Acta Universitatis Agriculturae Sueciae

SLU

Doctoral Thesis No. 2020:71
Faculty of Forest Sciences

Establishment and growth of Scots pine and Norway spruce

A comparison between species

Oscar Nilsson

Establishment and growth of Scots pine and Norway spruce

A comparison between species

Oscar Nilsson
Faculty of Forest Sciences
Southern Swedish Forest Research Centre
Alnarp

SWEDISH UNIVERSITY
OF AGRICULTURAL
SCIENCES

DOCTORAL THESIS

Alnarp 2020

Acta Universitatis agriculturae Sueciae
2020:71

Cover: Silhouettes of pine and spruce
(Images by Andrew Martin and Clker-Free-Vector-Images from Pixabay)

ISSN 1652-6880
ISBN (print version) 978-91-7760-660-4
ISBN (electronic version) 978-91-7760-661-1

Print: SLU Service/Repro, Alnarp 2020

Establishment and growth of Scots pine and Norway spruce

Abstract

The two by far most common and economically important tree species in Sweden are Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst). Despite a long history and tradition of silvicultural research on these species, few studies comparing their growth at the same sites have been performed, preventing accurate species comparisons. Hence, the goal of this thesis was to examine growth differences between Scots pine and Norway spruce at different rotation stages and disentangle potential underlying reasons for the observed differences. To do so, field experiments with both species growing together were utilized, and the importance of species choice was highlighted. In **Papers I-II** it was shown that Scots pine seedlings had a higher early growth, and nitrogen (N) uptake was found to be a reason for the initial growth response. Site preparation was favorable for the growth of both species, however, Norway spruce seedlings were severely hampered in the low nutrient environment created by removing all the organic material. Such practices should be avoided when planting Norway spruce. It was also concluded that N_2-fixation in fine roots did not explain the superior initial N uptake of Scots pine. In **Paper III** it was found that Scots pine produced 126% more stem wood than Norway spruce after 57 years. No overyielding could be found when both species grew in a mixture. However, a mixture provides several other benefits compared to monocultures. Species choice determines long-term possibilities and limitations and is important for more reasons than only growth parameters, as it has a significant influence on biodiversity and ecosystem services on different scales (**Paper IV)**. In this regard, Scots pine has a potential to provide several win-wins. This thesis puts species choice in a wider context by increasing the scientific knowledge regarding growth patterns, growth responses, ecosystem services and biodiversity.

Keywords: *Pinus sylvestris*, *Picea abies*, regeneration, nitrogen, seedlings, mixed forest, competition, growth, site preparation, ecosystem services, biodiversity

Author's address: Oscar Nilsson, SLU, Southern Swedish Forest Research Centre, P.O. Box 49, 230 53 Alnarp, Sweden

Etablering och tillväxt hos gran och tall – en jämförelse mellan arter

Sammanfattning

Gran (*Picea abies*) och tall (*Pinus sylvestris*) är de två överlägset vanligaste och ekonomiskt viktigaste trädslagen i Sverige. Trots en lång och gedigen historia och tradition av skogsskötselforskning, så finns det få studier som jämför arternas tillväxt på samma mark. Denna brist på studier försvårar möjligheten att göra tillförlitliga tillväxtjämförelser mellan arterna. Ett av målen i denna avhandling var att utvärdera tillväxtsskillnader mellan gran och tall i olika skeden under omloppstiden, samt att utröna potentiella orsaker för dessa skillnader. Därav studerades experiment där båda trädslagen växte tillsammans och trädslagsval belystes i ett vidare perspektiv. I **papper I-II** visades att tallplantorna växte bättre än granplantorna de första åren efter utplantering och att kväveupptaget var en viktig anledning till denna skillnad. Markbehandlingsmetoden där markprofilen vändes uppochner gynnade båda trädslagen, medans granens tillväxt reducerades i den markbehandling som tog bort allt organiskt material och således stora delar av växtplatsens tillgängliga näringsinnehåll. Därför bör markbehandlingar som avlägsnar stora mängder humus undvikas vid granplantering. Resultat från **papper II** visade även att kvävefixering i finrötter inte förklarar tallens högre initiala kväveupptag. I **papper III** hade tall producerat över dubbelt så mycket stamved som gran efter 57 år. I försöket ingick förutom monokulturer av gran och tall även blandskog av båda trädslagen men ingen blandskogseffekt kunde påvisas. Blandskogen har dock flera andra fördelar jämfört med trädslagsrena bestånd. Trädslagsvalet är ett av markägarens viktigaste beslut, det bestämmer de långsiktiga förutsättningarna och är viktigt av andra anledningar än endast tillväxtsaspekter. I **papper IV** visades att tallskogar tillhandahåller en avsevärt högre nivå av ekosystemtjänster och biodiversitet. Denna avhandling sätter trädslagsvalet i ett större sammanhang än endast biomassaproduktion.

Nyckelord: *Pinus sylvestris*, *Picea abies*, föryngring, kväve, plantor, blandskog, konkurrens, tillväxt, markberedning, ekosystemtjänster, biodiversitet

Författarens adress: Oscar Nilsson, Sveriges lantbruksuniversitet, Institutionen för Sydsvensk Skogsvetenskap, postbox 49, 230 53 Alnarp, Sverige

Dedication

Till min älskade familj

Smiles are free
Friendships are priceless
Invest in both
Dylan Brooks, student at North Carolina State University

If you can dream it, you can do it
Walt Disney

A people without the knowledge of their past history, origin and culture is like a tree without roots
Marcus Garvey, Jamaican politician

Contents

List of publications 9

List of figures 11

Abbreviations 15

1. Introduction 17
   - 1.1 Scots pine and Norway spruce 19
   - 1.2 Regeneration 19
   - 1.3 N uptake and N_2-fixation 21
   - 1.4 Productivity 22
   - 1.5 Mixed forest 23
   - 1.6 Biodiversity and ecosystem services 26

2. Thesis aims 27

3. Material and methods 29
   - 3.1 Regeneration studies (**I-II**) 29
     - 3.1.1 Study sites and field measurements (**I-II**) 29
     - 3.1.2 Nitrogen aspects sampling and analyzes (**II**) 31
   - 3.2 Mixture experiment (**III**) 31
   - 3.3 Review study (**IV**) 31

4. Main results and discussion 33
   - 4.1 Early growth of Scots pine and Norway spruce (**I**) 33
   - 4.2 N uptake, retranslocation and N_2-fixation in Scots pine and Norway spruce (**II**) 36
   - 4.3 Productivity of Scots pine and Norway spruce in monoculture and mixture (**III**) 40
     - 4.3.1 The “million-dollar question” 45
   - 4.4 Implications of replacing Scots pine with Norway spruce (**IV**) 47

5. Conclusions and implications 51

6. Future perspectives 55

References 57

Acknowledgements 71

Appendix 75

List of publications

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

I. Nilsson, O., Hjelm, K., Nilsson, U. (2019). Early growth of planted Norway spruce and Scots pine after site preparation in Sweden. *Scandinavian Journal of Forest Research*, 34 (8), 678-688

II. Nilsson, O., Nilsson, U., Näsholm, T., Cook, R., Hjelm, K. Nitrogen uptake, retranslocation and potential N_2-fixation in Scots pine and Norway spruce seedlings. (manuscript)

III. Holmström, E., Goude, M., Nilsson, O., Nordin, A., Lundmark, T., Nilsson, U. (2018). Productivity of Scots pine and Norway spruce in central Sweden and competitive release in mixtures of the two species. *Forest Ecology and Management*, 429, 287-293

IV. Felton, A., Petersson L., Nilsson, O., Witzell, J., Cleary, M., Felton, A. M., Björkman, C., Sang, Å. O., Jonsell, M., Holmström, E., Nilsson, U., Rönnberg, J., Kalén, C. and Lindbladh, M. (2020). The tree species matters: Biodiversity and ecosystem service implications of replacing Scots pine production stands with Norway spruce. *Ambio*, 49 (5), 1035-1049

Papers I and III-IV are reproduced with the permission of the publishers.

The contribution of Oscar Nilsson to the papers included in this thesis was as follows:

I. Developed the research idea together with co-authors and performed field work. Compiled and analyzed the data. Wrote the manuscript in collaboration with the co-authors.

II. Developed the research idea together with co-authors. Performed field and laboratory work. Compiled and analyzed the data. Wrote the manuscript in collaboration with the co-authors.

III. Participated in developing the research idea with co-authors and participated in writing the manuscript.

IV. Participated in developing the research idea. Wrote parts of the manuscript in collaboration with co-authors.

List of figures

Figure 1. Pictures from the early days of forest research. Left: State Forest Research Institute (Forstliga försöksanstalten) first director *jägmästare* Alexander Maass at plot number 1 outside Lycksele, Västerbotten in northern Sweden in 1902, the same year as the institute was established. Right: Professor Edvard Wibeck having fika (coffee and something sweet) at a burned site outside Torp, Medelpad in northern Sweden in 1920. (Photos: SLU – Forest library) 18

Figure 2. Forestry students (*jägmästarstudenter*) listening carefully to professor Anders Wahlgren (white hat) and professor Tor Jonsson (peaked white cap) at plot number 17, in a Scots pine stand outside Robertsfors, Västerbotten in northern Sweden in 1914. (Photo: SLU – Forest library).. 18

Figure 3. Illustration of the types of over- and underyielding (based on Hector, 1998; Fridley, 2001). Two monocultures of different productivity are plotted, A and B, and the theoretical mixture of them (the sum of half of the productivity of both monocultures). If a mixture of A and B has lower productivity than the higher producing monoculture (in this case A), but higher productivity than the theoretical mixture, it overyields but non-transgressively. If the productivity in the mixture is greater than the most productive monoculture, it transgressively overyields. Similar types of underyielding outcomes are also possible. 24

Figure 4. Locations of the four sites used in the regeneration studies (**Papers I-II**). 1 = NorthPoor, 2 = NorthFertile, 3 = SouthPoor and 4 = SouthFertile (Nilsson et al., 2019)... 30

Figure 5. Photo illustrating an excavator performing the deep soil cultivation treatment at the NorthPoor site used in the regeneration studies (**Papers I-II**) (Photo: Olle Sjölin - Skogforsk). 30

Figure 6. Observed leading shoot growth (cm) following the three site preparation treatments at the four experimental sites of Scots pine (SP) and Norway spruce (NS) seedlings during the first six or five growing seasons at the northern and southern sites, respectively. Site preparation treatments: Control (no site preparation), Removed Humus (RH) and Deep Soil Cultivation (DSC). Different letters next to an observed mean indicate significant differences within site and growing season according to the Tukey multiple comparison difference test (Nilsson et al., 2019)......................... 35

Figure 7. Photos from two field sites. Top left: Norway spruce seedlings experiencing growth check, and well-growing Scots pines 5 years after planting in the RH treatment at the SouthFertile site. Top right: Norway spruce and Scots pine saplings thriving in the DSC treatment at the SouthFertile site 5 years after planting. Bottom left: Slow growth of both species 6 years after planting in the RH treatment at the NorthPoor site. Bottom right: Improved leading shoot lengths of Norway spruce 6 years after planting in the DSC treatment at the NorthPoor site (Photos: top left; Nils-Anders Färdmo, the remainder; Oscar Nilsson)....................................... 36

Figure 8. N_{dfu} as a percentage of N in needles of new shoots derived from uptake at the sites across site preparation treatments. The asterisk indicates significant differences between species. 37

Figure 9 (a-c). N_{dfu} as percent of N in needles of new shoots derived from uptake against leading shoot growth the following year for Scots pine (hollow figures, dashed line) and Norway spruce (solid figures, full line) after: (a) the first growing season at all sites; (b) the second growing season at all except the NorthPoor site; (c) the second growing season at the NorthPoor site. 38

Figure 10. Mean standing volume (m^3 ha^{-1}) for all blocks (n = 9) in the experiment for Scots pine in monoculture (SP.mono), Norway spruce in monoculture (NS.mono), the mixture of the two species (Mix) and the theoretical mixture (T.mix). Error bars represent the standard deviation between blocks (Holmström et al. 2018). 40

Figure 11. Photos from the Främlingshem site during 2018. Top left: Norway spruce in monoculture. Top right: Scots pine in monoculture. Bottom: Mixture of Scots pine and Norway spruce. (Photos: Oscar Nilsson) 42

Figure 12. Frequency distribution of stems in diameter classes, all blocks. Upper panel, 12a, Scots pine in pure and mixed treatments. Lower panel, 12b, Norway spruce in pure and mixed treatments (Holmström et al. 2018). 43

Figure 13. Forestry students (*jägmästarstudenter*) listening carefully to Kramfors AB forest director *jägmästare* Eric Ronge teaching about thinning close to Bosundet, Ångermanland in northern Sweden in 1924. (Photo: SLU – Forest library) 76

Figure 14. Forestry students (*jägmästarstudenter*) at an old coniferous mixed stand with 854 m^3 standing volume. Professor Manfred Näslund, *jägmästare* Folke Thörn and *jägmästare* Carlsson-Ingerstedt can be seen in the middle of the photo, Johannishus, Blekinge in southern Sweden in 1924 (Photo: SLU – Forest library) 76

Abbreviations

DSC	Deep Soil Cultivation
HD	Height-Diameter
MAI	Mean Annual Increment
N_{dfr}	Nitrogen derived from retranslocation in needles of new shoots
N_{dfu}	Nitrogen derived from uptake in needles of new shoots
NFI	National Forest Inventory
PAI	Periodic Annual Increment
RH	Removed Humus
SI	Site Index

1. Introduction

The silvicultural tradition in Sweden has a long history; the first handbook was published already during the 18th century (Rosensten, 1737). The first higher forestry education *jägmästarutbildningen* started at The Royal Forest Institute in 1829, with the purpose to educate in forest management and contribute to the development of forest research (Kardell, 2004). The State Forest Research Institute (Forstliga försöksanstalten) was formed in 1902 with the task of enhancing forest management and biological knowledge through experiments and surveys (Schotte, 1917). The scientific research history about Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst) is rigorous, as thousands of studies have been carried out since the first documented regeneration experiment of Scots pine was established in 1887 by *jägmästare* Thorsten Örtenblad (Kardell, 2004). One of the first experimental field trials was sown with both Scots pine and Norway spruce seeds in 1888-1890 and established at several locations in southern and central Sweden (Wibeck, 1912). A unique exception, as most of the subsequent silvicultural research was conducted on an individual species level, thereby preventing accurate species comparisons for site-species recommendations. Up until today, both species have been thoroughly but separately studied down to the molecular level, as mapping of the Norway spruce genome has been done (Nystedt et al., 2013), and is soon to be expected for Scots pine.

Figure 1. Pictures from the early days of forest research. Left: State Forest Research Institute (Forstliga försöksanstalten) first director *jägmästare* Alexander Maass at plot number 1 outside Lycksele, Västerbotten in northern Sweden in 1902, the same year as the institute was established. Right: Professor Edvard Wibeck having fika (coffee and something sweet) at a burned site outside Torp, Medelpad in northern Sweden in 1920. (Photos: SLU – Forest library)

Figure 2. Forestry students (*jägmästarstudenter*) listening carefully to professor Anders Wahlgren (white hat) and professor Tor Jonsson (peaked white cap) at plot number 17, in a Scots pine stand outside Robertsfors, Västerbotten in northern Sweden in 1914. (Photo: SLU – Forest library)

1.1 Scots pine and Norway spruce

Scots pine and Norway spruce are by far the most common and economically important tree species in Sweden, each comprising approximately 40% of the standing volume (SLU, 2020). Scots pine is a pioneer species with rapid initial growth and early culmination of mean annual increment (MAI). The species is adapted to cope with recurrent fires, and has poor shade tolerance (Engelmark & Hytteborn, 1999). Scots pine is characterized by a high stress tolerance, which allows it to grow well in a wide range of soil conditions. It can hence occupy habitats that are unfavorable for other tree species, by tolerating different combinations of stress, extreme acidity and alkalinity, waterlogging and drought (Kelly & Connolly, 2000). Scots pine can form pure stands at nutrient poor sites where few other tree species can compete (Engelmark & Hytteborn, 1999). Other adaptations are a deep root system that makes it more wind resistant, and thick bark protecting from fire (Lundmark, 1988).

