem, and the number of trees with overlapping root systems, on average, was 4 trees m^{-2} across all blocks and treatments. This study provides novel insights into how belowground competition and active roots can be mapped in forest management experiments, which is valuable for future research.

Although the indirect LAI measurements did not detect increases between years, they provided important insight into the seasonal variation within years, along with the needle fall data. The higher proportion of needle senescence in the summer 2023, which was observed for all treatments, likely indicates a drought adaptation strategy of Scots pine trees.

Thinning form and strategies: Selective thinning from below showed significantly higher mean annual DBH increments for the individual trees (cm $year^{-1}$) than the schematic thinning. Schematically thinned stands, if thinned only once, resulted in more heterogeneous forests, although total volume and stand basal area did not significantly differ between selective and schematic thinning. These stand structure differences started to diminish if the stands were thinned again using selective thinning, which allowed better-quality stems to be retained at a later stage.

If volume production is the main goal, choosing one thinning form over the other will have little impact at the end of the rotation for Scots pine stands. However, if thinning only once, schematic thinning will require a longer rotation to reach a specific target diameter in the stand.

The findings from this thesis can be used to improve thinning guidelines and as a basis for managing resilient Scots pine forests under climate change.

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Popular science summary

Scots pine is one of the most important tree species in Europe and it represents approximately 40% of the total standing volume in Swedish forests. Growing this species in dense, even-aged stands has been an efficient, predictable and profitable method for providing fibre, timber and bioenergy. Harvesting is usually done in one or two commercial thinnings during mid rotation, in addition to final felling. Thinnings can be done with double purposes: to procure an early income and to shape the future of the forest stand by selections on which trees to harvest or to retain. Currently, Swedish thinning templates are made to balance between maintaining a high density for increased production and reducing the risk of tree mortality due to self-thinning, using site fertility (nitrogen availability) as an index for how much to harvest. However, Swedish conditions for forestry are changing because of global warming. In areas where nitrogen has always been considered as the main limiting factor to tree growth, we can now see indications of increasing water deficit. If water becomes a limiting factor in Swedish forests, due to a higher frequency and intensity of years with extreme drought events, then we might need to re-consider management strategies in Scots pine stands.

This thesis provides important knowledge for understanding how Scots pine trees behave in response to thinning and environmental conditions. In thinned stands, and especially the heavily thinned ones (with more than 60% removal of the basal area), a swift response in allocation strategies in the aboveground biomass was detected. The dominant trees in the thinned stands grew faster in diameter at breast height and leaf area for each tree, but did not differ in height growth for the same set of trees, when compared to the unthinned plots. The trees in the thinned plots generally presented a longer living crown. These responses were detected within three years after thinning. The results also show that thinning, especially heavy thinning, has a high potential to be an effective alternative to mitigate drought stress in Scots pine forests in the boreal zone, by using water more efficiently to produce wood, at least in the short-term.

Populärvetenskaplig sammanfattning

Tall är ett av de viktigaste trädslagen i Europa och det står för cirka 40% av den totala volymen i svenska skogar. Tall sköts oftast i täta, likåldriga bestånd och det har varit en effektiv, förutsägbar och lönsam metod för att tillhandahålla fiber, virke och bioenergi. Avverkning sker vanligtvis i en eller två kommersiella gallringar och sen en slutavverkning. Gallringarna göras ofta med dubbla syften: att generera en tidig inkomst och att forma framtiden för beståndet genom urval av vilka träd som ska avverkas eller behållas. De gallringsmallar som används, utgår från bonitet och ska balansera mellan en hög täthet för ökad produktion men inte så tät att det orsakar självgallring. Förutsättningarna för skogsbruk förändras dock på grund av den globala uppvärmningen; i områden där kväve tidigare har ansetts vara den mest begränsande faktorn för tillväxt kan vi nu se indikationer på ökande vattenbrist. Om vatten blir en begränsande faktor i svenska skogar, på grund av en högre frekvens och intensitet av år med extrema torkahändelser, kan vi behöva ompröva skötselstrategier i tallbestånden.

Den här avhandlingen ökar förståelsen hur tall svarar på gallring. I gallrade bestånd, och särskilt efter hård gallring (med mer än 60 % grundyteuttag), uppmättes en snabb respons och förändring i allokering i biomassa ovanjord.

De dominerande träden i de gallrade bestånden växte snabbare i brösthöjdsdiameter och bladarea för enskilda träd, men inte i höjdtillväxt jämfört med träd i ogallrade ytor. Träden i de gallrade ytorna hade i allmänhet en längre levande krona. Skillnaderna uppmättes redan inom tre år efter gallring. Resultaten visar också att gallring, särskilt hård gallring, har potential att vara ett effektivt alternativ för att mildra torkstress i tallskogar i den boreala zonen, genom att använda vatten mer effektivt på färre träd, åtminstone på kort sikt.

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IV

forests

Article

Select or Not? Comparing the Impact of Selective and Schematic Thinning on Scots Pine Tree Growth and Stand Structure

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Abstract: The first commercial thinning usually entails a high cost in harvest operations and a low resulting income. From a practical forestry perspective, a schematic spatial selection might be more efficient than a selective approach. Therefore, this study aimed to compare basal area, total and standing volumes, and periodic annual increment (PAI), as well as stand structure, between different thinning designs (selective and schematic thinning) and strategies (thinning once or more than once) over a long-term monitoring period of Scots pine (*Pinus sylvestris*) plantations in Sweden. We also evaluated the relevancy of distance-dependent competition indices (CIs) in individual tree growth models by comparing growth model predictions with the use of distance-dependent and distance-independent CIs. Despite higher heterogeneity in schematically thinned stands, there were no significant differences in standing and total volumes ($m^3 \cdot ha^{-1}$) among treatments in the short or long term. Although the inclusion of a distance-dependent CI improved the model slightly, distance-independent models predicted diameter growth just as effectively. Schematic thinning could be a viable option for a first commercial thinning or one-time thinning if, at least, one more thinning is included in the management plan, or if the motivating interest is mainly volume.