Norway spruce is a late successional species with slower initial growth, but more sustained over time (Lundmark, 1988). As a shade-tolerant species, needles of Norway spruce can adapt to grow in dark conditions, and it can replace its needles if the conditions change (Gebauer et al., 2011). The canopy in Norway spruce stands is of high density (Goude et al., 2019), which is a competitive advantage since it restricts other tree species from establishing underneath. Compared with Scots pine, Norway spruce is more sensitive to uprooting and windthrow (Peltola et al., 2000; Valinger & Fridman, 2011). The species is naturally adapted to sites without frequent fires and relies more on gap dynamics caused by windthrow, stem breakage or disturbances where suppressed trees are released as competition locally decreases (Engelmark & Hytteborn, 1999).

1.2 Regeneration

Regeneration is a critical stage in forestry as it sets the conditions for the future silvicultural possibilities and can be seen as the start of a long-term commitment. In Sweden, more than 80% of the Swedish forest clearcuts are regenerated by planting of either Scots pine or Norway spruce (Bergquist et al., 2011). Several different aggravating factors arise in this phase (Burdett, 1990), which can lead to possible negative financial impacts. Poor survival and slow initial growth should be avoided as it is important for seedlings to grow fast after planting in order to reduce the time when they are most exposed to severe stress by e.g., insects, browsing, frost and competing vegetation (Nilsson et al., 2010).

An effective way to mitigate stress factors at regeneration is mechanical site preparation (Nilsson et al., 2010; Sikström et al., 2020). Mechanical site preparation improves growth by reducing competition for nutrients and water, and risk for frost and pine weevil damage, while it at the same time often increases nutrient mineralization, water availability, soil temperatures, etc. (Nilsson & Örlander, 1999; Langvall et al., 2001; Thiffault et al., 2004; Lebel et al., 2008; Nordlander et al., 2011; Löf et al., 2012; Johansson et al., 2013; Thiffault et al., 2013). Mechanical site preparation has also shown long-term positive growth effects (Boateng et al., 2006; Johansson et al., 2013; Prevost & Dumais, 2018; Hjelm et al., 2019). As a consequence of the positive effects, 92% of the regeneration area to be planted in Sweden is mechanically site prepared (SFA, 2014), commonly by disc trenching or mounding.

Scots pine has been reported to initially grow faster than Norway spruce (Wibeck, 1912; Örlander et al., 1990b; Johansson et al., 2015; Luoranen, 2018; Nilsson et al., 2019). A common problem for Norway spruce seedlings is growth check, also referred to as planting shock, which restricts seedling growth during the first years after planting to varying degrees (Grossnickle, 2000). Several studies have reported a poor initial growth of Norway spruce, dating back to Wibeck (1912), who found most seedlings being < 0.5 m tall 19-21 years after sowing on *Calluna* heathlands in southern and central Sweden. Jonsson (2001) reported a dominant height of 2 m, 15 years after regeneration for the experiment in **Paper III** (central Sweden). Örlander et al. (1990b) reported an average height < 0.5 m after 23 years in burned- or control treatments, and < 2 m after ploughing treatments at a site 50 km from the Baltic seacoast in northern Sweden. Nilsson et al. (2012) reported an average height of Norway spruce seedlings of 1.5 m after 15 years across 12 sites in northern Sweden.

A major issue hindering the establishment of Scots pine is the “browsing dilemma”. Due to high game densities, the risk of browsing damage is perceived as high by forest owners, making them hesitant to invest in planting Scots pine even on the most appropriate sites (Lodin et al., 2017). The hunting community (of which many forest owners are members) commonly wants to maintain high population densities of game. Such high densities, in combination with intensive forestry and the effects these have on forage availability and distribution, leads to a high browsing pressure and high damage in Swedish forests. Browsing of Scots pine shoots by moose (*Alces alces*) and other ungulates in young stands can regionally be severe. For example, the Swedish national young stand browsing inventory (ÄBIN) showed that on average 43% of Scots pine saplings had browsing damage made by cervids during 2016-2020 (SFA, 2020), with high possible economic losses as a consequence (Nilsson et al., 2016). Other types of browsing damage, such as browsing of Norway spruce seedlings by roe deer (*Capreolus capreolus*) (Bergquist & Örlander, 1998) and bark stripping in Norway spruce stands by red deer (*Cervus elaphus*) can locally be severe (Månsson & Jarnemo, 2013; Jarnemo et al., 2014). These facts are likely forming the composition of the future forests, and recent data from 2015-2018 indicates that the proportion of forest area in Sweden with Scots pine stands (> 1500 Scots pine stems ha^{-1}, 1-4 m in height) is 7.6% for all regenerated forest land, and only 1.5% in southern Sweden, indicating a substantial decrease of the species in the future (Ara, 2020, unpublished data, November 2020).

1.3 N uptake and N_2-fixation

Forest ecosystems in the boreal zone are nitrogen (N) limited (Vitousek & Howarth, 1991; Fenn et al., 1998; Bergh et al., 1999) just like many other terrestrial and marine ecosystems in the world (Tamm, 1991; Vitousek et al., 1997). It is hence crucial for seedlings to establish a sufficient N uptake after outplanting (Margolis & Brand, 1990). N can be derived from internal sources of storage by retranslocation, or from external sources by mineralization of soil organic matter, N_2-fixation, organic N uptake via mycorrhiza to roots, N deposition or fertilization (Näsholm et al., 1998; Millard & Grelet, 2010). For a seedling or a tree, retranslocation of N that has been taken up previously is of utmost importance, as approximately 50% of the N use comes from retranslocated N and the remaining 50% from new uptake, but the variation is rather high (Millard & Grelet, 2010). The relative dependency of retranslocated N is lower in high N environments because of high N uptake.

N can also be added to an ecosystem by N_2-fixation, by for example free-living or endophytic diazotrophs (bacteria and archaea). N_2-fixation can be found in, for example, aboveground tree residues (Brunner & Kimmins, 2003), roots (Granhall & Lindberg, 1978; Mäkipää et al., 2018), soil, foliage etc. (Son, 2001). Findings from Canada have shown bacteria living in internal tissues (endophytic diazotrophs) of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson) and hybrid white spruce (*Picea glauca x engelmannii*), possibly facilitating the species to grow well in nutrient poor environments (Padda et al., 2018; Puri et al., 2018).

Stable isotopes are an important tool in plant ecology to better understand how plants interact with their surrounding environment (Dawson et al., 2002; Fry, 2006). They can be used for various types of research, from microbial to whole landscape levels (Fry, 2006). The labeled substances' isotopic composition usually exceeds the natural occurring level, and is compared to the background level (Dawson et al., 2002). A way to quantify N uptake and retranslocation in seedlings or trees is by using the ^{15}N isotope. A typical approach is to add ^{15}N to the soil, including a control where no ^{15}N has been added.

1.4 Productivity

Traditionally, Scots pine is recommended to be used on dry poor to intermediate fertile sites (Albrektson et al., 2012) as many previous non-experimental studies have found that Scots pine performs better on such sites compared to Norway spruce. Leijon (1979) found that Norway spruce grew better or similar than Scots pine on all site types in a study of adjacent stands. Öyen and Tveite (1998) found in a similar survey study of 92 adjacent stands in Norway that Norway spruce had a 100% higher potential growth than Scots pine. Ekö et al. (2008) used national forest inventory (NFI) data to estimate potential growth ratios of Scots pine and Norway spruce and found a better growth of Norway spruce in southern Sweden with decreasing differences between the species with increasing latitude.

However, recent experiments have contrasted above studies showing Scots pines' potential to grow better than Norway spruce on intermediate and fertile sites. Jonsson (2001) found in an experiment in central Sweden that Scots pine had a 165% higher total volume compared to Norway spruce after 40 years, and in the same experiment Holmström et al. (2018) reported a 126% higher total volume of Scots pine after 57 years. Nilsson et al. (2012) examined productivity of Scots pine and Norway spruce in an experiment at 12 sites, spanning over a wide fertility gradient in northern Sweden. Scots pine produced on average 240% more total volume across sites at a total age of 52-82 years. Norway spruce only matched growth of Scots pine at one very fertile site. Drössler et al. (2018) found that the growth of Scots pine had 17% (southern Sweden) to 844% (northern Sweden) higher total volume production than Norway spruce at ages between 26-57 years. The study included seven sites across Sweden with monocultures of both species and mixtures. Nevertheless, Vollbrecht et al. (1995) reported Scots pine to have 21% lower MAI compared to Norway spruce after 40 years at a fertile west-facing slope in southwestern Sweden. It should be taken into consideration that thinning was carried out four times down to a basal area of 18-19 m^2 ha^{-1} for Scots pine and 27-28 m^2 ha^{-1} for Norway spruce, which could have skewed the results in favor of Norway spruce.

1.5 Mixed forest

An alternative to monocultures of Scots pine or Norway spruce is to grow them in a mixture. Mixed forests in Sweden are common, but the proportion depends on the definition used (Appendix 1). For example, the Swedish National Forest Inventory (NFI) showed that the amount of mixed forest can vary from 20%-74%. The lower proportion of mixed forest comes from the standard monoculture classification, while the higher proportion comes from an alternative threshold (SLU, 2019).

When mixing two species there are a few possible production outcomes of how the mixing affects productivity (i.e., growth, total volume or biomass) according to del Río et al. (2018) (Figure 3):

1) "Transgressive overyielding", i.e., productivity of the mixed stand is higher than the productivity of the highest producing monoculture,

2) "non-transgressive overyielding", i.e., productivity of the mixed stand is higher than the theoretical mixture (the sum of half of the productivity of both monocultures, from here-on referred to as "theoretical mixture"),

3) "non-degressive underyielding", i.e., productivity in the mixed stand is lower than the theoretical mixture,

4) "degressive underyielding", i.e., productivity in the mixed stand is lower than the worst growing monoculture.

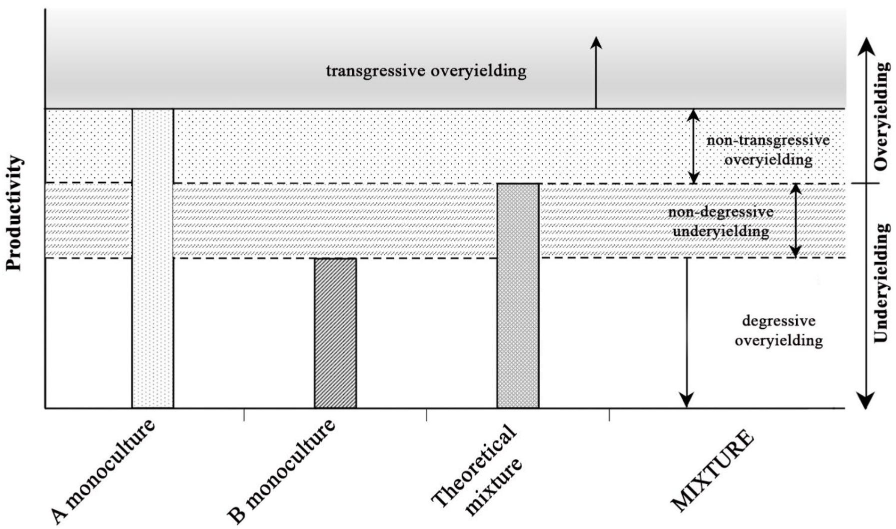

Figure 3. Illustration of the types of over- and underyielding (based on Hector, 1998; Fridley, 2001). Two monocultures of different productivity are plotted, A and B, and the theoretical mixture of them (the sum of half of the productivity of both monocultures). If a mixture of A and B has lower productivity than the higher producing monoculture (in this case A), but higher productivity than the theoretical mixture, it overyields but non-transgressively. If the productivity in the mixture is greater than the most productive monoculture, it transgressively overyields. Similar types of underyielding outcomes are also possible.

An increase in growth of mixtures is in theory explained by complementary effects, meaning that species use different available resources. Another explanation could be facilitation, meaning that one species enables the other species to increase resource utilization, such as when one species can fixate atmospheric N_2 (Pretzsch, 2018). Both types of overyielding indicates beneficial interspecific interactions, which are of special scientific interest, and have been found in several survey studies of mixed and monoculture stands (Pretzsch, 2018), including mixed stands of Scots pine and Norway spruce (Bielak et al., 2014).

There are few published experiments in northern Europe investigating growth of Scots pine and Norway spruce in mixtures. Lindén and Agestam (2003) found a non-significant trend that volume increment in mixture was higher than in monocultures (transgressive-overyielding). Most sites in Sweden in the study of Drössler et al. (2018) did not show overyielding, however transgressive-overyielding was observed at the site in southern Sweden where Lindén and Agestam conducted their study. Furthermore, Jonsson (2001) found a significant non-transgressive overyielding, as the volume growth of the Scots pine-Norway spruce mixture was higher than the theoretical mixture, but not higher than the Scots pine monoculture.

However, there are other reasons than only volume production for growing mixed forests. Other important aspects are regulatory potential benefits in terms of decreased risk for windthrow, pests and pathogens (Felton et al., 2016). Aesthetics and outdoor recreation could be expected to increase in a mixed forest compared to monocultures as mixtures are often aesthetically preferred (Gundersen & Frivold, 2008), probably due to openness and higher understory light levels (Eriksson et al., 2012). In addition, mixtures of Scots pine and Norway spruce would, compared to Norway spruce monocultures, increase the range of environmental conditions and increase the potential variety of habitats (Felton et al., 2016). Hence, compared to monocultures of Norway spruce, a mixture seems to be beneficial for biodiversity, cultural- and regulatory services, as well as providing provisioning advantages, economic flexibility (Felton et al., 2016) and an insurance against low production.

1.6 Biodiversity and ecosystem services

The provisioning ecosystem service of wood production is of major importance in Sweden, indicated by annual harvest levels (85 million m^3), and possible utilization rates of the forest (5% of the productive forest land is formally protected) (SLU, 2020). A first approach to a modern sustainable forestry was made in 1993 when the Swedish Forest Act gave equal status to environmental and production objectives (Gov. bill 1992/93:226). Hence, today's forests provide a wide range of ecosystem services and support forest biodiversity (Felton et al., 2020a). For example, Sweden's forests are supposed to provide environments for non-timber forest products, recreation, as well as crucial habitats for biodiversity. Since the Swedish Forest Act of 1993 came into place, important biodiversity indicators such as amount of broadleaf trees and dead wood has increased significantly (Jonsson et al., 2016; SLU, 2020), and the amount of dead wood at different stages of decay is crucial for thousands of species (Berg et al., 2002; Stokland et al., 2012).

Outdoor recreation connected to forests is a strong tradition in Sweden (Fredman et al., 2014). Visiting the forest for hunting, collection of non-timber forest products, physical activities or to just experience the pleasure and beauty of nature are important for the public (Lisberg Jensen & Ouis, 2014). These recreation activities provides probable wellbeing and mental health benefits (Oh et al., 2017; Buckley et al., 2019). Collection of bilberry (*Vaccinum myrtillus*) is a common activity motivating forest visits. Bilberry is one of the most important wild berry species, collected for both household consumption and sale (Lindhagen & Bladh, 2013; Sténs & Sandström, 2013). Mushroom picking is another activity with long tradition. The total annually collected amount can be more than 15 million liters (Yrjölä, 2002). Furthermore, hunting can be added to list of benefits that forests produce, with an estimated value exceeding 300 million Euros (Boman & Mattsson, 2012).

2. Thesis aims

The overarching goal of this thesis was to examine growth differences between Scots pine and Norway spruce in different stages during a rotation, to disentangle potential underlying reasons for differences, and thereby expand the knowledge basis regarding growth patterns and growth responses. In addition, an aim was to provide increased basic scientific knowledge regarding site-specific tree species choice.

In the first part of the thesis (**Paper I**), early growth of Scots pine and Norway spruce seedlings was evaluated for different site preparation treatments at fertile- and poor sites in northern and southern Sweden. In the second part (**Paper II**), reasons behind initial growth responses from the first study was examined using a stable isotope to investigate relationships between N uptake and retranslocation. Potential N_2-fixation was also studied by acetylene reduction assay. In the third part (**Paper III**), the growth of mature Scots pine and Norway spruce in mixtures or monocultures in central Sweden was investigated to further determine species differences found in the first and second study. In the fourth part (**Paper IV**), the importance of species choice was highlighted in a wider context by compiling existing literature regarding implications of a species shift from Scots pine to Norway spruce in southern Sweden, focusing on stand- and landscape scale.

The following objectives were addressed in this thesis:

I. To determine establishment and early growth responses of Scots pine and Norway spruce, and examine possible reasons for differences between species (**Papers I-II**).

II. To determine the productivity of Scots pine and Norway spruce as monocultures and mixtures, and assess biodiversity and a wide range of ecosystem services connected to both species, as well as possible implications of a species shift from Scots pine to Norway spruce (**Papers III-IV**).

3. Material and methods

To address the specific objectives of this thesis, field experiments were used (**Papers I and III**), a combination of field experiments and laboratory experiments (**Paper II**), as well as a review study (**Paper IV**). In this section, the material and methods are briefly summarized; further details can be found in the individual papers.

3.1 Regeneration studies (**I-II**)

3.1.1 Study sites and field measurements (**I-II**)

The four trials used in these studies were selected to represent fertile and poor sites in northern and southern Sweden, and were designated: NorthPoor, NorthFertile, SouthPoor and SouthFertile (Figure 4). The trials were established in 2011 and 2012. At all sites, a split-plot design with four blocks was applied. Three site preparation treatments were applied over the entire main plot (7 x 8 m, i.e., not spot-wise): control (no site preparation); removed humus (RH, i.e., removal of the organic layer); and deep soil cultivation (DSC, i.e., inverting the entire soil profile) (Figure 5). Containerized Norway spruce and Scots pine seedlings of suitable provenances were randomly planted within the main plots with a 1 x 1 m spacing. Seedlings were measured (height from the ground, diameter at ground level, and length of leading shoot) after planting and after every growing season during 5-6 years.

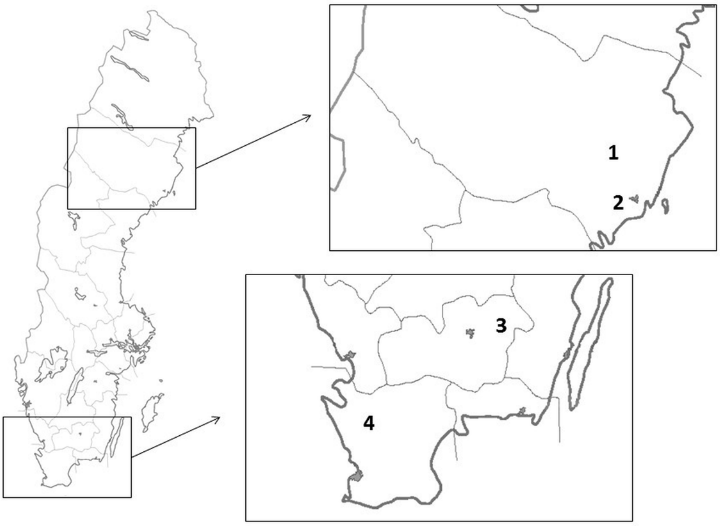

Figure 4. Locations of the four sites used in the regeneration studies (**Papers I-II**). 1 = NorthPoor, 2 = NorthFertile, 3 = SouthPoor and 4 = SouthFertile (Nilsson et al., 2019).

Figure 5. Photo illustrating an excavator performing the deep soil cultivation treatment at the NorthPoor site used in the regeneration studies (**Papers I-II**) (Photo: Olle Sjölin – Skogforsk).

3.1.2 Nitrogen aspects sampling and analyzes (**II**)

The natural occurring atom % abundance level of ^{15}N is 0.3663, compared to 99.6337 of ^{14}N (Fry, 2006). In this study, the seedlings were enriched with ^{15}N at the nursery to a baseline concentration. By knowing the starting value of the ^{15}N isotope in the seedlings from the nursery, the concentration of ^{15}N in new needles indicates uptake of unlabeled N, and how much the seedling has depended on retranslocation. The proportion of N in needles of new shoots derived from N acquisition in the field ("N derived from uptake" or N_{dfu}) and the proportion of N in needles of new shoots derived from N retranslocation ("N derived from retranslocation" or N_{dfr}) was calculated after the two first growing seasons.

In order to analyze potential N_2-fixation capacity, fine roots from seedlings of both species were sampled in every treatment plot during late spring and early autumn 2017, i.e., after 5-7 growing seasons. Fine roots were collected and stored until the start of the laboratory analyzes. Samples were analyzed using a 24-hours acetylene reduction assay using a gas chromatograph (Perkin Elmer Inc. Clarus 500 GC).

3.2 Mixture experiment (**III**)

The Främlingshem trial used in this study is located in central Sweden. It was regenerated in 1956 by sowing mixed seeds of Scots pine and Norway spruce. Ten blocks of monocultures of both species and a mixture were established a few years after the sowing by applying early pre-commercial thinning to on average 2873 stems ha^{-1}. The mixed treatment was done with approximately half of that stem number for each species. Diameter of all trees and heights of sample trees were recorded in 2014 to calculate standing volume. Increment cores were also taken to estimate the current growth rate (PAI, periodic annual increment), by measuring the ring-width growth during the last five-year period.

3.3 Review study (**IV**)

Available research about differences in ecosystem services and biodiversity in stands of Scots pine and Norway spruce was reviewed to evaluate implications of a species shift from Scots pine to Norway spruce.

Selected topics frequently raised by forest stakeholders including damages, production, biodiversity and recreation connected to stand conversion were investigated. Consequences of a conversion from Scots pine to Norway spruce were then examined with a focus on the following ecosystem services and biodiversity:

- ***Cultural services***
  Aesthetics and recreation

- ***Provisioning services***
  Biomass production and wood products

- ***Regulatory services***
  Abiotic and biotic risks, climate suitability

- ***Biodiversity***
  Vascular plants, bryophytes, birds, large herbivores etc.

Boolean search terms were used to find relevant peer-reviewed studies. For example, search terms used to find relevant studies on biodiversity of birds were: (''Scots pine'' OR ''*Pinus sylvestris*'' OR ''Norway spruce'' OR ''Picea abies'') AND ''bird*''. Databases used were Web of Science (http://www.isiwebofknowledge.com/), Google Scholar (http://scholar.google.com.se), and Scopus (https://www.elsevier.com/solutions/scopus). Published studies, books and reports were also obtained from colleagues and reference lists. Studies conducted in even-aged stands of Scots pine or Norway spruce in Fennoscandia were prioritized.

4. Main results and discussion

4.1 Early growth of Scots pine and Norway spruce (**I**)

In this study, the species' survival and growth was monitored at both fertile and poor sites in northern and southern Sweden after site preparation of various intensity. No significant differences in growth responses of either species to site preparation treatments during the first year were detected, consistent with previous studies on boreal coniferous species (Löf, 2000; Johansson et al., 2005). Significant differences in the growth response were first detected after two or three years, which is in line with findings of Örlander et al. (1996b). Scots pine subsequently grew more rapidly at all sites and in all site preparation treatments (Figures 6 and 7). Norway spruce most closely matched Scots pine's leading shoot growth and total stem volume at the SouthFertile site. The difference between the two species was generally most pronounced in the RH site preparation, in which the humus layer and hence large proportions of available nutrients were removed. The finding of a more rapid early growth of Scots pine compared to Norway spruce is in accordance with many studies from both Finland and Sweden (Örlander et al., 1990b; Johansson et al., 2015; Luoranen, 2018).

Growth of both species was highest following DSC site preparation at most sites (Figure 6). In DSC plots, seedlings' early growth was relatively poor in the north, but they subsequently outperformed seedlings in the other treatment plots, possibly due to increased mineralization and nutrient availability, which previously has been observed after site preparation (Örlander et al., 1990a; Schmidt et al., 1996; Lebel et al., 2008). In addition, growth check of Norway spruce, which is a common phenomenon

(Grossnickle, 2000), was detected following every treatment in the second growing season, and throughout the entire study period following the RH treatment (Figures 6 and 7). This may have been due to the removal of nutrients, especially nitrogen, in the organic layer, as found in other studies (Simard et al., 2003; Powers et al., 2005). Interestingly, differences in leading shoot growth and total stem volume of Scots pine seedlings between DSC and RH treatment were found at the poor but not the fertile sites. This may indicate that improvements in nutrient availability following the DSC treatment at poor sites have contributed to their increased growth.

There were no significant treatment differences in the growth of Scots pine seedlings at the SouthFertile site (Figure 6), indicating that they acquire enough nutrients to maximize stem volume growth, even when the humus layer was removed. The SouthFertile site seems to be so fertile that it might not be necessary nor possible to increase growth for either of the two species. In addition to soil nutrients, other factors may also have been affected by the site preparation. Low soil temperature often limits growth, but can be increased by soil scarification (Örlander et al., 1990a; Grossnickle, 2000, 2005; Thiffault et al., 2013). Soil temperature was generally lowest, and field vegetation cover was highest in the control plots. The increases in soil temperature and reduction of competing field vegetation associated with the RH treatment probably at least partially compensated for the accompanying removal of nutrients.

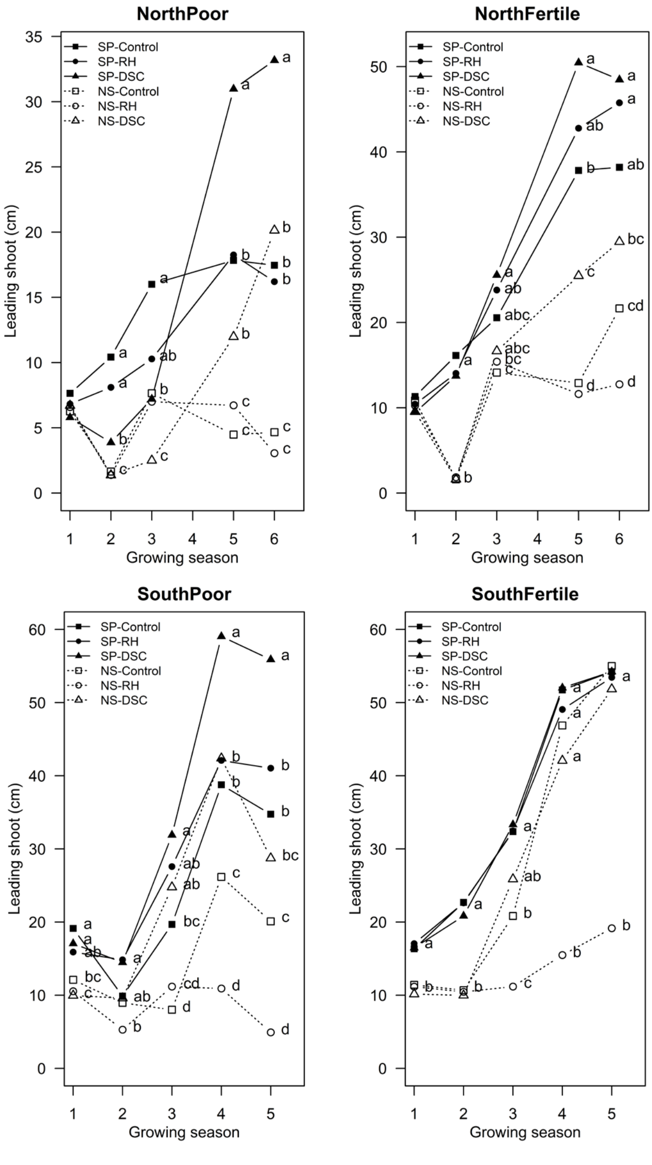

Figure 6. Observed leading shoot growth (cm) following the three site preparation treatments at the four experimental sites of Scots pine (SP) and Norway spruce (NS) seedlings during the first six or five growing seasons at the northern and southern sites, respectively. Site preparation treatments: Control (no site preparation), Removed Humus (RH) and Deep Soil Cultivation (DSC). Different letters next to an observed mean indicate significant differences within site and growing season according to the Tukey multiple comparison difference test (Nilsson et al., 2019).

Figure 7. Photos from two field sites. Top left: Norway spruce seedlings experiencing growth check, and well-growing Scots pines 5 years after planting in the RH treatment at the SouthFertile site. Top right: Norway spruce and Scots pine saplings thriving in the DSC treatment at the SouthFertile site 5 years after planting. Bottom left: Slow growth of both species 6 years after planting in the RH treatment at the NorthPoor site. Bottom right: Improved leading shoot lengths of Norway spruce 6 years after planting in the DSC treatment at the NorthPoor site (Photos: top left; Nils-Anders Färdmo, the remainder; Oscar Nilsson).

4.2 N uptake, retranslocation and N_2-fixation in Scots pine and Norway spruce (**II**)

In this study, underlying reasons for initial growth patterns from **Paper I** were examined using the stable isotope ^{15}N. The proportion of N in needles of new shoots derived from N acquisition in the field (“N derived from uptake” or N_{dfu}) and the proportion of N in needles of new shoots derived from N retranslocation (“N derived from retranslocation” or N_{dfr}) was calculated.

N_{dfu} was significantly higher for Scots pine compared to Norway spruce, indicating that Norway spruce had a higher dependency on N_{dfr} (Figure 8). Seedlings of both species were still dependent on old N from the nursery after two growing seasons at the harshest site (NorthPoor), whereas seedlings at the other three sites almost had reached asymptotic levels of ^{15}N (Figure 8).

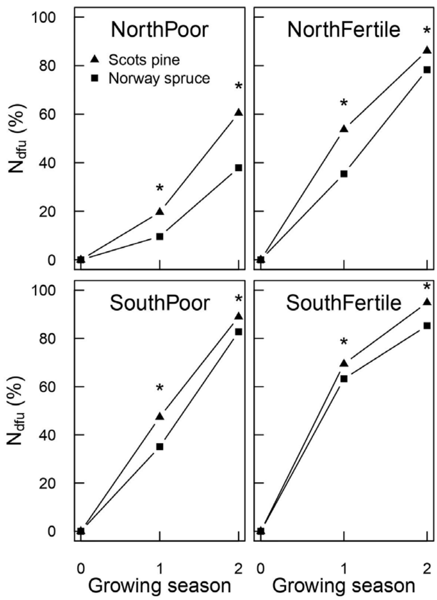

Figure 8. N_{dfu} as a percentage of N in needles of new shoots derived from uptake at the sites across site preparation treatments. The asterisk indicates significant differences between species.

The relationship between N_{dfu} after the first growing season and leading shoot growth the following year across all sites clearly showed that increased N_{dfu} led to an increased leading shoot growth ($p < 0.0001$) (Figure 9a). However, for Norway spruce in the north, especially at the NorthFertile site, there was a tendency that leading shoot growth the second year had no relationship to N_{dfu} the first growing season (Figure 9a). Indicating that there may be other limiting factors besides N, such as low soil temperature, poor access to water or lack of other nutrients (Margolis & Brand, 1990; Grossnickle, 2000). A relationship between N_{dfu} after the second growing season and leading shoot growth next year was found at the NorthPoor site (Figure 9c) and for the other three sites (Figure 9b). The pattern that increased N uptake leads to increased leading shoot growth the following year are in line with previous research (Nilsson & Örlander, 1999; Grossnickle, 2000; Nordborg et al., 2003).