Keywords: forest management; pine; competition indices

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1. Introduction

Thinning is one of the main management practices in forestry, as it plays a key part in the increase in individual tree growth and the regulation of wood quality [1]. Important reasons for thinning include removing low-quality stems [2], increasing resource availability (e.g., water, light, and nutrients) for the remaining trees [1,3], diversifying forest structure and generating income before final felling [4], and reducing mortality rates due to self-thinning [5,6]. In Swedish forestry, the first commercial thinning usually entails thinning selectively from below, i.e., the biggest, most productive trees are kept on the stand and the smallest and/or damaged trees are harvested, when the dominant trees reach a height of over 11–12 m [7]. The 1960s saw an increase in mechanization in harvest operations, accompanied by a higher thinning intensity in early stages, consequently reducing intensity as the stands got older [1,8]. In that particular context, the possibility of having complete systematized thinning operations became a topic of interest [1]. When it comes to the first commercial thinning specifically, forest owners are still often reluctant to perform systematized thinning due to the high cost of harvest operations and the low income derived from it [9]. The importance of finding a more cost-efficient thinning method is, therefore, as prevalent now as it was decades ago, a fact shown by various other studies [1,9–11]. In their study, for example, the authors of [12] showed that mechanized line thinning increased productivity and enabled low-cost thinning operations in comparison to conventional single-tree selection thinning.

Schematic thinning, i.e., boom-corridor cuttings, can lower the number of damaged trees and reduce fuel consumption and emissions, offering not only an attractive economical alternative, but a more environmental friendly one [13]. Potentially, schematic thinning also increases biodiversity due to a more heterogeneous stand structure developing [11,14], especially if it is a mixed forest or if there is ingrowth of other tree species.

Scots pine (*Pinus sylvestris*) is the most well-distributed conifer species worldwide [15]. It is considered to be a shade-intolerant, light-demanding species [16], and it has been reported that competition leads to reduced diameter increment in stands of this species [17]. While using another study's [18] competition index (CI), the authors of [19] found that competition in four types of Scots pine stand structures (a mature even-aged stand, a plantation, one with oak understory, and an uneven-aged stand) presented a negative relationship to stem diameter in all stands. When evaluating the relationship between current diameter increment and the CI, the authors suggested that, in low stand densities (<1000 stems·ha^{-1}), the competition between trees may not cause severe growth limitation [19].

The success of the first commercial thinning in Scots pine stands and further stand development is highly dependent on precommercial thinning (PCT), with early and intensive PCT generally increasing merchantable volume and the profitability of harvested wood during the first commercial thinning [20]. However, the maintenance of a high stem density, e.g., >3000 stems·ha^{-1}, in the early development of Scots pine stands has been shown to promote good external wood quality with smaller branches [21].

Thinning can be selective, systematic, or half-systematic [1,10]. The first is generally applied on the basis of size selection, i.e., dominant and codominant trees are prioritized, with the removal of smaller and/or damaged trees (thinning from below), or bigger trees are removed from the stand to allow the suppressed, subdominant trees to grow better (thinning from above) [8,10]. Schematic thinning, on the other hand, refers to when the thinning design is chosen on the basis of a spatial selection, e.g., thinning in corridors, regardless of tree size; it can be implemented in different ways and have different nomenclatures, such as row thinning [22], corridor thinning [11], systematic thinning [1], and boom-corridor thinning (BCT) [23,24], with trees of all sizes being removed proportionally [25]. If the distance between rows is small, an alternative to this is to use narrow harvesting machines or to increase the number of adjacent rows to be removed [22].

Growth rates vary considerably within different diametric classes in a stand, and one cause of that is the variation in competition by other trees [26,27]. A larger crown will generally result in high increment performance for a tree, while also reducing light availability for its neighbors [28].

Having a better understanding of what impacts growth variation is essential for predicting stand development and evaluating forest resistance and resilience to environmental change [27]. Other authors have previously suggested that the effect of competition on the growth of individual trees and stand development can be best predicted if the coordinates for all trees are known, potentially making the model more accurate and enabling the effective evaluation of different spatial distribution designs derived from, for example, systematic thinning, half-systematic thinning, or selective thinning [26,29]. Individual-tree-based growth models generally include an index designed to quantify the degree of competitive stress on individual trees in a stand [18]. The models can be distance-dependent or distance-independent. The former requires that the model has information on the location of the trees [30]. CIs depend on the position, dimensions, and number of trees, and they can be based on the weighted distance of neighboring trees (competitors), selected through an empirical rule, which are located within a certain distance from the subject tree [30,31]; CIs are usually included in individual tree growth models as an explanatory variable [32].

CIs are important tools in forest management and help determine how much of the growing space of an individual is occupied by others, potentially reflecting more successfully the growth of individual trees [33–35]. CIs can assume asymmetry or symmetry when it comes to the partitioning of resources and neighborhood effects [31], i.e., "the tree with the highest influence captures all the resources available at that spot" (asymmetric distribution), or the opposite, when the resources are assumed to be shared among the trees proportionally, depending on their local influence function values (symmetric distribution) [36]. CIs generally assume that there is asymmetry on the effects caused by the neighboring trees and the way that the tree responds to them [33].

Within this context, this study compares different thinning designs (selective and schematic thinning) and strategies (by thinning once or more than once), using long-term monitoring of a set of Scots pine stands in Sweden. Furthermore, we enquire whether or not the spatial arrangement of trees influences single tree growth.

From a practical forestry perspective, it could be economically relevant for forest owners to know if the spatial selection of thinned trees significantly affects productivity, rather than a size selection. Therefore, this study aimed to investigate if spatial selection affects stand growth. We hypothesized the following:

H1. *There will be no significant differences among thinning treatments in pine stand basal area, periodic annual increment (PAI), or in mean diameter growth.*

H2. *Distance-independent models will be as effective for predicting diameter growth as the distance-dependent model.*

2. Materials and Methods

2.1. Experimental Design

The data were obtained from a long-term thinning experiment established in Sweden [7] in young Scots pine plantations, using a site for each block, with three exceptions in which there were two blocks on the same site. Each block contained two randomized plots with the respective treatments (selective and schematic thinning). The stands were planted between 1949 and 1958 as a provenance trial, and the thinning experiment was then established between 1974 and 1981, when the stands were, on average, 25 years old, in a total of 16 blocks. The original spacing and stem density from the planting were maintained, and ingrowth was removed in blocks where it had appeared. The spacing between the trees was 1.5 m × 1.5 m; on the basis of the planting design, we created coordinate systems for each treatment plot with the spatial location of each tree (Figure 1). The treatment plots ranged from 0.05 to 0.2 ha in size. Surrounding the treatment plots was also a buffer zone of trees with the same treatment (varying 2–5 m in width), but none of the trees in the buffer zone were measured. In this study, we reduced the net plots by trimming at least 3 m of distance off the plot edges, such that all subject trees had known size and distance to all neighboring trees within at least 3 m.