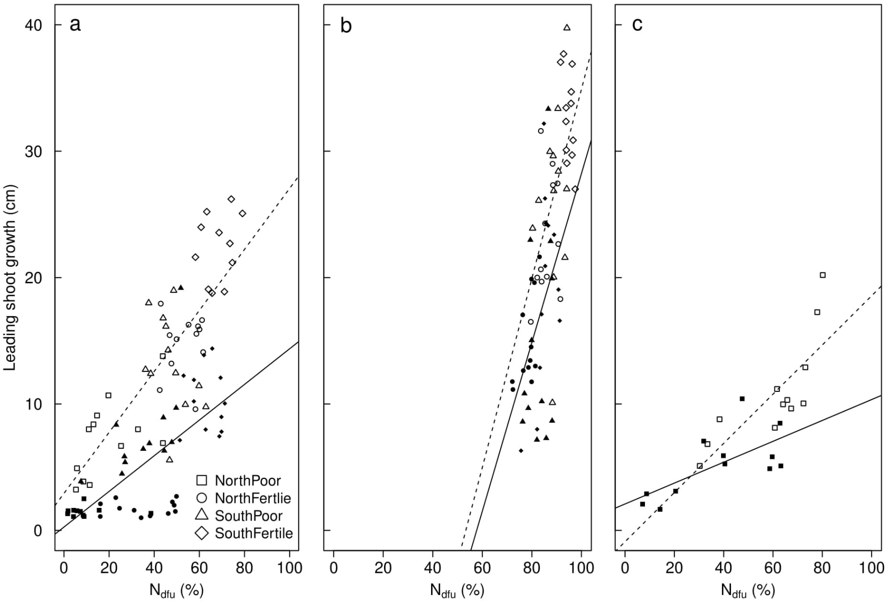

Figure 9 (a-c). N_{dfu} as percent of N in needles of new shoots derived from uptake against leading shoot growth the following year for Scots pine (hollow figures, dashed line) and Norway spruce (solid figures, full line) after: (a) the first growing season at all sites; (b) the second growing season at all except the NorthPoor site; (c) the second growing season at the NorthPoor site.

The approach of ^{15}N dilution used in our study differed from the typical approaches (Barraclough, 1995; Murphy et al., 2003; Millard & Grelet, 2010). In our study, we chose to enrich the seedlings to high levels of ^{15}N in the nursery and followed the N_{dfu} and N_{dfr} in new needles. A strength of our approach is that seedlings were cultivated from seed to the stage at which they were planted with a known ^{15}N content and the entire seedling was homogenously labelled.

The other part of this study investigated potential N_2-fixation capacity in fine roots. The results indicated a higher potential N_2-fixation of Scots pine ($p < 0.0001$) across sites, both at the spring and autumn samplings. Studies from Sweden have shown that Scots pine can grow well in bare mineral soil plots in Sweden with low N levels (Kardell, 2010; Nilsson et al., 2019), and thus maybe get their N from an unknown source. These prior observations led to a hypothesis that this unknown source could be N_2-fixation. Studies from Canada have reported that lodgepole pine can grow well on gravel mining pits with a lack of topsoil and essential plant nutrients such as N (Chapman & Paul, 2012), suggesting that N_2-fixation could be involved in the unexpected good growth at these types of sites (Padda et al., 2018; Puri et al., 2018). However, the results from our study showed that in Sweden, the unknown N source is not from N_2-fixation in fine roots during the establishment phase. This was based on a sensitivity analysis showing a contribution of N_2-fixation to total annual N uptake of around 0.1%. The annual addition of N from N_2-fixation was hence disregarded for the N_{dfu} and N_{dfr} variables.

The N_2-fixation results found in our study is in contrast to findings by Granhall and Lindberg (1978), who found that Norway spruce had higher rates of N_2-fixation. However, our values for Norway spruce are similar to those reported by Mäkipää et al. (2018) in older trees from Finland, despite their focus on coarser roots. Mäkipää et al. (2018) upscaled their results for Norway spruce to stand level N_2-fixation per hectare and reported values of 0.06 and 0.15 kg ha^{-1} $year^{-1}$, which is a fraction of the total N uptake of mature trees (Korhonen et al., 2013; Sponseller et al., 2016). Comparing N_2-fixation capacities of fine roots found in our study with feather mosses, our rates were around 100 times lower (DeLuca et al., 2002; Leppänen et al., 2013; Stuiver et al., 2016).

A possible limitation in our study is that we approximated potential N_2-fixation, which could be an overestimation compared to actual N_2-fixation as no control vials with fine root samples without acetylene were analyzed. Importantly, any corrections (of naturally emitted ethylene) would only lead to a lower N_2-fixation capacity.

4.3 Productivity of Scots pine and Norway spruce in monoculture and mixture (**III**)

In this study at Främlingshem, growth differences between Scots pine and Norway spruce found in **Papers I-II** were further investigated later in the rotation, as well as their potential growth in mixtures. Standing volume (m^3 ha^{-1}) of Scots pine in monoculture plots was 126 % higher than Norway spruce after 57 years (Figure 10).

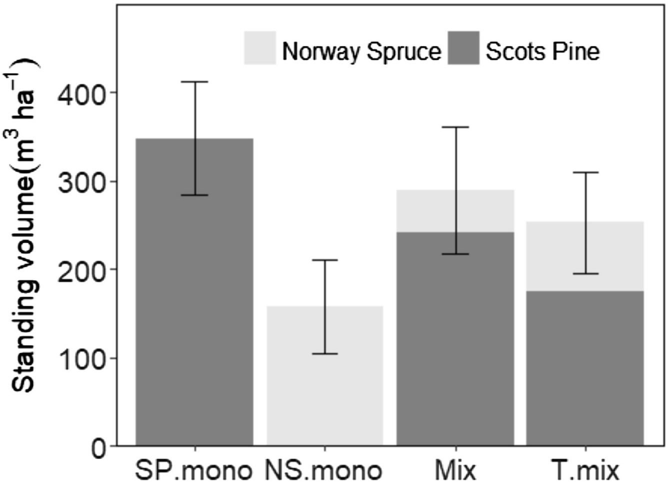

Figure 10. Mean standing volume (m^3 ha^{-1}) for all blocks (n = 9) in the experiment for Scots pine in monoculture (SP.mono), Norway spruce in monoculture (NS.mono), the mixture of the two species (Mix) and the theoretical mixture (T.mix). Error bars represent the standard deviation between blocks (Holmström et al. 2018).

The mixture of Scots pine and Norway spruce had a non-significant higher standing volume and PAI during the last five-year period than the theoretical mixture (i.e., a tendency of non-transgressive overyielding) (Figure 10). The standing volume of Scots pine was higher in the mixture, while it was lower for Norway spruce when compared with the theoretical mixture (Figures 10 and 11). The PAI estimation still showed significantly higher growth rate of Scots pine than Norway spruce, meaning that total production was still diverging. The PAI also indicated a shift in growth relations between treatments with time. The standing volume of the mixture was significantly higher than the theoretical mixture in 1999 (non-transgressive overyielding) (Jonsson, 2001), but not in 2014. This trend between the mixture and theoretical mixture could be because of the species' different growth patterns. Further, transgressive overyielding of Scots pine and Norway spruce mixtures have previously only been observed at one site in southern Sweden, where a mixture produced 8% higher total volume than the highest producing monoculture (Drössler et al., 2018).

The diameter distributions of the two species in monocultures and mixtures showed that the effect of increased or decreased competition probably was more important for explaining the results than complementary or facilitation effects (Figure 12a-b). The diameter distributions of Scots pine in monoculture and mixture is similar to the diameter distribution in high- and low density stands (Pettersson, 1993), suggesting a spacing effect. That Scots pine had higher diameters in mixture (Figure 12a) was also found by Lindén and Agestam (2003). In our study, the different diameter distribution patterns of the subdominant Norway spruce in monoculture and mixture indicates increased competition from Scots pine when growing together (Figure 12b), which is in line with other studies (Forrester & Smith, 2012; Pretzsch et al., 2015). Scots pine also had a lower height-diameter ratio (HD-ratio) in the mixture, another sign of reduced competition, as low ratios often are found in low density plantations or after heavy thinning (Wallentin, 2007). For Norway spruce, the HD-ratio was higher in the mixture for higher diameter classes, thus indicating increased competition.

The finding that Scots pine had a higher total growth compared to Norway spruce is consistent with results from Nilsson et al. (2012) who found that Scots pine on average had produced 240% more stem wood compared to Norway spruce in experiments with both species planted on the same sites in northern Sweden. Drössler et al. (2018) also found that Scots pine would grow comparably well on three fertile sites in southern Sweden, showing the potential of Scots pine even on those kinds of sites. This fact may be explained by the low initial growth of Norway spruce observed in many experiments (Wibeck, 1912; Björkman, 1953; Örlander et al., 1990b; Jonsson, 2001; Nilsson et al., 2012).

Figure 11. Photos from the Främlingshem site during 2018. Top left: Norway spruce in monoculture. Top right: Scots pine in monoculture. Bottom: Mixture of Scots pine and Norway spruce. (Photos: Oscar Nilsson)

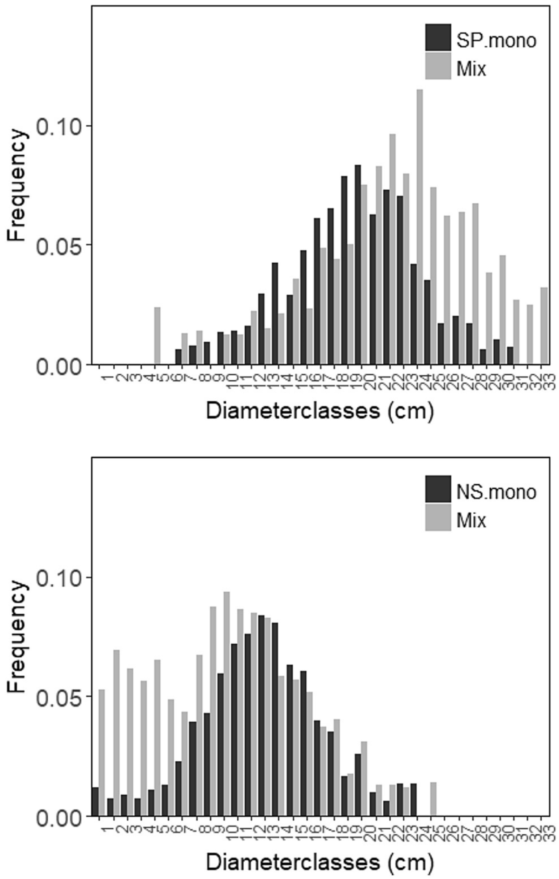

Figure 12. Frequency distribution of stems in diameter classes, all blocks. Upper panel, 12a, Scots pine in pure and mixed treatments. Lower panel, 12b, Norway spruce in pure and mixed treatments (Holmström et al. 2018).

An important aspect to take into account is that growth characteristics of both species varies, Scots pine being a “sprinter” with a rapid initial growth and Norway spruce being a “slow-starter” with a more sustained growth. Hence, the timing of the comparison affects the production outcomes. Therefore, comparing the growth in younger stages is problematic, and should ideally instead be done over a full rotation until the culmination of MAI. Another complication regarding growth comparisons is the complexity of providing similar conditions and comparable silvicultural treatments throughout a full rotation of two different species, to make the results as comparable as possible.

Establishing a mixture in the regeneration phase reduces the risk of a full rotation with unnecessarily low production, which could happen if the slower growing species is selected. A mixture is also an insurance to species-specific biotic or abiotic damages occurring any time during the rotation made by browsing, pests or pathogens, etc. More than 80% of the Swedish clearcuts are regenerated by planting only one of Scots pine or Norway spruce (Bergquist et al., 2011), a safer bet could be to at least consider a mixture of both species.

A drawback with this study is that it is only one site, which makes it hard to draw any general conclusions. The dilemma regarding which species to choose is complex, as previous studies are showing contradicting results. Results from the few existing experiments shows that Scots pine in general has a better or similar growth compared to Norway spruce (Jonsson, 2001; Nilsson et al., 2012; Drössler et al., 2018), with some exceptions (Vollbrecht et al., 1995). A second way to compare the growth between the species is by using survey data from paired stands with similar conditions growing in the proximity of each other. Such studies in Sweden (Leijon, 1979) and Norway (Öyen & Tveite, 1998) shows a superiority of Norway spruce, except at poor or dry sites. A third way to compare growth of both species is by using national forest inventory (NFI) data to estimate site index (SI) by using site properties (such as field vegetation, see Hägglund & Lundmark, 1977), and then compare outcomes from growth models. This third way was done by Ekö et al. (2008) who found that Norway spruce in Sweden on average had a 43% higher potential growth, where differences increased with decreasing latitude.

4.3.1 The "million-dollar question"

As many studies show similar or better growth of Scots pine compared to Norway spruce in scientific experimental setups, it leads to the "million-dollar question":

Why does Scots pine production compare better to Norway spruce in scientific field experiments than in survey studies?

There is no question that scientific field experiments are superior to survey studies when comparing potential production of two or more tree species. However, problems with field experiments are that they are limited in the representation of site properties and they may only reflect the first part of the rotation. Therefore, various types of survey studies or measurements in temporary plots have been used to overcome these drawbacks. However, it turns out that results from scientific field experiments are different from results of survey studies or comparing SI.

Problems with using survey studies or studies comparing SI could for example be:

- Previous management history and owner goals are unknown.
- Site-species selection, "as you sow, so shall you will reap". Using Scots pine only on poor sites may not allow reliable growth comparisons between the two species.
- Management guidelines typically include thinning to a lower basal area for Scots pine (over-thinning), which may result in an underestimation of potential Scots pine production.
- Potential errors in converting SI from one species to the other.

Problems with using scientific field experiments could for example be:

- Old experiments use old seedling material and often without mechanical site preparation. Modern mechanical site preparation and seedling material may comparatively improve growth of Norway spruce more than for Scots pine.
- New experiments with modern seedling material and mechanical site preparation only enable comparisons early in a rotation when trees are still young, as it takes a long time to grow a full rotation. Early comparisons between tree species are not ideal and may be misguiding.

- The influence of prescribed burning on growth of either tree species in old experiments, as it was a more common site preparation method used in the past.

It may be important to keep in mind that prescribed burning was done before sowing in **Study III**. The effect of prescribed burning on the growth of Norway spruce has shown contradicting results in previous studies. For example, early studies in southern and central Sweden showed that prescribed burning in general affected the growth of Norway spruce negatively (Wibeck, 1912). In addition, a study involving burning and ploughing treatments in northern Sweden also showed that Norway spruce grew less after prescribed burning compared to ploughing and untreated control (Örlander et al., 1990b). Growth was reduced by 50% for the species at a site in northern Sweden after prescribed burning compared to the unburned control after 40 years (Kardell & Laestadius, 1987). It was found that SI for Norway spruce was negatively affected by prescribed burning, indicating lower growth, in a study of 800 stands across Sweden (Elfving, 1983). However, no clear negative growth effect was found for the species in a study of two experiments in central and northern Sweden after 16 years of growth (Nykvist, 2000). In addition, there was no indication of lower production of Norway spruce relative to Scots pine on sites that were burned compared to not burned in a study at 12 locations in northern Sweden (Nilsson et al., 2012). Further, a positive growth response was found with increasing fire severity for Norway spruce in northern Sweden after one growing season (Bansal et al., 2014).

For Scots pine on the other hand, growth following prescribed burning has also shown inconsistent patterns. For example, Scots pine has been reported to grow better after prescribed burning in Sweden (Wibeck, 1912) and Finland (Mäkitalo, 1999; Mäkitalo et al., 2010). SI of Scots pine has also been found to be positively affected by prescribed burning, indicating increased growth (Elfving, 1983). However, inconsistent results of Scots pines' growth after prescribed burning was found in a study at three sites in northern Sweden, (Örlander et al., 1996a). Nevertheless, fire severity could be a key factor influencing soil nutrients and controlling the effect on growth, as high fire severity led to a reduced growth in the mentioned study. Further, Scots pine grew best in the intermediate burn after one growing season in northern Sweden (Bansal et al., 2014), indicating that variation in fire severity may lead to variable growth responses.