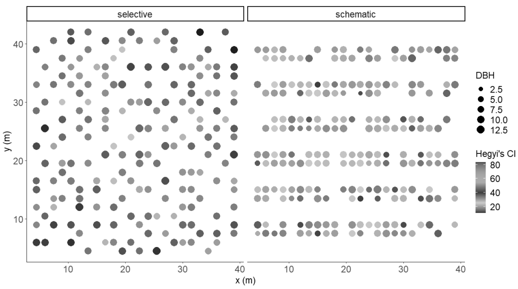

Figure 1. Representation of the spatial location of the trees for one of the sites after establishing the thinning treatments (selective or schematic). The size of the points is based on the diameter at breast height (DBH), i.e., bigger points represent bigger trees. The colors in the scale express the competition based on one of the calculated distance-dependent competition indices in this study (Hegyi's in this case). Higher CIs indicate that the tree is suffering from more competition.

The 16 blocks were located In eight regions in Sweden, between latitudes 56°40′ N and 66°04′ N (the counties Kronoberg, Västerbotten, Västernorrland, Norrbotten, Dalarna, Jämtland, Kalmar, and Halland) (Figure 2, Table 1). The experimental design consisted of two levels of thinning treatments, selective and schematic thinning, randomized within blocks during first thinning. Over time, the blocks were managed with two different experimental plans, where 10 of the blocks had no further thinning, only measurements of living and dead trees. The other six blocks were thinned more than once, according to a thinning template and with the same thinning strategy for both treatments. This resulted in two different experiments.

Figure 2. Map of the sites included in the study.

Table 1. Description of the study sites.

Study Sites	Location	Year of Last Revision	No. of Revisions	Age *	Establishment of Treatments *	H_{dom} (m) *	Site Index (H_{100}) **	Coordinates		Number of Thinnings
								E	N	
1034	Kronoberg	2010	4	21	1978	8.15	27.5	15°01′	56°44′	1
1038	Västerbotten	2022	4	29	1979	8.53	23.5	18°48′	64°22′	1
1039	Dalarna	1999	4	28	1978	8.5	23.5	14°27′	61°29′	1
1040	Norrbotten	1999	3	28	1976	8.15	23	21°23′	66°04′	1
1041	Jämtland	2003	5	25	1974	8.45	25	14°32′	63°08′	1
1042	Västernorrland	2022	5	26	1977	8.4	24.5	17°10′	63°50′	1
10,432 ***	Jämtland	1984	3	32	1974	11.4	28.5	16°18′	63° 49′	1
1051	Västernorrland	1999	3	25	1980	7.95	24.5	15°22′	62°20′	1
1053	Jämtland	2003	3	24	1981	7.55	24	14°32′	63°08′	1
1033	Kalmar	1998	5	22	1976	10.25	31.5	15°43′	57°47′	3
1035	Kalmar	1998	4	25	1980	10.5	28	15°45′	57°47′	2
10,431 ***	Jämtland	2022	5	32	1974	11.8	27.5	16°18′	63° 49′	2
1050	Västernorrland	1999	4	29	1978	9.55	25	16°13′	63°28′	2
8097	Halland	2018	7	18	1974	7	28	13°04′	56°40′	4

* At the time of the first revision, when the thinning treatments were established; ** Site index calculated for the current age of the stands; *** Blocks 10,431 and 10,432 are presently in the same site, but different thinning strategies were applied for each one; hence, they are included separately here, unlike other pairs of blocks present in the same site.

In the first thinning, both treatments had a basal area removal of the same intensity (50% intensity), with the selective thinning being performed from below and the schematic thinning being applied on the basis of a spatial selection (two rows were harvested, two rows were kept).

The thinning ratio, i.e., the ratio of mean diameter between harvested trees and retained trees, describes the used thinning type [8]. Since thinning from below consists of harvesting, mostly, the smallest trees, the ratio is lower than 1.0. In contrast, in thinning from above, the thinning ratio is over 1.0 [8]. Schematic thinning, however, is based on spatial selection, regardless of tree size, e.g., corridor thinning; the thinning ratio should theoretically be 1, or close to 1. Mean thinning ratios for the treatments were 0.72 and 0.97, respectively.

Later thinning, if applied, was performed as selective thinning from below with 25% intensity for both treatments.

All trees with a height over 1.3 m were numbered and registered for remeasurements over all revisions, starting with the first revision at the time of conducting the thinning treatments, prior to harvest. Stem diameter at 1.3 m height (dbh) was measured on every tree together with height on 20 sample trees. Each revision provided data on the dbh of all trees, status of the trees (e.g., thinned or not, dead or alive), and height of sample trees. The experiments were measured at minimum three times and at most seven times, with the monitoring period from 1974 to 2022 (Table 1). The time for remeasurements varied among sites, with an increased interval across revisions as the stands got older. On average, it ranged from 8 to 10 years.

2.2. Treatment Comparisons

The treatment effect on stand level was tested by comparing PAI between the first two revisions, and standing and total volumes for the second and the last revisions. On average, the time between the first and second revisions was 6 years. Additionally, we also compared the mean annual increment (MAI) between the selective and schematic thinning treatments. PAI establishes a relation between tree growth (in this case, specifically volume growth) "over a certain period to the length of the period" [37], whereas MAI refers to the current size of a tree in relation to its age [37].

A visual representation of the data was obtained by plotting the diameter distribution of the different blocks, the treatments (selective or schematic), and thinning strategies (thinning once or more than once). Additionally, to test the heterogeneity, we calculated the Gini coefficient [38,39] to measure the heterogeneity of forests as a function of certain variables, e.g., diameter, basal area, and growth. In the case of our study, we used arithmetic mean diameter. As a way to further showcase the heterogeneity, the coefficient of variation (CV) was calculated. We also compared quadratic mean diameter (QMD) among the thinning treatments in the short term (first revision at the time of thinning). For the long-term analysis, we compared both the treatments and the thinning strategies, i.e., blocks that were only thinned once with treatments maintained after first thinning, and blocks that were thinned more than once, using data from the last revision.

The data were analyzed using the statistical and graphics software R (version 4.0.4) (R Core Team 2021). To test for potential statistical difference among treatments on a stand level, the data were computed with mixed-effects models using the nmle package in R. Plots within sites were considered a random effect. We tested PAI ($m^3 \cdot ha^{-1} \cdot a^{-1}$) between the first two revisions (revision 1 after thinning and revision 2 before thinning), and standing volume ($m^3 \cdot ha^{-1}$) between the second (before second thinning) and last revisions as response variables. The Tukey test (0.95 level of confidence) was used to test the difference in basal area, total and standing volumes, and QMD among the different treatments.

2.3. Comparing Growth Predictions with and without Competition Indices

The measured growth between revisions 1 and 2 was used for the development of 5 year interval growth functions with and without CIs. Thereafter, the functions were applied for dbh increment over 5 and 10 years, respectively, after first commercial thinning. We used the individual tree models with no CI (BA-base), with distance-dependent CI (BA-DDCI), and with distance-independent CI (BA-DICI) to predict diameter growth and, subsequently, basal area on a stand level to see how well the models performed in comparison to the original stand-level data (BA-stand) (Figure 3).

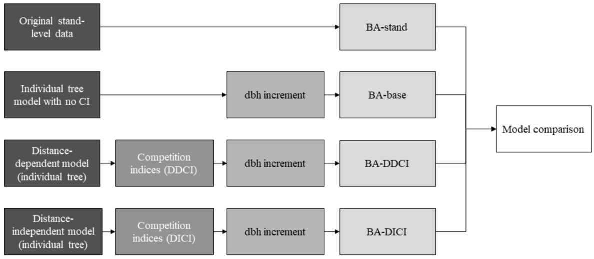

Figure 3. Description of the model comparison process.

The individual tree dbh growth base model was fitted to the data (Equation (1)), with no CI, using the 5 year diameter growth as the response variable. Only trees within the net plots were used as subject trees. Plots within sites were used as random effects using the lme function in the nlme package. Treatment (selective and schematic thinning) was initially tested, but was proven to be nonsignificant and, therefore, removed from the final model.

$$I_{dbh5} = \beta_0 + (\beta_1 dbh) + (\beta_2 SI) + (\beta_3 BA) + b_i + e_i, \quad (1)$$

where I_{dbh5} is the 5 year diameter increment (cm), dbh is the diameter at breast height (cm), SI is the scaled site index ranging from 0 to 1 (lowest to highest SI, respectively), BA is the basal area ($m^2 \cdot ha^{-1}$), b_i is a random factor, and e_i is the error term. β_0 is a constant and β_i denotes coefficients.

Thereafter, the CIs were added to the base model, creating a total of five models (Equation (2)).

$$I_{dbh5} = \beta_0 + (\beta_1 dbh) + (\beta_2 SI) + (\beta_3 BA) + (\beta_4 CI) + b_i + e_i, \quad (2)$$

where CI is the added competition index.

Additionally, we created a final function in which we included age at last revision as a covariate (Equation (3)).

$$I_{dbh5} = \beta_0 + (\beta_1 dbh) + (\beta_2 SI) + (\beta_3 BA) + (\beta_4 CI) + (\beta_5 age) + bi + e_i, \quad (3)$$

where age refers to the age of the trees at the last revision.

The models met the normality assumptions. To correct for heteroscedasticity, we used an exponential weight function. Since the models did not have the same fixed effects, we used the maximum likelihood (ML) method. R^2 values for all models were calculated with the MuMIn package. To check for multicollinearity amongst the explanatory variables in the model, we calculated the variance inflation factor (VIF).

We calculated and implemented two distance-dependent and three distance-independent CIs into the base growth model. The neighboring trees (competitors, *j*) were selected regardless of their distances to the subject tree (*i*), i.e., every tree that was not the subject tree was selected as a competitor, with the distances between the trees being incorporated into the calculation of the distance-dependent CIs. Five models using asymmetric competition were developed [40]. In total, there were 3267 and 3240 subject trees in the net plots in revisions 2 and 3, respectively, excluding outliers and dead trees. We used Spearman's rank correlation to examine the relationship between the CIs and 5 year diameter increment for individual trees.

The evaluation of model performance for predicting 5 year diameter increment was initially conducted using the Akaike information criterion (AIC). The same models were used for predicting 10 year diameter growth and final growth. The model comparisons were then used to test the second hypothesis.

3. Results

3.1. Treatment Effect on Stand and Individual Tree Growth

Basal area ($m^2 \cdot ha^{-1}$) did not differ among treatments in the short term, on average, 6 years after thinning (p = 0.214), nor did it differ in the long term, on average, 35 years after first thinning, for stands that were thinned once (p = 0.092) or more than once (p = 0.736). Although there was no significant difference, mean basal area was higher for the schematic thinning than in the selective thinning in the short and long terms. There were no statistical differences among the treatments on stand-level data for PAI between the first two revisions (p = 0.850) or standing volume on the second revision (p = 0.768). Conditional R^2 values for the models were 0.936 and 0.931, respectively, i.e., the variance was well explained by the fixed and random effects. Additionally, no significant difference among treatments was found when evaluating MAI over a long term for either thinning strategy, i.e., sites that were thinned only once (p = 0.230) and more than once (p = 0.661). Total volume in the last revision did not present significant differences among treatments for the blocks that were thinned only once (p = 0.060) (Figure 4). The same can be said for the blocks that received more than one thinning (p = 0.673) (Figure 4). Standing volume also did not differ significantly among treatments at the last revision.