A possible indication that fire severity could play an important role in specific tree-species growth response is found in **Paper I**. In that study, the growth of Norway spruce was severely hampered at all sites in the RH treatment that removed the entire organic layer, which could be comparable to a burn with a high fire severity. The negative effect on the growth of Scots pine in this treatment was comparably lower, and there was no negative growth response at the most fertile site (SouthFertile). That Scots pine can grow well at sites where the entire organic layer has been removed has also been shown in other studies in Sweden (Kardell, 2010). Hence, the growth of Norway spruce may have been more negatively affected by high-severity burning compared to Scots pine in old scientific experiments.

4.4 Implications of replacing Scots pine with Norway spruce (**IV**)

In this study, the importance of tree species choice was emphasized in a wider context, and implications of a shift from Scots pine to Norway spruce regarding ecosystem services and biodiversity in southern Sweden was investigated. Regarding biodiversity, a shift in tree species has complex implications, as projections depend on the scale. At the stand level scale, the diversity of bryophytes and birds were projected to increase, while the diversity of large herbivores and vascular plants were projected to decrease. Light levels can be very low in Norway spruce stands, restricting the cover of vascular plants but not the cover of bryophytes (Petersson et al., 2019). The diversity decrease of large herbivores probably stems from two main reasons, the first being that other tree species than Norway spruce are preferred by browsers (Månsson et al., 2007). The second reason is that available forage for cervids such as moose can be restricted in dense low light stands (Felton et al., 2020b), and important forage species such as dwarf shrubs have decreased during the last 20 years due to for example denser forest stands (Hedwall & Brunet, 2016). The bird diversity is projected to increase, as studies have found possible higher diversity in Norway spruce forests (Lindbladh et al., 2019), however, Scots pine forests can exclusively support certain species (Gjerde & Saetersdal, 1997). A change in community composition at a landscape scale was projected for all biodiversity components mentioned, except for large herbivores.

Impacts of a conversion on ecosystem services were assessed in three main categories being: provisioning, regulatory and cultural services. Firstly, production outcomes and wood products provided were projected to be negatively influenced by a conversion from Scots pine to Norway spruce (Table 1).

Secondly, regulatory services were divided into abiotic and biotic risks. All abiotic risks, such as damage from climate, storms, drought, and frost were expected to have negative outcomes from a conversion from Scots pine to Norway spruce (Table 1). Only fire damage had uncertain outcomes. Most biotic risks were also projected to have negative outcomes of a conversion, as increased damage from bark beetle and root rot is highly probable. Browsing damage had a contradicting projected outcome. A conversion would most likely decrease the damage in stands that are regenerated with Norway spruce instead of Scots pine but increase on a landscape scale since the browsing pressure in the remaining Scots pine stands will be increased.

Thirdly, all cultural services were projected to have a negative outcome from a conversion (Table 1). Scots pine has been preferred over Norway spruce in aesthetic visual preference studies (Tyrväinen et al., 2003). Recreational values such as hiking, hunting and berry-picking were hence also projected to decrease, as a conversion most likely would lead to darker Norway spruce forests. For example, the cover of *Vaccinium* spp. has been found to be almost non-existent in Norway spruce forests in southern Sweden, compared to a cover of around 50% in Scots pine forests (Petersson et al., 2019). A conversion could in turn decrease the important contribution berries have as a food resource for animals, decreasing populations of birds and game species, and reduce the benefit of recreational activities such as bird watching, hunting and berry-picking.

The outcome for ecosystem services and biodiversity from a conversion from Scots pine to Norway spruce was complex, and came from three main related negative interacting sources. The first source was risks specific to Norway spruce, the second was risks with Norway spruce growing on unsuitable sites, and the third was the risk of an augmented uniform Norway spruce landscape. The above described risks and implications of a conversion highlights the importance of species choice in a broader context. Planting Norway spruce in unsuitable environments would not only influence growth negatively as described in **Papers I-II**, but it would also have wide economical, ecological and cultural implications.

A major mitigation effort to slow down or stop this uncontrolled experiment should be in focus as soon as possible, as the ongoing conversion spiral would likely further increase the browsing pressure in the remaining Scots pine stands, further reinforcing the use of Norway spruce (Wallgren et al., 2013; Bergqvist et al., 2014). One mitigation method could be mixed stands of both species, as it can have several benefits compared to monocultures such as risk reduction, increased forest habitat variation and societal benefits (Gundersen & Frivold, 2008; Felton et al., 2016). Establishing a mixed forest could, for example be done by planting both species, or using natural regeneration of one species combined with planting of the other. An example of the latter is the combination method, where planting of Norway spruce is combined with natural regeneration of Scots pine. The combination method was considered to have potential and experiments were established, but these were not followed after stand establishment since an early evaluation showed restricted potential (Nilsson et al., 2006). Unfortunately, species choice at regeneration seems to be driven by beliefs and tradition of which species will have the best growth on a site and browsing risk, and not always on science.

Table 1. Expected implications at the stand level of pine conversion to spruce for ecosystem services. Outcomes are graded in terms of positive outcomes ''↑'', negative outcomes ''↓'', and uncertain outcomes ↕. ''Effect modifier'' indicates management that has a strong impact on outcomes. Confidence levels (i.e. *,**,***) are ''possible'', ''probable'', and ''highly probable'' outcomes, but are not relevant to ''uncertain'' outcomes (Felton et al. 2020)

Ecosystem services	Positive or negative outcomes	Effect modifiers
Provisioning		
Biomass production	↓*	Varies with type and extent of disturbance (e.g. browsing pressure vs. storm damage)
Product diversity	↓**	
Wood prices	↕	
Cultural		
Forest aesthetics	↓**	
Hiking	↓**	
Hunting	↓*	
Bilberry picking	↓***	
Stress recovery	↓**	Potential to improve in urban areas
Regulatory services		
Abiotic risks		
Projected outcomes due to:		
Climate damage	↓**	Extent of future GHG emissions
Storm damage	↓***	When thinning and harvest takes place
Drought damage	↓***	
Fire damage	↕	Ignition risk may be lower in spruce, but damage higher if a fire occurs; unknown implications of spruce on dry sites
Frost damage	↓***	
Biotic risks		
Projected outcomes due to:		
Browsing damage	↑***	However, conversion may increase / focus landscape scale damage
Spruce bark beetle damage	↓***	
Other bark beetle damage	↓**	Tree stress may allow other bark beetles to become pest species
Root rot damage	↓***	Higher spruce stem densities are likely to increase risks

5. Conclusions and implications

The overarching goal of this thesis was to examine growth differences between Scots pine and Norway spruce in different stages during the rotation, to investigate possible reasons for the differences, and to put species choice in a wider context. Thereby, the knowledge basis regarding growth patterns, growth responses and species choice has been improved.

Planted Scots pine seedlings outgrew Norway spruce seedlings at all sites in diverse environments (**Paper I**), which is consistent with previous studies (Johansson et al., 2015; Luoranen, 2018). Site preparation was favorable for both species as it increased survival and growth, and this is consistent with previous research (reviews by Löf et al., 2012; Sikström et al., 2020), suggesting that it should be done before planting. In low nutrient environments, early growth of Norway spruce was severely hampered compared to Scots pine that grew relatively, which is in line with previous research (Kardell, 2010). The results suggest that site preparation techniques removing large amounts of organic material should be avoided when planting Norway spruce.

N uptake and dependence on N retranslocation was found to be a reason for the initial growth responses found in **Paper I**, when it was investigated by the use of ^{15}N-labelled seedlings (**Paper II**). Both species followed similar trajectories regarding N uptake and retranslocation, but Scots pine had higher N uptake and higher leading shoot growth the following year. However, increased N uptake for Norway spruce in the north after the first growing season did not increase leading shoot growth the second growing season, indicating other possible limiting factors. As the role of retranslocated N diminished after the second growing season, it can be concluded that N uptake following outplanting is crucial, and retranslocated N is insufficient for satisfactory seedling growth. Instead, effective silviculture by optimizing site-species choice and suitable site preparation should be practiced. In addition, fertilization could possibly be an add-on to increase both initial- and long term growth for both species, as it has been shown to increase growth in previous studies (Timmer & Morrow, 1984; Nambiar & Fife, 1991; Munson et al., 1993; Nordborg & Nilsson, 2003; Nordborg et al., 2003; Johansson et al., 2012; Thiffault et al., 2017). Slow-release fertilizer could be of particular interest as Thiffault and Jobidon (2006) found promising results. As seedlings also take up organic N, fertilization with the amino acid arginine is a possible alternative to have the seedlings well supplied with N and improve growth (Näsholm et al., 2009; Gruffman et al., 2012; Wilson et al., 2013). Low rates of potential N_2-fixation capacity in fine roots of Scots pine and Norway spruce were also determined. Although differences were detected between species, the contribution of N_2-fixation to N acquisition was minuscule.

Scots pine produced 126% more stem wood than Norway spruce after 57 years and production was still diverging, but no overyielding was found (**Paper III**). In the mixture, Scots pine seemed to grow as if being in a wider spacing (Wallentin, 2007), while Norway spruce suffered from increased competition. However, establishing a mixture reduces the risk of sub-optimal species choice, and could be an insurance against low survival, low production or species-specific damages. **Paper III** is hence a good example of a long-term experiment with good statistical design, and is highly valuable for a general understanding, showing why forest owners could consider establishing a mixed forest. The drawback is that it only represents one site, making it difficult to draw general conclusions.

The conversion of Scots pine sites to Norway spruce can be seen as a large-scale uncontrolled experiment, as every stand converted is further reinforcing uncertainties, risks and possible future implications (**Paper IV**). A conversion from Scots pine stands to Norway spruce mostly had negative effects on ecosystem services and forest biodiversity. For example, the lower light levels typically found in Norway spruce stands (Petersson et al., 2019) had many negative biodiversity implications. Ecosystem services were to the vast majority deemed to have negative outcomes from a conversion from

Scots pine to Norway spruce, and stemmed from risks specific to Norway spruce, risks specific to Norway spruce growing on unsuitable sites, and risks with an increased uniform Norway spruce landscape. A conversion would likely decrease the browsing damage at a stand scale, as Norway spruce is less palatable for cervids (SFA, 2020). Nevertheless, at a landscape scale, the browsing pressure in the remaining stands would potentially increase, and by that reinforce the conversion spiral (Wallgren et al., 2013; Bergqvist et al., 2014). Unfortunately, the risk of browsing seems to override most other concerns regarding risks and potentially low growth of Norway spruce on unsuitable sites (Lidskog & Sjodin, 2014; Lodin et al., 2017), as it seems like forest owners, at least in southern Sweden are following the saying "Spruce or Lose". Hence, a key issue with the potential to unlock the major part of the complex conditions regarding species choice and regionally extremely low use of Scots pine would likely be to in some way resolve the "browsing dilemma".

Further, using Norway spruce at inappropriate sites would likely decrease forest growth, causing economical losses for the forest owners and reduced carbon sequestration. Scots pine probably has the potential to grow similarly or better than Norway spruce, not only on poor or dry sites, but up to rather high fertile site types, while having vital biodiversity benefits and providing significant higher levels of diverse crucial ecosystem services, providing win-wins in several dimensions. These findings from **Papers III-IV** have highlighted the importance of not losing Scots pine in the Swedish forest landscape in the long term, particularly in southern Sweden. It has also clarified for the public, decision makers, forest owners and forest managers, possible implications of a conversion of Scots pine stands to Norway spruce, and expected results if the conversion is not halted and reversed. Nevertheless, it does not mean to regenerate with Scots pine everywhere and to completely stop using Norway spruce, which would also have severe negative implications. A better approach would probably be to do it the "lagom"[1] way.

[1] "Lagom" is a Swedish word with a complicated English translation. It usually refers to something like: "just about enough but not too much or too little".

Finally, my results have further expanded on previous limited scientific knowledge regarding growth comparisons between Sweden's by far two most common and economically valuable tree species. It has given possible ecophysiological explanations, elucidated the importance of species choice from the elemental level to landscape scales. In addition, it has pin-pointed the vast possibilities of questions that warrants further attention in future studies.

6. Future perspectives

Because of the lack of long- and short-term studies of the two species at the same site with a statistically sound design, there is high potential for enhancing the scientific knowledge in several aspects.

Due to the complexity of the soil-plant ecosystem, more sophisticated studies than, for example, traditional fertilization studies could be a way to further enhance our understanding. Hence, future studies of establishment and growth could focus on disentangling limiting factors for both species by optimization studies further studying the role of N uptake and retranslocation. Regarding N_2-fixation, some of the limitations in my thesis could be addressed by accounting for naturally-emitted ethylene from fine roots, and by quantifying the contribution of N_2-fixation at a per seedling or per hectare basis. A wider span of root diameter classes and different tree ages could also be studied.

Higher frequency of droughts, predicted by climate models (de Groot et al., 2013; Flannigan et al., 2013), and a stronger interest in the use of prescribed burning for nature conservation and fuel management (McKenzie et al., 2004; Conedera et al., 2009) may increase fire occurrence. This development calls for more research focused on how both species establish and grow following fire and interaction between tree species and fire severity, a knowledge gap identified in this thesis. Long-term comparative studies of Scots pine and Norway spruce with unburned controls are rare in Scandinavia, and previous research has not revealed a consistent pattern of growth responses.

A potential addition to the silvicultural toolbox that might help mitigating a conversion of Scots pine stands to Norway spruce could be establishing mixed forests of both species by using planted Norway spruce and naturally regenerated Scots pine (Nilsson et al., 2006). There was previously a large interest in this method, but no follow-up has been carried out after the first early evaluation.

The planting of Norway spruce by default, particularly in southern Sweden, could potentially be mitigated if the economic consequences of Norway spruce on unsuitable sites were visible for forest owners and policy makers. Regarding the "million dollar question" and if survey data methods or scientific field experiments is the best way to evaluate and compare the potential growth of both species, I would place my bet on experiments being more reliable, and by that, pin-pointing the crucial need of more. A nationwide study with both species growing in monocultures and mixtures in a scientific experimental setup spanning over a wide gradient of fertility- and moisture classes, could potentially be an eye-opener for the forestry sector and the public. Growth and impacts on biodiversity in such experiments should also test different silvicultural regimes (i.e., different combinations of site preparation methods, spacing, thinning, fertilization, etc.). However, to get whole-rotation results from such studies takes a long time due to Sweden's northern location and slow forest growth. Meanwhile, we need reliable models enabling us to make good simulations and test different silvicultural regimes in both monocultures and mixed forests.

There is much work ahead to be done!

References

Albrektson, A., Elfving, B., Lundqvist, L., & Valinger, E. (2012). *Skogsskötselserien. 1, Skogsskötselns grunder och samband*. Jönköping: Skogsstyrelsen.

Ara, M. (2020). *Precommercial thinning in Swedish forests*. unpublished data. Southern Swedish Forest Research Centre. Swedish University of Agricultural Sciences.

Bansal, S., Jochum, T., Wardle, D. A., & Nilsson, M. C. (2014). The interactive effects of surface-burn severity and canopy cover on conifer and broadleaf tree seedling ecophysiology. *Canadian Journal of Forest Research, 44*(9), 1032-1041. doi:10.1139/cjfr-2014-0112

Barraclough, D. (1995). N-15 isotope dilution techniques to study soil nitrogen transformations and plant uptake. *Fertilizer Research, 42*(1-3), 185-192. doi:10.1007/bf00750513

Berg, A., Gärdenfors, U., Hallingbäck, T., & Noren, M. (2002). Habitat preferences of red-listed fungi and bryophytes in woodland key habitats in southern Sweden - analyses of data from a national survey. *Biodiversity and Conservation, 11*(8), 1479-1503. doi:10.1023/a:1016271823892

Bergh, J., Linder, S., Lundmark, T., & Elfving, B. (1999). The effect of water and nutrient availability on the productivity of Norway spruce in northern and southern Sweden. *Forest Ecology and Management, 119*(1-3), 51-62. doi:10.1016/s0378-1127(98)00509-x

Bergquist, J., & Örlander, G. (1998). Browsing damage by roe deer on Norway spruce seedlings planted on clearcuts of different ages - 1. Effect of slash removal, vegetation development, and roe deer density. *Forest Ecology and Management, 105*(1-3), 283-293. doi:10.1016/s0378-1127(97)00297-1

Bergquist, J., Eriksson, A., & Fries, C. (2011). Skogsstyrelsen Polytax 5/7 återväxttaxering: Resultat från 1999-2009. *Rapport Skogsstyrelsen*.