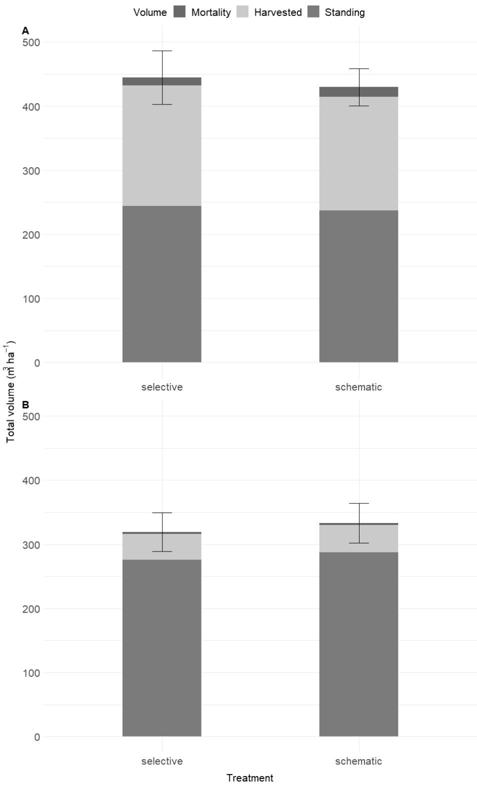

Figure 4. Total volume production ($m^3 \cdot ha^{-1}$) of the blocks thinned more than once (**A**) and only once (**B**), expressed on stacked bar charts with mortality, harvested, and standing volumes. The error bar represents the standard error of the total volume among the thinning treatments. The site index ranged from 23 to 29 for blocks that were thinned once and from 24 to 32 for blocks that were thinned more.

Mean arithmetic diameter growth (cm·year^{-1}) was significantly higher for the selective thinning treatment (0.32 cm·year^{-1}) in comparison to the schematic thinning (0.29 cm·year^{-1}) for sites that were thinned only once (p = 0.012). On the other hand, for sites that had more than one thinning, that difference was not significant (p = 0.948), with mean diameter growth being 0.42 cm·year^{-1} for both thinning treatments.

3.2. Stand Structure

For the sites that maintained the initial treatment, i.e., those that were thinned only once, stand structure was more heterogeneous for the schematic thinning treatment, since there were a higher number of smaller trees, as well as greater stem density, in general, along with a higher Gini coefficient and CV (Figure 5, Table 2). As a result, mean dbh was mostly concentrated in bigger diameter classes for the selective thinning, in comparison to the schematic thinning (Figure 5). For sites that were thinned more than once, that tendency started to disappear and heterogeneity was no longer significant among treatments (Figure 6, Table 2).

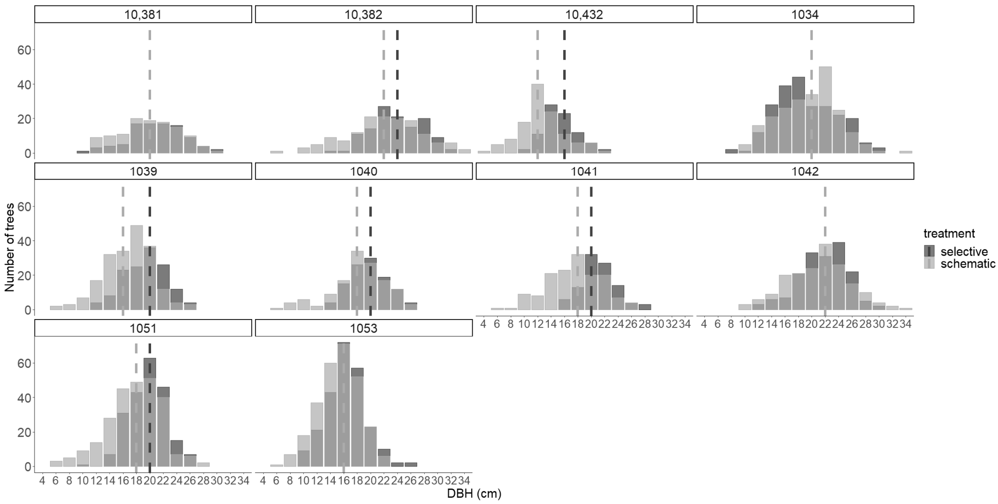

Figure 5. Diameter distribution for sites that were thinned only once. The x-axis value represents the upper limit of the dbh class. The y-axis represents the number of trees on the plot. The dashed lines represent the mean dbh value for each treatment. When only one dashed line appears, it means that the dbh means for both treatments were in the same class.

Table 2. Coefficient of variation and Gini coefficient calculated in the first and last revisions. N is the number of blocks, and sd is standard deviation.

		First Revision			Last Revision		
Treatment	**Thinning Strategy**	**N**	**CV% ± sd**	**Gini Coefficient ± sd**	**N**	**CV% ± sd**	**Gini Coefficient ± sd**
Selective	Thinned once	10	18.17 ± 1.78	0.10 ± 0.010	10	17.47 ± 3.12	0.10 ± 0.018
Schematic	Thinned once	10	29.59 ± 4.65	0.16 ± 0.025	10	23.98 ± 1.89	0.13 ± 0.010
Selective	Thinned more	6	16.54 ± 1.47	0.09 ± 0.009	6	13.16 ± 1.42	0.07 ± 0.008
Schematic	Thinned more	6	28.11 ± 3.13	0.16 ± 0.018	6	15.27 ± 3.46	0.08 ± 0.019

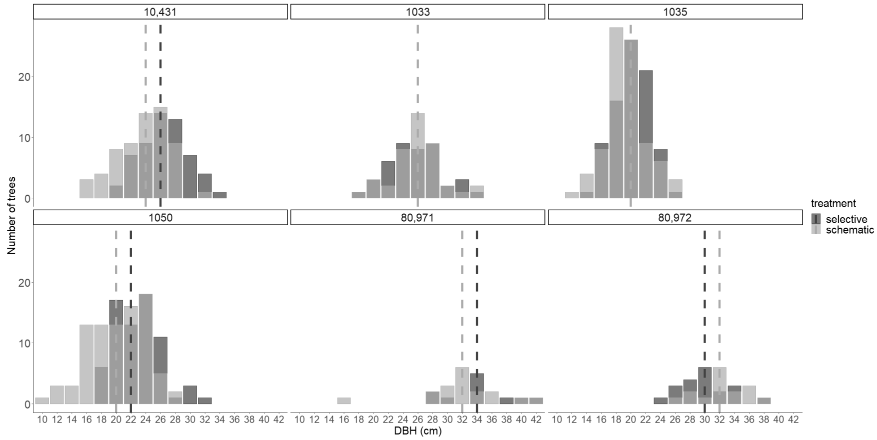

Figure 6. Diameter distribution for sites that were thinned more than once. Each number on the x-axis represents the upper number of the diameter class. The y-axis represents the number of trees on the plot. The dashed lines represent the mean dbh value for each treatment. When only one dashed line appears, it means that the dbh means for both treatments were in the same class.

QMD was significantly different between treatments at the time of first thinning due to the thinning designs that were established and the thinning ratios derived from them ($p < 0.0001$) (Figure 7). When evaluating QMD at the time of the last revision, the thinning strategies differed significantly ($p < 0.0001$), as did the treatments in blocks that had only one thinning ($p = 0.0147$) (Figure 8). There was no significant difference between treatments when there was more than one thinning ($p = 0.3735$).

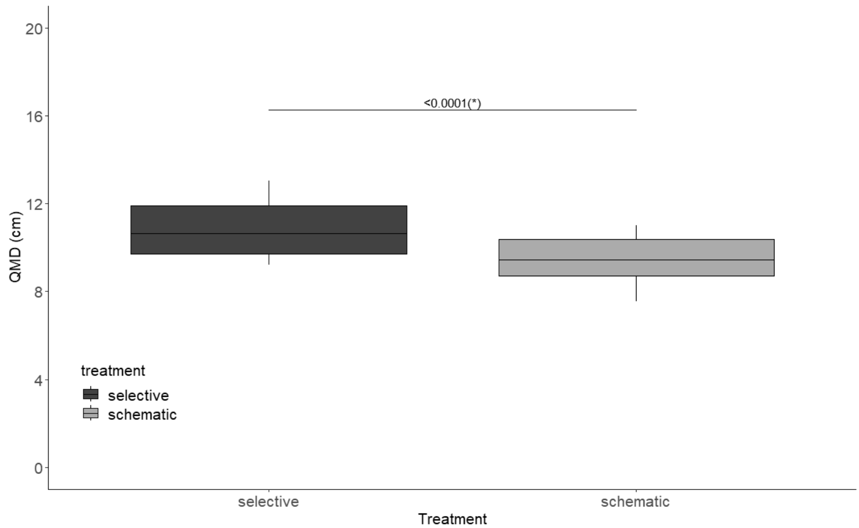

Figure 7. Evaluation of quadratic mean diameter between treatments (selective and schematic) and different thinning strategies (one thinning and more than one thinning) at the time of the first thinning. (*) indicates significant differences using the Tukey test ($p < 0.05$).

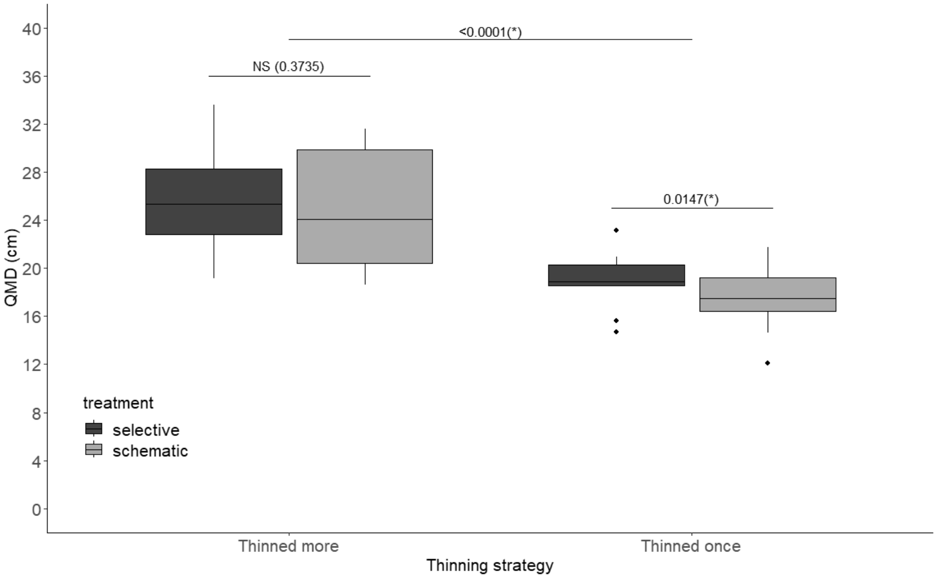

Figure 8. Evaluation of quadratic mean diameter between treatments (selective and schematic) and different thinning strategies (one thinning and more than one thinning) in the last revision. NS means "not significant" ($p \geq 0.05$); (*) indicates significant differences using the Tukey test ($p < 0.05$).

3.3. Competition Indices and Model Performance

All of the computed CIs (distance-dependent and distance-independent), using Spearman's rank correlation coefficient (rho), presented a negative relationship with 5 year individual tree diameter increment (Table 3).

Table 3. Spearman's rank correlation coefficient between 5 year individual tree increment and the competition indices.

Competition Index		Spearman's rho
Hegyi (Hey)	Distance-dependent	−0.4945112
Lorimer_(Lor1)		−0.4416078
Wyk (BAL)	Distance-independent	−0.5403026
CoFe (BAR)		−0.5864578
LOR_(Lor2)		−0.551673

Model performance did not differ across treatments. However, the addition of CIs to the growth model slightly improved its performance according to AICc. The model that best predicted 5 year dbh increment and best explained the variation in the data was a distance-dependent model using Hegyi's CI (BA_DDCI_Hey, Tables 4 and 5, Figure 9), which differed significantly to other models. The model with no CI (BA_BASE) and one of the distance-independent ones (BA_DICI_Lor2) were ranked as less suitable models. The CI in the latter was not significant (Table 4).

Table 4. Models for predicting 5 year dbh increment for individual trees.