Bergqvist, G., Bergström, R., & Wallgren, M. (2014). Recent browsing damage by moose on Scots pine, birch and aspen in young commercial forests - effects of forage availability, moose population density and site productivity. *Silva Fennica, 48*(1). doi:10.14214/sf.1077

Bielak, K., Dudzinska, M., & Pretzsch, H. (2014). Mixed stands of Scots pine (Pinus sylvestris L.) and Norway spruce Picea abies (L.) Karst can be more productive than monocultures. Evidence from over 100 years of observation of long-term experiments. *Forest Systems, 23*(3), 573-589. doi:10.5424/fs/2014233-06195

Björkman, E. (1953). Om orsakerna till granens tillväxtsvårigheter i nordsvensk skogsmark. [Summary: factors arresting early growth of the spruce after

plantation in northern Sweden]. *Norrlands Skogsvårdförbunds Tidskrift* (2), 285-316.
Boateng, J. O., Heineman, J. L., McClarnon, J., & Bedford, L. (2006). Twenty year responses of white spruce to mechanical site preparation and early chemical release in the boreal region of northeastern British Columbia. *Canadian Journal of Forest Research, 36*(10), 2386-2399. doi:10.1139/x06-197
Boman, M., & Mattsson, L. (2012). The hunting value of game in Sweden: Have changes occurred over recent decades? *Scandinavian Journal of Forest Research, 27*(7), 669-674. doi:10.1080/02827581.2012.683533
Brunner, A., & Kimmins, J. P. (2003). Nitrogen fixation in coarse woody debris of Thuja plicata and Tsuga heterophylla forests on northern Vancouver Island. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 33*(9), 1670-1682. doi:10.1139/x03-085
Buckley, R., Brough, P., Hague, L., Chauvenet, A., Fleming, C., Roche, E., Sofija, E., & Harris, N. (2019). Economic value of protected areas via visitor mental health. *Nature Communications, 10*. doi:10.1038/s41467-019-12631-6
Burdett, A. N. (1990). Physiological processes in plantation establishment and the development of specifications for forest planting stock. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 20*(4), 415-427. doi:10.1139/x90-059
Chapman, W. K., & Paul, L. (2012). Evidence that Northern Pioneering Pines with Tuberculate Mycorrhizae are Unaffected by Varying Soil Nitrogen Levels. *Microbial Ecology, 64*(4), 964-972. doi:10.1007/s00248-012-0076-0
Conedera, M., Tinner, W., Neff, C., Meurer, M., Dickens, A. F., & Krebs, P. (2009). Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation. *Quaternary Science Reviews, 28*(5-6), 555-576. doi:10.1016/j.quascirev.2008.11.005
Dawson, T. E., Mambelli, S., Plamboeck, A. H., Templer, P. H., & Tu, K. P. (2002). Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics, 33*, 507-559. doi:10.1146/annurev.ecolsys.33.020602.095451
de Groot, W. J., Flannigan, M. D., & Cantin, A. S. (2013). Climate change impacts on future boreal fire regimes. *Forest Ecology and Management, 294*, 35-44. doi:https://doi.org/10.1016/j.foreco.2012.09.027
del Río, M., Pretzsch , H., Alberdi, I., Bielak, K., Bravo, F., Brunner, A., Condés, S., Ducey, M. J., Fonseca, T., von Lüpke, N., Pach, M., Peric, S., Perot, T., Souidi, Z., Spathelf, P., Sterba, H., Tijardovic, M., Tomé, M., Vallet, P., & Bravo-Oviedo, A. (2018). Characterization of Mixed Forests. In A. Bravo-Oviedo, H. Pretzsch, & M. del Río (Eds.), *Dynamics, Silviculture and Management of Mixed Forests* (Vol. 31, pp. 27-72). Cham: Springer International Publishing AG.
DeLuca, T. H., Zackrisson, O., Nilsson, M. C., & Sellstedt, A. (2002). Quantifying nitrogen-fixation in feather moss carpets of boreal forests. *Nature, 419*(6910), 917-920. doi:10.1038/nature01051

Drössler, L., Agestam, E., Bielak, K., Dudzinska, M., Koricheva, J., Liziniewicz, M., Lof, M., Mason, B., Pretzsch, H., Valkonen, S., & Wellhausen, K. (2018). Over- and underyielding in time and space in experiments with mixed stands of Scots pine and Norway Spruce. *Forests, 9*(8). doi:10.3390/f9080495

Ekö, P.-M., Johansson, U., Petersson, N., Bergqvist, J., Elfving, B., & Frisk, J. (2008). Current growth differences of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula pendula* and *Betula pubescens*) in different regions in Sweden. *Scandinavian Journal of Forest Research, 23*(4), 307-318. doi:10.1080/02827580802249126

Elfving, B. (1983). Den nya skogens produktion. *Sveriges Skogsvårdsförbunds Tidskrift, 83*(4-5), 7-16.

Engelmark, O., & Hytteborn, H. (1999). *Swedish plant geography: Coniferous forests* (H. Rydin, P. Snoeijs, & M. Diekmann Eds.). Uppsala: Opulus press AB.

Eriksson, L., Nordlund, A. M., Olsson, O., & Westin, K. (2012). Recreation in Different Forest Settings: A Scene Preference Study. *Forests, 3*(4), 923-943. doi:10.3390/f3040923

Felton, A., Nilsson, U., Sonesson, J., Felton, A. M., Roberge, J. M., Ranius, T., Ahlstrom, M., Bergh, J., Bjorkman, C., Boberg, J., Drossler, L., Fahlvik, N., Gong, P., Holmstrom, E., Keskitalo, E. C. H., Klapwijk, M. J., Laudon, H., Lundmark, T., Niklasson, M., Nordin, A., Pettersson, M., Stenlid, J., Stens, A., & Wallertz, K. (2016). Replacing monocultures with mixed-species stands: Ecosystem service implications of two production forest alternatives in Sweden. *Ambio, 45*, S124-S139. doi:10.1007/s13280-015-0749-2

Felton, A., Petersson, L., Nilsson, O., Witzell, J., Cleary, M., Felton, A. M., Björkman, C., Sang, Å. O., Jonsell, M., Holmström, E., Nilsson, U., Rönnberg, J., Kalén, C., & Lindbladh, M. (2020a). The tree species matters: Biodiversity and ecosystem service implications of replacing Scots pine production stands with Norway spruce. *Ambio, 49*(5), 1035-1049. doi:10.1007/s13280-019-01259-x

Felton, A. M., Holmström, E., Malmsten, J., Felton, A., Cromsigt, J., Edenius, L., Ericsson, G., Widemo, F., & Wam, H. K. (2020b). Varied diets, including broadleaved forage, are important for a large herbivore species inhabiting highly modified landscapes. *Scientific Reports, 10*(1). doi:10.1038/s41598-020-58673-5

Fenn, M. E., Poth, M. A., Aber, J. D., Baron, J. S., Bormann, B. T., Johnson, D. W., Lemly, A. D., McNulty, S. G., Ryan, D. F., & Stottlemyer, R. (1998). Nitrogen excess in North American ecosystems: predisposing factors, ecosystem responses, and management strategies. *Ecological Applications, 8*(3), 706-733. doi:10.2307/2641261

Flannigan, M., Cantin, A. S., de Groot, W. J., Wotton, M., Newbery, A., & Gowman, L. M. (2013). Global wildland fire season severity in the 21st century.

Forest Ecology and Management, 294, 54-61. doi:https://doi.org/10.1016/j.foreco.2012.10.022

Forrester, D. I., & Smith, R. G. B. (2012). Faster growth of Eucalyptus grandis and Eucalyptus pilularis in mixed-species stands than monocultures. *Forest Ecology and Management, 286*, 81-86. doi:https://doi.org/10.1016/j.foreco.2012.08.037

Fredman, P., Stenseke, M., & Sandell, K. (2014). *Friluftsliv i förändring : studier från svenska upplevelselandskap*. Stockholm: Carlsson.

Fridley, J. D. (2001). The influence of species diversity on ecosystem productivity: how, where, and why? *Oikos, 93*(3), 514-526. doi:10.1034/j.1600-0706.2001.930318.x

Fry, B. (2006). *Stable isotope ecology* (Vol. 521): Springer.

Gebauer, R., Volarik, D., Urban, J., Borja, I., Nagy, N. E., Eldhuset, T. D., & Krokene, P. (2011). Effect of thinning on anatomical adaptations of Norway spruce needles. *Tree Physiology, 31*(10), 1103-1113. doi:10.1093/treephys/tpr081

Gjerde, I., & Saetersdal, M. (1997). Effects on avian diversity of introducing spruce Picea spp plantations in the native pine Pinus sylvestris forests of western Norway. *Biological Conservation, 79*(2-3), 241-250. doi:10.1016/s0006-3207(96)00093-6

Goude, M., Nilsson, U., & Holmstrom, E. (2019). Comparing direct and indirect leaf area measurements for Scots pine and Norway spruce plantations in Sweden. *European Journal of Forest Research, 138*(6), 1033-1047. doi:10.1007/s10342-019-01221-2

Granhall, U., & Lindberg, T. (1978). Nitrogen fixation in some coniferous forest ecosystems. *Ecological Bulletins (Stockholm)*(26), 178-192.

Grossnickle, S. C. (2000). *Ecophysiology of northern spruce species : The performance of planted seedlings.* Ottawa: NRC Research Press.

Grossnickle, S. C. (2005). Importance of root growth in overcoming planting stress. *New Forests, 30*(2-3), 273-294. doi:10.1007/s11056-004-8303-2

Gruffman, L., Ishida, T., Nordin, A., & Näsholm, T. (2012). Cultivation of Norway spruce and Scots pine on organic nitrogen improves seedling morphology and field performance. *Forest Ecology and Management, 276*, 118-124. doi:10.1016/j.foreco.2012.03.030

Gundersen, V. S., & Frivold, L. H. (2008). Public preferences for forest structures: A review of quantitative surveys from Finland, Norway and Sweden. *Urban Forestry & Urban Greening, 7*(4), 241-258. doi:https://doi.org/10.1016/j.ufug.2008.05.001

Hector, A. (1998). The effect of diversity on productivity: detecting the role of species complementarity. *Oikos, 82*(3), 597-599. doi:10.2307/3546380

Hedwall, P. O., & Brunet, J. (2016). Trait variations of ground flora species disentangle the effects of global change and altered land-use in Swedish forests during 20 years. *Global Change Biology, 22*(12), 4038-4047. doi:10.1111/gcb.13329

Hjelm, K., Nilsson, U., Johansson, U., & Nordin, P. (2019). Effects of mechanical site preparation and slash removal on long-term productivity of conifer plantations in Sweden. *Canadian Journal of Forest Research, 49*(10), 1311-1319. doi:10.1139/cjfr-2019-0081

Holmström, E., Goude, M., Nilsson, O., Nordin, A., Lundmark, T., & Nilsson, U. (2018). Productivity of Scots pine and Norway spruce in central Sweden and competitive release in mixtures of the two species. *Forest Ecology and Management, 429*, 287-293. doi:10.1016/j.foreco.2018.07.008

Hägglund, B., & Lundmark, J. E. (1977). Site index estimation by means of site properties. Scots pine and Norway spruce in Sweden. *Studia Forestalia Suecica*(138), 38pp.

Jarnemo, A., Minderman, J., Bunnefeld, N., Zidar, J., & Mansson, J. (2014). Managing landscapes for multiple objectives: alternative forage can reduce the conflict between deer and forestry. *Ecosphere, 5*(8). doi:10.1890/es14-00106.1

Johansson, K., Söderbergh, I., Nilsson, U., & Allen, H. L. (2005). Effects of scarification and mulch on establishment and growth of six different clones of *Picea abies*. *Scandinavian Journal of Forest Research, 20*(5), 421-430. doi:10.1080/02827580500292121

Johansson, K., Langvall, O., & Bergh, J. (2012). Optimization of environmental factors affecting initial growth of Norway spruce seedlings. *Silva Fennica, 46*(1), 27-38. doi:10.14214/sf.64

Johansson, K., Ring, E., & Högbom, L. (2013). Effects of pre-harvest fertilization and subsequent soil scarification on the growth of planted *Pinus sylvestris* seedlings and ground vegetation after clear-felling. *Silva Fennica, 47*(4), 1-18.

Johansson, K., Hajek, J., Sjölin, O., & Normark, E. (2015). Early performance of Pinus sylvestris and Picea abies - a comparison between seedling size, species, and geographic location of the planting site. *Scandinavian Journal of Forest Research, 30*(5), 388-400. doi:10.1080/02827581.2014.987808

Jonsson, B. (2001). Volume yield to mid-rotation in pure and mixed sown stands of Pinus sylvestris and Picea abies in Sweden. *Studia Forestalia Suecica*(211), 19 pp.

Jonsson, B. G., Ekström, M., Esseen, P. A., Grafström, A., Ståhl, G., & Westerlund, B. (2016). Dead wood availability in managed Swedish forests - Policy outcomes and implications for biodiversity. *Forest Ecology and Management, 376*, 174-182. doi:10.1016/j.foreco.2016.06.017

Kardell, L., & Laestadius, L. (1987). Longterm yield of Norway spruce (Picea abies) after prescribed burning. An example from mid-Sweden. *Sveriges Skogsvårdsförbunds Tidskrift, 85*(3), 19-30.

Kardell, L. (2004). *Svenskarna och skogen, Del 2: Från baggböleri till naturvård.* Ödeshög: Skogsstyrelsen.

Kardell, L. (2010). *Skogsenergiförsöken 1977-2008. Report nr:111.* Uppsala: SLU Department of environmental forestry.

Kelly, D., & Connolly, A. (2000). A review of the plant communities associated with Scots Pine (*Pinus sylvestri*s L.) in Europe, and an evaluation of putative indicator/specialist species. *Sistemas y recursos forestales, 9*(1), 15-40.

Korhonen, J. F. J., Pihlatie, M., Pumpanen, J., Aaltonen, H., Hari, P., Levula, J., Kieloaho, A. J., Nikinmaa, E., Vesala, T., & Ilvesniemi, H. (2013). Nitrogen balance of a boreal Scots pine forest. *Biogeosciences, 10*(2), 1083-1095. doi:10.5194/bg-10-1083-2013

Langvall, O., Nilsson, U., & Örlander, G. (2001). Frost damage to planted Norway spruce seedlings - influence of site preparation and seedling type. *Forest Ecology and Management, 141*(3), 223-235. doi:10.1016/s0378-1127(00)00331-5

Lebel, P., Thiffault, N., & Bradley, R. L. (2008). *Kalmia* removal increases nutrient supply and growth of black spruce seedlings: An effect fertilizer cannot emulate. *Forest Ecology and Management, 256*(10), 1780-1784. doi:10.1016/j.foreco.2008.02.050

Leijon, B. (1979). *Tallens och granens produktion på lika ståndort*. Umeå: SLU, institutionen för skogsskötsel.