Model	Response Variable	Parameter	Estimates	Std. Error	*p*-Value	Marginal R^2	Conditional R^2	Random Variance
BA_BASE	5 year dbh increment	intercept	1.4507	0.1778	<0.0001	0.70	0.80	
		dbh (cm)	0.1979	0.004	<0.0001			
		basal area ($m^2 \cdot ha^{-1}$)	−0.1420	0.0149	<0.0001			
		scaled SI	1.0592	0.1883	0.0143			
		sites: plots (random)						0.09
BA_DDCI_Hey	5 year dbh increment	intercept	1.7319	0.1920	<0.0001	0.67	0.77	
		dbh (cm)	0.1728	0.0068	<0.0001			
		basal area ($m^2 \cdot ha^{-1}$)	−0.1329	0.0151	<0.0001			
		scaled SI	1.0340	0.1981	0.0201			
		DDCI * (Hegyi)	−0.0086	0.0019	<0.0001			
		sites:plots (random)						0.10
BA_DDCI_Lor1	5 year dbh increment	intercept	1.5979	0.1906	<0.0001	0.68	0.78	
		dbh (cm)	0.1853	0.0066	<0.0001			
		basal area ($m^2 \cdot ha^{-1}$)	−0.1379	0.0150	<0.0001			
		scaled SI	1.0405	0.1947	0.0179			
		DDCI * (Lorimer)	−0.0007	0.0003	0.0211			
		sites: plots (random)						0.10
BA_DICI_Wyk	5 year dbh increment	intercept	1.2540	0.1903	<0.0001	0.70	0.80	
		dbh (cm)	0.2271	0.0095	<0.0001			
		basal area ($m^2 \cdot ha^{-1}$)	−0.1639	0.0162	<0.0001			
		scaled SI	1.0731	0.1921	0.0152			
		DICI ** (BAL)	0.0221	0.0065	0.0007			
		sites: plots (random)						0.09
BA_DICI_Lor2	5 year dbh increment	intercept	1.4922	0.1849	<0.0001	0.70	0.79	
		dbh (cm)	0.1936	0.0064	<0.0001			
		basal area ($m^2 \cdot ha^{-1}$)	−0.1401	0.0148	<0.0001			
		scaled SI	1.0595	0.1887	0.0139			
		DICI ** (Lor)	−0.00001	0.00002	0.4203			
		sites: plots (random)						0.09
BA_DICI_CoFe	5 year dbh increment	intercept	1.4145	0.1772	<0.0001	0.71	0.8	
		dbh (cm)	0.2030	0.0045	<0.0001			
		basal area ($m^2 \cdot ha^{-1}$)	−0.1439	0.0145	<0.0001			
		scaled SI	1.0599	0.1874	0.0155			
		DICI ** (BAR)	0.000003	0.000002	0.0293			
		sites: plots (random)						0.09

* DDCI = distance-dependent competition index; ** DICI = distance-independent competition index.

Table 5. Ranking of the tested models, from best to worst, based on the Akaike information criterion.

Model	AICc
BA_DDCI_Hey	5258.54a
BA_DICI_Wyk	5268.97b
BA_DICI_CoFe	5273.71c
BA_DDCI_Lor1	5273.97c
BA_BASE	5278.1d
BA_DICI_Lor2	5279.33d

When comparing the predictions of basal area ($m^2 \cdot ha^{-1}$) for 5, 10, and 35 years after thinning (average time at the last revision), they did not significantly differ among all tested models, with and without CIs (Figure 10).

The analysis using VIF presented no major multicollinearity issues, with similar studies suggesting that a value of less than 10 is acceptable [41,42]. The highest value was close to 6 for one of the distance-independent models (BA_DICI_Wyk), with the initial dbh and DICI presenting values of 5.52 and 5.63, respectively. All other models and their explanatory variables presented a VIF of less than 3.

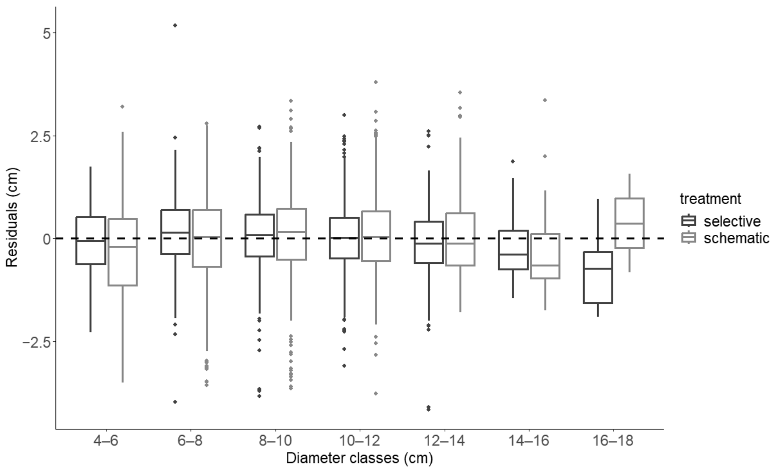

Figure 9. Residual plot of the distance-dependent model using Hegyi's competition index (BA_DDCI_Hey), considering only trees with dbh ≥ 4 cm.

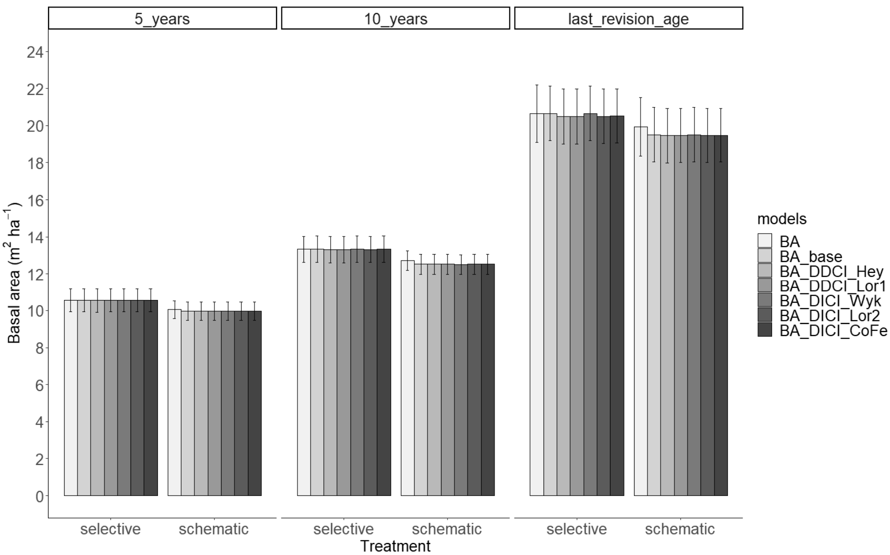

Figure 10. Basal area ($m^2 \cdot ha^{-1}$) predictions using different models and over time (5, 10, and 35 years (last revision age) (average time)) after thinning. The last graph had age included in the model, considering the latest revision. "BA" indicates the real basal area value. "BA_base" has no competition index. "BA_DDCI_Hey" and "BA_DDCI_Lor1" are distance-dependent models. "BA_DICI_Wyk", "BA_DICI_Lor2", and "BA_DICI_CoFe" are distance-independent models.