Leppänen, S. M., Salemaa, M., Smolander, A., Mäkipää, R., & Tiirola, M. (2013). Nitrogen fixation and methanotrophy in forest mosses along a N deposition gradient. *Environmental and Experimental Botany, 90*, 62-69. doi:10.1016/j.envexpbot.2012.12.006

Lidskog, R., & Sjödin, D. (2014). Why do forest owners fail to heed warnings? Conflicting risk evaluations made by the Swedish forest agency and forest owners. *Scandinavian Journal of Forest Research, 29*(3), 275-282. doi:10.1080/02827581.2014.910268

Lindbladh, M., Petersson, L., Hedwall, P. O., Trubins, R., Holmström, E., & Felton, A. (2019). Consequences for bird diversity from a decrease in a foundation speciesreplacing Scots pine stands with Norway spruce in southern Sweden. *Regional Environmental Change, 19*(5), 1429-1440. doi:10.1007/s10113-019-01480-0

Lindén, M., & Agestam, E. (2003). Increment and yield in mixed and monoculture stands of Pinus sylvestris and Picea abies based on an experiment in southern Sweden. *Scandinavian Journal of Forest Research, 18*(2), 155-162. doi:10.1080/02827580310003722

Lindhagen, A., & Bladh, G. (2013). Trender i bär- och svampplockning : ett exempel på hur kvantitativ och kvalitativ metod kan kombineras. In M. S. K. S. Peter Fredman & M. Anders (Eds.), *Friluftsliv i förändring : resultat från ett forskningsprogram : slutrapport* (pp. 63-80). Stockholm: Naturvårdsverket.

Lisberg Jensen, E., & Ouis, P. (2014). *Det gröna finrummet: etnicitet, friluftsliv och naturumgängets urbanisering*. Stockholm: Carlssons.

Lodin, I., Brukas, V., & Wallin, I. (2017). Spruce or not? Contextual and attitudinal drivers behind the choice of tree species in southern Sweden. *Forest Policy and Economics, 83*, 191-198. doi:10.1016/j.forpol.2016.11.010

Lundmark, J.-E. (1988). *Skogsmarkens ekologi: ståndortsanpassat skogsbruk. D. 2 Tillämpning*. Jönköping: Skogsstyrelsen.
Luoranen, J. (2018). Autumn versus spring planting: the initiation of root growth and subsequent field performance of Scots pine and Norway spruce seedlings. *Silva Fennica, 52*(2). doi:10.14214/sf.7813
Löf, M. (2000). Influence of patch scarification and insect herbivory on growth and survival in *Fagus sylvatica* L., *Picea abies* L. Karst. and *Quercus robur* L. seedlings following a Norway spruce forest. *Forest Ecology and Management, 134*(1-3), 111-123. doi:10.1016/s0378-1127(99)00250-9
Löf, M., Dey, D. C., Navarro, R. M., & Jacobs, D. F. (2012). Mechanical site preparation for forest restoration. *New Forests, 43*(5-6), 825-848. doi:10.1007/s11056-012-9332-x
Margolis, H. A., & Brand, D. G. (1990). An ecophysiological basis for understanding plantation establishment. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 20*(4), 375-390. doi:10.1139/x90-056
McKenzie, D., Gedalof, Z., Peterson, D. L., & Mote, P. (2004). Climatic change, wildfire, and conservation. *Conservation Biology, 18*(4), 890-902. doi:10.1111/j.1523-1739.2004.00492.x
Millard, P., & Grelet, G. A. (2010). Nitrogen storage and remobilization by trees: ecophysiological relevance in a changing world. *Tree Physiology, 30*(9), 1083-1095. doi:10.1093/treephys/tpq042
Munson, A. D., Margolis, H. A., & Brand, D. G. (1993). Intensive silvicultural treatment - Impacts on soil fertility and planted conifer response. *Soil Science Society of America Journal, 57*(1), 246-255. doi:10.2136/sssaj1993.03615995005700010043x
Murphy, D. V., Recous, S., Stockdale, E. A., Fillery, I. R. P., Jensen, L. S., Hatch, D. J., & Goulding, K. W. T. (2003). Gross nitrogen fluxes in soil: Theory, measurement and application of N-15 pool dilution techniques. In D. L. Sparks (Ed.), *Advances in Agronomy, Vol 79* (Vol. 79, pp. 69-118). San Diego: Elsevier Academic Press Inc.
Månsson, J., Kalen, C., Kjellander, P., Andren, H., & Smith, H. (2007). Quantitative estimates of tree species selectivity by moose (Alces alces) in a forest landscape. *Scandinavian Journal of Forest Research, 22*(5), 407-414. doi:10.1080/02827580701515023
Månsson, J., & Jarnemo, A. (2013). Bark-stripping on Norway spruce by red deer in Sweden: level of damage and relation to tree characteristics. *Scandinavian Journal of Forest Research, 28*(2), 117-125. doi:10.1080/02827581.2012.701323
Mäkipää, R., Huhtiniemi, S., Kaseva, J., & Smolander, A. (2018). Asymbiotic nitrogen fixation on woody roots of Norway spruce and silver birch. *Canadian Journal of Forest Research, 48*(2), 172-179. doi:10.1139/cjfr-2017-0270

Mäkitalo, K. (1999). Effect of Site Preparation and Reforestation Method on Survival and Height Growth of Scots Pine. *Scandinavian Journal of Forest Research, 14*(6), 512-525. doi:10.1080/02827589908540816

Mäkitalo, K., Alenius, V., Heiskanen, J., & Mikkola, K. (2010). Effect of soil physical properties on the long-term performance of planted Scots pine in Finnish Lapland. *Canadian Journal of Soil Science, 90*(3), 451-465.

Nambiar, E. K. S., & Fife, D. N. (1991). Nutrient retranslocation in temperate conifers. *Tree Physiology, 9*(1-2), 185-207. doi:10.1093/treephys/9.1-2.185

Nilsson, O., Hjelm, K., & Nilsson, U. (2019). Early growth of planted Norway spruce and Scots pine after site preparation in Sweden. *Scandinavian Journal of Forest Research, 34*(8), 678-688. doi:10.1080/02827581.2019.1659398

Nilsson, U., & Örlander, G. (1999). Vegetation management on grass-dominated clearcuts planted with Norway spruce in southern Sweden. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 29*(7), 1015-1026. doi:10.1139/cjfr-29-7-1015

Nilsson, U., Örlander, G., & Karlsson, M. (2006). Establishing mixed forests in Sweden by combining planting and natural regeneration - Effects of shelterwoods and scarification. *Forest Ecology and Management, 237*(1-3), 301-311. doi:10.1016/j.foreco.2006.09.053

Nilsson, U., Luoranen, J., Kolström, T., Örlander, G., & Puttonen, P. (2010). Reforestation with planting in northern Europe. *Scandinavian Journal of Forest Research, 25*(4), 283-294. doi:10.1080/02827581.2010.498384

Nilsson, U., Elfving, B., & Karlsson, K. (2012). Productivity of Norway spruce compared to Scots pine in the interior of northern Sweden. *Silva Fennica, 46*(2), 197-209.

Nilsson, U., Berglund, M., Bergquist, J., Holmstrom, H., & Wallgren, M. (2016). Simulated effects of browsing on the production and economic values of Scots pine (Pinus sylvestris) stands. *Scandinavian Journal of Forest Research, 31*(3), 279-285. doi:10.1080/02827581.2015.1099728

Nordborg, F., & Nilsson, U. (2003). Growth, damage and net nitrogen uptake in Picea abies (L.) Karst. seedlings, effects of site preparation and fertilisation. *Annals of Forest Science, 60*(7), 657-666. doi:10.1051/forest:2003058

Nordborg, F., Nilsson, U., & Örlander, G. (2003). Effects of different soil treatments on growth and net nitrogen uptake of newly planted Picea abies (L.) Karst. seedlings. *Forest Ecology and Management, 180*(1-3), 571-582. doi:10.1016/s0378-1127(02)00650-3

Nordlander, G., Hellqvist, C., Johansson, K., & Nordenhem, H. (2011). Regeneration of European boreal forests: Effectiveness of measures against seedling mortality caused by the pine weevil *Hylobius abietis*. *Forest Ecology and Management, 262*(12), 2354-2363. doi:10.1016/j.foreco.2011.08.033

Nykvist, N. (2000). Effects of clearfelling, slash removal and prescribed burning on amounts of plant nutrients in biomass and soil. *Studia Forestalia Suecica, 210*, 1-43.

Nystedt, B., Street, N. R., Wetterbom, A., Zuccolo, A., Lin, Y. C., Scofield, D. G., Vezzi, F., Delhomme, N., Giacomello, S., Alexeyenko, A., Vicedomini, R., Sahlin, K., Sherwood, E., Elfstrand, M., Gramzow, L., Holmberg, K., Hallman, J., Keech, O., Klasson, L., Koriabine, M., Kucukoglu, M., Kaller, M., Luthman, J., Lysholm, F., Niittyla, T., Olson, A., Rilakovic, N., Ritland, C., Rossello, J. A., Sena, J., Svensson, T., Talavera-Lopez, C., Theissen, G., Tuominen, H., Vanneste, K., Wu, Z. Q., Zhang, B., Zerbe, P., Arvestad, L., Bhalerao, R., Bohlmann, J., Bousquet, J., Gil, R. G., Hvidsten, T. R., de Jong, P., MacKay, J., Morgante, M., Ritland, K., Sundberg, B., Thompson, S. L., Van de Peer, Y., Andersson, B., Nilsson, O., Ingvarsson, P. K., Lundeberg, J., & Jansson, S. (2013). The Norway spruce genome sequence and conifer genome evolution. *Nature, 497*(7451), 579-584. doi:10.1038/nature12211

Näsholm, T., Ekblad, A., Nordin, A., Giesler, R., Högberg, M., & Högberg, P. (1998). Boreal forest plants take up organic nitrogen. *Nature, 392*(6679), 914-916. doi:10.1038/31921

Näsholm, T., Kielland, K., & Ganeteg, U. (2009). Uptake of organic nitrogen by plants. *New Phytologist, 182*(1), 31-48. doi:10.1111/j.1469-8137.2008.02751.x

Oh, B., Lee, K., Zaslawski, C., Yeung, A., Rosenthal, D., Larkey, L., & Back, M. (2017). Health and well-being benefits of spending time in forests: systematic review. *Environmental Health and Preventive Medicine, 22*(71), (18 October 2017)-(2018 October 2017).

Örlander, G., Gemmel, P., & Hunt, J. (1990a). Site preparation: a Swedish overview. In *FRDA Report*. Victoria, Canada: BC Ministry of Forests.

Örlander, G., Hallsby, G., & Sundkvist, H. (1990b). *Överlevnad och tillväxt hos tall (Pinus sylvestris (L.)) och gran (Picea abies (L.) Karst) samt näringsförhållanden 23 år efter plantering på helplöjd respektive bränd hedmark. Rapport nr 26*. Umeå: Sveriges lantbruksuniversitet.

Örlander, G., Egnell, G., & Albrektson, A. (1996a). Long-term effects of site preparation on growth in Scots pine. *Forest Ecology and Management, 86*(1-3), 27-37. doi:10.1016/s0378-1127(96)03797-8

Örlander, G., Nilsson, U., & Hällgren, J.-E. (1996b). Competition for water and nutrients between ground vegetation and planted *Picea abies*. *N.Z. J. For. Sci, 26*, 99-117.

Öyen, B. H., & Tveite, B. (1998). *A comparison of site index class and potential stem volume yield between different tree species growing on equal sites in west Norway*. Norsk institutt for skogsforskning, Ås.

Padda, K. P., Puri, A., & Chanway, C. P. (2018). Isolation and identification of endophytic diazotrophs from lodgepole pine trees growing at unreclaimed gravel mining pits in central interior British Columbia, Canada. *Canadian*

Journal of Forest Research, 48(12), 1601-1606. doi:10.1139/cjfr-2018-0347

Peltola, H., Kellomäki, S., Hassinen, A., & Granander, M. (2000). Mechanical stability of Scots pine, Norway spruce and birch: an analysis of tree-pulling experiments in Finland. *Forest Ecology and Management, 135*(1-3), 143-153. doi:10.1016/s0378-1127(00)00306-6

Perkin Elmer Inc. Clarus 500 GC. *Waltham, Massachusetts, USA.*

Petersson, L., Holmström, E., Lindbladh, M., & Felton, A. (2019). Tree species impact on understory vegetation: Vascular plant communities of Scots pine and Norway spruce managed stands in northern Europe. *Forest Ecology and Management, 448*, 330-345. doi:10.1016/j.foreco.2019.06.011

Pettersson, N. (1993). The effect of density after precommercial thinning on volume and structure in Pinus Sylvestris and Picea Abies stands. *Scandinavian Journal of Forest Research, 8*(1-4), 528-539. doi:10.1080/02827589309382799

Powers, R. F., Scott, D. A., Sanchez, F. G., Voldseth, R. A., Page-Dumroese, D., Elioff, J. D., & Stone, D. M. (2005). The North American long-term soil productivity experiment: Findings from the first decade of research. *Forest Ecology and Management, 220*(1-3), 31-50. doi:10.1016/j.foreco.2005.08.003

Pretzsch, H., del Rio, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Dirnberger, G., Drössler, L., Fabrika, M., Forrester, D., Godvod, K., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Matovic, B., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schutze, G., Schweig, J., Skrzyszewski, J., Sramek, V., Sterba, H., Stojanovic, D., Svoboda, M., Vanhellemont, M., Verheyen, K., Wellhausen, K., Zlatanov, T., & Bravo-Oviedo, A. (2015). Growth and yield of mixed versus pure stands of Scots pine (Pinus sylvestris L.) and European beech (Fagus sylvatica L.) analysed along a productivity gradient through Europe. *European Journal of Forest Research, 134*(5), 927-947. doi:10.1007/s10342-015-0900-4

Pretzsch, H. (2018). Growth and Structure in Mixed-Species Stands Compared with Monocultures: Review and Perspectives. In A. Bravo-Oviedo, H. Pretzsch, & M. del Río (Eds.), *Dynamics, Silviculture and Management of Mixed Forests* (Vol. 31, pp. 131-183). Cham: Springer International Publishing AG.

Prevost, M., & Dumais, D. (2018). Long-term growth response of black spruce advance regeneration (layers), natural seedlings and planted seedlings to scarification: 25th year update. *Scandinavian Journal of Forest Research, 33*(6), 583-593. doi:10.1080/02827581.2018.1430250

Puri, A., Padda, K. P., & Chanway, C. P. (2018). Evidence of endophytic diazotrophic bacteria in lodgepole pine and hybrid white spruce trees growing in soils with different nutrient statuses in the West Chilcotin region of British Columbia, Canada. *Forest Ecology and Management, 430*, 558-565. doi:10.1016/j.foreco.2018.08.049

Rosensten, A. (1737). *Tanckar, om skogars skiötzel eller Underrättelse om alla willa träns natur och egenskaper, som finnes uti Sweriges rike, huru de kunna och böra, antingen genom såning eller ock plantering updragas, at däraf ofelbart, med god och hastig fortgång winna skog på behörige orter af slättbygderne, som deraf nu lida stor brist på brännе, byggningz timber samt alla andra til huushåldning nödige och omistelige träwaror. Hwarjämte följer ett bihang om allehanda fruchtbärande : träns skiötzel, som höra til trägårdar. Wälment utgifne af Anders Rosensten. Stads Major.* Lund: Ludvig Decreaux, directeur öfwer kongl. academiens priviligerade tryckerij i Lund.

Schmidt, M. G., Macdonald, S. E., & Rothwell, R. L. (1996). Impacts of harvesting and mechanical site preparation on soil chemical properties of mixed-wood boreal forest sites in Alberta. *Canadian Journal of Soil Science, 76*(4), 531-540. doi:10.4141/cjss96-066

Schotte, G. (1917). Skogsförsöksanstaltens tillkomst och uppgift. In G. Schotte (Ed.), *Meddelanden från Statens Skogsförsöksanstalt* (Vol. 13-14, pp. 11-14). Stockholm: Statens Skogsförsöksanstalt.