4. Discussion

We show in this study that both selective and schematic thinning are useful strategies in early harvests. In this experiment, by design, only the thinning ratio differed among the treatments after thinning, but not the remaining basal area. With this approach, a schematic thinning will create stands with more stems, albeit smaller. This resulted in no significant difference in stand basal area, over a short or long term. It also resulted in an increased mean diameter in the selective thinning. However, when later thinnings were performed (selective thinning from below), the difference between the early treatment of selective and schematic disappeared.

Unlike what we found in our study, despite the selective thinning treatment having a higher mean diameter increment, the authors of [1] found no statistical differences in mean diameter growth among the thinned treatments (selective, half-systematic, and systematic) when working with Scots pine and Norway spruce stands in Finland. The authors argued, however, that a higher mean diameter increment for a selective thinning based on basal area removal, as was the case in our study, makes sense since "the growing space released by the removed trees is more evenly distributed among all the trees remaining on a plot". When working with a 35 year old Douglas fir stand to compare growth among unthinned, strip-thinned, and selectively thinned, the authors of [43] also found that individual tree growth was higher in the selective thinning than in the plots with strip thinning. Our first hypothesis was, therefore, partly rejected, since, although there were no significant differences among treatments in stand basal area and PAI, arithmetic diameter growth was significantly higher for the selective thinning treatment.

Different management goals and thinning strategies can result in a varied stand structure and resource distribution in the short term, potentially also affecting forest development in the long term [44]. The authors of [11] argued that different thinning treatments will promote "very different effects on vertical stand structure, habitat diversity, and light conditions". In a different study, the authors of [45] found that crown attributes in Scots pine were significantly larger in intensive thinning from below (66% of basal area removal) in comparison to the systematic thinning and thinning from above treatments, which could be one reason to explain the higher individual tree diameter growth found in the selective thinning i.e., potentially higher photosynthetic rates, due to a larger crown. The authors of [44], who did not specifically work with corridors on their thinning simulations, argued that light distribution may not vary so much among different stand structures, which could be the reason why, in our study, we did not see significant differences in basal area in the short and long terms after thinning.

Furthermore, a higher number of stems in the schematic thinning and the potential that some trees have to benefit from the increased resource availability along the corridors end up making the treatments comparable when it comes to total stand volume [7], compensating for the lower growth [1]. The forests look structurally different, i.e., the plots with corridors have higher stem density and a higher number of smaller trees, making them more heterogeneous, while the plots with selective thinning present a more homogenous structure, even though both treatments had the same amount of basal area removed in the first thinning and in subsequent thinning (for six of the blocks). Other studies have shown that schematic thinning treatments, such as BCT, resulted in a more heterogeneous forest, similar to the results from [9,14,46,47]. Schematic thinning will generally not improve the external wood quality of the remaining trees [25].

Our models with CIs for comparison of stand basal area performed very well in the short term, regardless of being spatially dependent or not, especially for the plots with selective thinning. Despite the AICc showing a significantly higher efficiency in prediction and explanation of the variation in the data for one of distance-dependent models (BA_DDCI_Hey), we saw that estimated stand basal area using the predicted diameter growth did not differ among the models (distance-dependent or -independent), thus confirming our second hypothesis. The slightly better, but not significant, performance for the selective thinning treatment was probably due to the fact that the models underperformed for trees in smaller diameter classes, which were mostly found in the schematic thinning treatment. In their study, the authors [48] also found little difference in predictive ability between distance-dependent and distance-independent models, when working on 11 year old *Pinus radiata* plantations in Italy with different thinning intensities; they argued that the costs to obtain the coordinates of trees "may be unjustified for growth prediction, at least in young conifer plantations".

By not choosing a specific method for competitor selection, such as the fixed radius method, one of the potential consequences in our analysis would be the presence of spatial autocorrelation among samples, since the trees were not independent from each other and were repeatedly analyzed, producing pseudo-replicates. To account for that, we included plots within sites as random effects in the models. Additionally, the authors of [34] went into detail about overlapping samples in their study, and one of their conclusions was that spatial autocorrelation was only detected for a very short search radius (3–4 m) and that "on average, this effect does not seem to introduce any type I statistical error".

With advances in technology and the continuing development of precision forestry [49], cheaper and less time-consuming methods could be implemented to obtain tree coordinates. However, perhaps, even more important for long-term predictions would be to use methods that could give us more information on crown development over a period of years; this was one of the limitations in our study, since changes in morphology could be important to understand growth patterns after competition release due to thinning [50]. When working with unevenly sized Norway spruce stands in Sweden, the authors of [51] mentioned that their model could have possibly been improved if they had a "more representative measure for the crown ratio".

5. Conclusions

Accordingly, on the basis of our findings, if production is the main goal, in addition to selective thinning, schematic thinning could also be a viable option for the first commercial thinning. If working with a one-time thinning system, schematic thinning will result in a longer rotation to get to a specific target diameter in the stand. However, if the main motivation is volume, the thinning design one chooses—selective or schematic—will amount to nonsignificant differences between treatments. If thinning is performed more than once, trees can be selectively thinned from below in later thinning, thereby promoting fast-growing, good-quality trees at a later stage. Nevertheless, it is important to highlight that the first commercial thinning in our study was performed when dominant height ranged 7–11.8 m among the different sites, i.e., there was no late first commercial thinning. In that way, codominant trees at this range of dominant height tend to develop really well after thinning, because of their live crown ratio, which is especially important for the schematically thinned stands due to a generally higher number of codominant trees in growing stock, in comparison to the selectively thinned ones. If the first thinning was applied later, the crown of codominant trees would suffer more to recover, consequently affecting growth. Therefore, further investigation would have to be conducted at sites in which first commercial thinning was performed at a later stage to evaluate if similar results to our study would be found.

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This thesis aims to explore the mechanistic basis of thinning responses in the short-term, through the establishment of thinning experiments in central Sweden, and to evaluate long-term thinning strategies, using a series of thinning experiments across Sweden. The results showed that the amount of retained basal area is more important for stand development than the spatial distribution of trees, and that thinning has the potential to contribute to greater resilience of Scots pine forests in the boreal zone.

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