SFA. (2014). Swedish Forest Agency, Swedish Statistical Yearbook of Forestry. Retrieved from https://www.skogsstyrelsen.se/globalassets/statistik/historisk-statistik/skogsstatistisk-arsbok-2010-2014/skogsstatistisk-arsbok-2014.pdf

SFA. (2020). Swedish Forest Agency, Skoglig betesinventering. Retrieved from https://www.skogsstyrelsen.se/abin

Sikström, U., Hjelm, K., Hanssen, K. H., Saksa, T., & Wallertz, K. (2020). Influence of mechanical site preparation on regeneration success of planted conifers in clearcuts in Fennoscandia-a review. *Silva Fennica, 54*(2). doi:10.14214/sf.10172

Simard, S. W., Jones, M. D., Durall, D. M., Hope, G. D., Stathers, R. J., Sorensen, N. S., & Zimonick, B. J. (2003). Chemical and mechanical site preparation: effects on *Pinus contorta* growth, physiology, and microsite quality on grassy, steep forest sites in British Columbia. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 33*(8), 1495-1515. doi:10.1139/x03-072

SLU. (2019). Swedish University of Agriultural Sciences, Forest statistics 2019. Retrieved from https://www.slu.se/globalassets/ew/org/centrb/rt/dokument/skogsdata/skogsdata_2019_webb.pdf

SLU. (2020). Swedish University of Agriultural Sciences, Forest statistics 2020. Retrieved from https://www.slu.se/globalassets/ew/org/centrb/rt/dokument/skogsdata/skogsdata_2020_webb.pdf

Son, Y. (2001). Non-symbiotic nitrogen fixation in forest ecosystems. *Ecological Research, 16*(2), 183-196. doi:10.1046/j.1440-1703.2001.00385.x

Sponseller, R. A., Gundale, M. J., Futter, M., Ring, E., Nordin, A., Näsholm, T., & Laudon, H. (2016). Nitrogen dynamics in managed boreal forests: Recent advances and future research directions. *Ambio, 45*, S175-S187. doi:10.1007/s13280-015-0755-4

Sténs, A., & Sandström, C. (2013). Divergent interests and ideas around property rights: The case of berry harvesting in Sweden. *Forest Policy and Economics, 33*, 56-62. doi:10.1016/j.forpol.2012.05.004

Stokland, J. N., Siitonen, J., & Jonsson, B. G. (2012). *Biodiversity in Dead Wood*. Cambridge: Cambridge University Press.

Stuiver, B. M., Gundale, M. J., Wardle, D. A., & Nilsson, M. C. (2016). Nitrogen fixation rates associated with the feather mosses Pleurozium schreberi and Hylocomium splendens during forest stand development following clear-cutting (vol 347, pg 130, 2015). *Forest Ecology and Management, 375*, 309-309. doi:10.1016/j.foreco.2016.05.038

Tamm, C. O. (1991). *Nitrogen in Terrestrial Ecosystems. Questions of Productivity, Vegetational Changes, and Ecosystem Stability* (Vol. 81). Berlin Heidelberg: Springer.

Thiffault, N., Titus, B. D., & Munson, A. D. (2004). Black spruce seedlings in a *Kalmia-Vaccinium* association: microsite manipulation to explore interactions in the field. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 34*(8), 1657-1668. doi:10.1139/x04-046

Thiffault, N., & Jobidon, R. (2006). How to shift unproductive *Kalmia angustifolia - Rhododendron groenlandicum* heath to productive conifer plantation. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 36*(10), 2364-2376. doi:10.1139/x06-090

Thiffault, N., Fenton, N. J., Munson, A. D., Hebert, F., Fournier, R. A., Valeria, O., Bradley, R. L., Bergeron, Y., Grondin, P., Pare, D., & Joanisse, G. (2013). Managing understory vegetation for maintaining productivity in black spruce forests: A synthesis within a multi-scale research model. *Forests, 4*(3), 613-631. doi:10.3390/f4030613

Thiffault, N., Titus, B. D., & English, B. (2017). Twenty-five years post-treatment conifer responses to silviculture on a *Kalmia*-dominated site in eastern Canada. *Forestry Chronicle, 93*(2), 161-170. doi:10.5558/tfc2017-022

Timmer, V. R., & Morrow, L. D. (1984). *Forest soils and treatment impacts : proceedings of the sixth North American Forest Soils Conference held at the University of Tennessee, Knoxville in June 1983.* Paper presented at the North American Forest Soils, Conference, Knoxville.

Tyrväinen, L., Silvennoinen, H., & Kolehmainen, O. (2003). Ecological and aesthetic values in urban forest management. *Urban Forestry & Urban Greening, 1*(3), 135-149. doi:https://doi.org/10.1078/1618-8667-00014

Valinger, E., & Fridman, J. (2011). Factors affecting the probability of windthrow at stand level as a result of Gudrun winter storm in southern Sweden. *Forest Ecology and Management, 262*(3), 398-403. doi:10.1016/j.foreco.2011.04.004

Vitousek, P. M., & Howarth, R. W. (1991). Nitrogen limitation on land and in the sea - how can it occur. *Biogeochemistry, 13*(2), 87-115.

Vitousek, P. M., Aber, J. D., Howarth, R. W., Likens, G. E., Matson, P. A., Schindler, D. W., Schlesinger, W. H., & Tilman, D. G. (1997). Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications, 7*(3), 737-750. doi:10.2307/2269431

Vollbrecht, G., Johansson, U., Eriksson, H., & Stenlid, J. (1995). Butt rot incidence, yield and growth pattern in a tree species experiment in southwestern Sweden. *Forest Ecology and Management, 76*(1/3), 87-93. doi:10.1016/0378-1127(95)03550-t

Wallentin, C. (2007). Thinning of Norway spruce. Doctoral dissertation. *Acta Universitatis Agriculturae Sueciae, 2007:29*.

Wallgren, M., Bergstrom, R., Bergqvist, G., & Olsson, M. (2013). Spatial distribution of browsing and tree damage by moose in young pine forests, with implications for the forest industry. *Forest Ecology and Management, 305*, 229-238. doi:10.1016/j.foreco.2013.05.057

Wibeck, E. (1912). *Om ljungbränning för skogskultur.* (Vol. 8). Stockholm: Statens Skogsforskningsanstalt.

Wilson, A. R., Nzokou, P., Guney, D., & Kulac, S. (2013). Growth response and nitrogen use physiology of Fraser fir (Abies fraseri), red pine (Pinus resinosa), and hybrid poplar under amino acid nutrition. *New Forests, 44*(2), 281-295. doi:10.1007/s11056-012-9317-9

Yrjölä, T. (2002). *Forest management guidelines and practices in Finland, Sweden and Norway. Tecnical report 11*: European Forest Institute.

Acknowledgements

Teamwork.

A PhD project is not done by one person alone, it is rather done by a group of people sharing knowledge, expertise and experience, always moving towards a common goal. A good team makes use of everyone's competencies and works together. Here I would like to thank everyone that have contributed to this work in any possible way, from the start to the finish.

First of all, thanks to both of my supervisors **Karin Hjelm** and **Urban Nilsson**, for believing in me and letting me be a part of your team! I would say that you two make up a perfect combination of supervisors. I have really enjoyed the trip with you during these years! **Karin**, you have always been very helpful and ready to answer my questions, or throwing them back to me in a reformulated way. Your professionalism, competence, guiding way, and calm manner is exceptional. **Urban**, here comes a long sentence as I would like to mention that you are a living encyclopedia when it comes to forest research, your expertise, helpful and friendly way is very inspirational and I have also enjoyed doing other things together like our jogging trips on a few different continents (even if you managed to beat me in North America), or watching the Crusaders play rugby in Christchurch, or playing *innebandy*[2] (you have some serious skills!), you even have the weight record for carrying heavy furniture from my last move. Astonishing. Thanks. That was two shorter sentences. Both of you are combining being very competent, and also nice persons that understand that there are sometimes also other things in life going on outside of work.

[2] *Innebandy*: Floorball in English, a somewhat more user-friendly sport performed indoors compared to the real sport, ice hockey. *Innebandy* is a traditional and important part of Swedish culture, as well as at the Southern Swedish Forest Research Centre. Despite last years' small decreasing participation numbers at the department, I am still certain that the trend can be halted and reversed.

I would also like to thank other players involved in this trip. Thanks to **Emma Holmström** for believing in me and always having your office door open. Your drive and capacity is unheard of, and I am grateful to have been working with you. Thanks to **Torgny Näsholm** for being extremely helpful, I just wish that I had contacted you earlier! **Rachel Cook**, thank you for sharing your knowledge and for being the best possible host ever for my family and me during the four months spent at North Carolina State University, assisting with everything from furnishing an empty apartment, to provide means of transportation. Thanks to **Euan Mason** for being a great host during my visit in New Zealand, and for sharing your indescribable knowledge, and musical skills. **Eric Agestam**, thank you for always being helpful and willing to share your knowledge. In the absolute end of my PhD studies, I got interested in the history of forest research and education (not the best timing to get stuck with that!) and realized that we share this interest. **Pelle Gemmel**, thanks for all inspiration during the first period of my PhD studies. **Adam Felton**, thanks for inviting me to write about production and other interesting things in the review.

P-M Ekö, Lars Drössler, **Vilis Brukas** and **Jörg Brunet**, thanks for being such great course leaders back in the days when I attended the EUROFORESTER master's program 2011-2012 at the Southern Swedish Forest Research Centre in Alnarp. It helped me to develop both my interest and attitude to forestry and forest research. I hope that EUROFORESTER will always continue, to give more students the same possibility to experience great education in a great place, and develop their future careers.

Andis Zvirgzdiņš and **Mikołaj Lula**, the "dynamic duo", thank you for being such good friends, colleagues and definitely most important, such devoted *innebandy* players. Also, thanks for helping out a desperate PhD student (me) to find figure 2 and draw figure 3. But I still wonder: When will we play tennis? **Guilherme Alexandre Stecher Justiniano Pinto**, or probably better **Gui**, it was a pleasure to get to know you, and experience our final push in the PhD studies together. It was awesome to have you around working late hours in Alnarp these last couple of months. **Isak Lodin**, it was a true pleasure to get to know you during these years. Too bad that we didn´t manage to watch more ice hockey games together, but luckily there are many more to come! **Adrian Villalobos**, thanks for the interesting discussions about Vikings and Sweden, it was very nice to get to know you.

Michelle Cleary & **Jonas Rönnberg**, thanks for being so kind and helpful with small kids' stuff. **Zhanna Möller**, **Violeta Kokos**, **Meelis Seedre**, **Ignacio "Nacho" Barbeito**, **Jaime Uria Diez, Jorge Aldea & Carmen Romeralo**, **Giulia Attocchi**, **Henrik Böhlenius** and **Per-Ola Hedwall**, thanks for being very nice colleagues, and among other things, all discussions about having small kids. **Igor Drobyshev**, thanks for the last minute advices. By the way, conversations with you are always interesting, regardless if in Swedish, English or Russian. **Annika Felton**, thanks for the last minute help about browsing. Thanks **Pär Fornling** for all the interesting discussions, you are a true professional in your field. **Lisa Petersson**, thank you for sharing your biodiversity knowledge. **Laura Juvany Canovas**, thank you for being a very friendly colleague, but next time you plan for a barbecue, ask me for advice instead.

My thanks extends to all past and present co-workers at the Southern Swedish Forest Research Centre, you have all helped me to truly enjoy my time: **Desiree**, **Eugene**, **Nils**, **Mateusz**, **Ola S**, **Carl**, **Renats**, **Matts**, **Mimmi**, **Katarina**, **Magnus L**, **Magnus M**, **Johanna**, **JP, Naran**, **Patrick, Kent**, **Klas**, and many more. Thanks to all of you. Special thanks to all current and former PhD students at the department: **Marta**, **Axelina**, **Emma S**, **Mattias**, **Tanya**, **Martin P**, **Martin G**, **Karin**, **Mostarin**, **Delphine**, **Ida W**, **Ida N**, **Hanna**, **Ewa**, **Rebecka**, **Noelia**, **Khaled**, **Joan**, and many more.

Thanks to all the people at the Department of Forest Ecology and Management in Umeå I got to know and work with. **Clydecia Spitzer**, you made all the statistics courses we took together so much more giving and fun. Thanks for your friendship and for the immense last minute support (or is it "last-minute" with a hyphen?). This thesis would have been so much worse without your help. Du är en klippa! **Artis Bečs**, your *innebandy* skills might not be your strongest side, but thanks for being such a great travel companion in Brazil and for your friendship. Also thanks to **Marie-Charlotte Nilsson Hegethorn** and **Kelley Gundale** for helping out with the root study. **Morgan Karlsson**, thanks for being a great laboratory companion. **Theresa Ibáñez**, thanks for the last minute fire help.

All of you who helped me during field work: **Nils-Anders "Nischa" Färdmo**, **Alessandra Salvalaggio**, **Ulla Nylander**, **Per Löfgren**, **Kristian "Krillan" Tufvesson**, **Kaisa Hammarstedt** and **Anette**, thank you. I would also like to extend thanks to **Örjan Kardell** at the Department of History at Uppsala University for detective work finding a "lost" photograph.

Thanks for always being there pappa **Bengt**, mamma **Elisabeth**, storebror **August** och lillasyster **Lisa**.

Last and most important, thanks to my beautiful wife **Yulia** and our wonderful kids. Я вас так сильно люблю!

Appendix

1. Definitions of stand types according to NFI (SLU, 2019)
Species' proportions are based on the share of basal area (m^{-2} ha^{-1}) in stands with an average height of 7 m or higher, or the share of crop trees or seedlings

- ***Scots pine forest***
  ≥ 65% Scots pine

- ***Norway spruce forest***
  ≥ 65% Norway spruce

- ***Lodgepole pine forest***
  ≥ 65% lodgepole pine

- ***Mixed-coniferous forest***
  None of the above, but ≥ 65% conifers

- ***Mixed forest***
  > 35% to < 65% broadleaves

- ***Broadleaf forest***
  ≥ 65% broadleaves, and < 45% valuable broadleaves[3]

- ***Valuable broadleaf forest***
  ≥ 65% broadleaves, and ≥ 45% valuable broadleaves

To better describe the proportion of monocultures in Sweden, an alternative 95% threshold for the monocultures described above was used in SLU (2019), which then classified around 74% of Sweden's forests as mixed. The proportion drops to 20% mixed forest when the typical threshold of 65% for the monocultures is used, as described above.

[3] Sometimes referred to as "noble broadleaves": oak, beech, elm, ash, lime, maple, hornbeam and cherry

Figure 13. Forestry students (*jägmästarstudenter*) listening carefully to Kramfors AB forest director *jägmästare* Eric Ronge teaching about thinning close to Bosundet, Ångermanland in northern Sweden in 1924. (Photo: SLU – Forest library)

Figure 14. Forestry students (*jägmästarstudenter*) at an old coniferous mixed stand with 854 m^3 standing volume. Professor Manfred Näslund, *jägmästare* Folke Thörn and *jägmästare* Carlsson-Ingerstedt can be seen in the middle of the photo, Johannishus, Blekinge in southern Sweden in 1924 (Photo: SLU – Forest library)

Acta Universitatis agriculturae Sueciae
Doctoral Thesis No. 2020:71

Despite a long history and tradition of silvicultural research in Sweden, few studies have compared the growth of Scots pine and Norway spruce at the same site. My findings show site-specific growth differences between the species at different stages in a rotation. In this thesis, possible underlying reasons for those growth responses were investigated. The thesis also highlights the importance of long-term experiments and discusses species choice in a wider context than only production.

Oscar Nilsson received his graduate education at the Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences (SLU). He holds M.Sc. degrees in Forest management and in Forestry from SLU, and in Forestry from North Carolina State University, USA.

Acta Universitatis agriculturae Sueciae presents doctoral theses from the Swedish University of Agricultural Sciences (SLU).

SLU generates knowledge for the sustainable use of biological natural resources. Research, education, extension, as well as environmental monitoring and assessment are used to achieve this goal.

Online publication of thesis summary: https://pub.epsilon.slu.se

ISSN 1652-6880
ISBN (print version) 978-91-7760-660-4
ISBN (electronic version) 978-91-7760-661-1