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Adapting forest regeneration to a changing climate

Matej Domevscik

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SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

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Cover: Possibly the bushiest Scots pine seedling in Sweden, completely unprepared for climate change (photo by Matej Domevscik).

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Adapting forest regeneration to a changing climate

Abstract

Forest regeneration in Sweden is increasingly challenged by the rapidly changing climate, making traditional management practices less reliable. Firstly, this thesis addresses these challenges by examining performance of main regeneration methods across Sweden in the context of variable growing conditions. The extreme drought of 2018, which is part of all studies included in this thesis, was used as an example of conditions expected to become more common in the future. Secondly, possible adaptations to these conditions were tested, including mechanical protections against pine weevil damage, changing of planting positions, addition of organic fertiliser, using coated seeds and applying natural regeneration. Results show that mechanical protections against pine weevils performed equally well as insecticide in a non-drought year, suggesting their potential as replacements. In a drought year, however, a synergistic response between drought and pine weevil damage was found, highlighting the interactions of different stressors on seedling establishment. Further, survival of nursery seedlings was significantly reduced by drought, but less so when they were planted directly in mineral soil and fertilised with arginine phosphate. Similarly, coated seeds were significantly influenced by moisture loss, mainly because of unsuccessful soil attachment, and achieved an average establishment rate of 56%. Additionally, methods of mechanical site preparation significantly increased survival of planted and naturally regenerated seedlings. Finally, these findings underscore the need for diverse and flexible management practices to ensure that the regeneration stage can adapt to the complex and evolving challenges posed by climate change. This approach, grounded in the principles of resistance, resilience, and transition adaptation, aligns with broader climate adaptation strategies and offers a roadmap for managing Sweden's forest regeneration amid increasing climatic uncertainty.

Keywords: forest regeneration; climate change; Scots pine; Norway Spruce; establishment; drought; pine weevil; coated seeds; climate adaptation.

Anpassning av skogsföryngring till ett förändrat klimat

Sammanfattning

Skogsföryngringen i Sverige utmanas alltmer av den snabba klimatförändringen, vilket gör traditionella skötselmetoder mindre tillförlitliga. För det första tar denna avhandling upp dessa utmaningar genom att undersöka resultaten av de mest förekommande föryngringsmetoderna i Sverige i ett förändrat klimat. Den extrema torkan år 2018, som är en del av samtliga studier i denna avhandling, användes som exempel på ett tillstånd som förväntas bli allt vanligare i framtiden. För det andra testades möjliga anpassningar till dessa förhållanden, inklusive mekaniska skydd mot skador på snytbagge, val av planteringspunkt, tillsats av organiskt gödselmedel, användning av belagda frön och applicering av naturlig föryngring. Resultaten visade att mekaniska skydd mot snytbagge fungerade lika bra som insekticider under ett år utan torka, vilket visar på deras potential som ersättning för insekticider. Under torka fann man dock synergistiska effekter mellan torka och snytbaggeskador, vilket belyser samspelet mellan olika stressfaktorer och hur de påverkar plantans etablering. Vidare visade resultaten att plantornas överlevnad reducerades vid torka, men att effekten var mindre när de planterades direkt i mineraljord och gödslades med argininfosfat. På liknande sätt påverkades också belagda frön av torka och fuktförlust, främst på grund av misslyckad vidhäftning till marken, och uppnådde en genomsnittlig etableringsgrad på 56 %. Dessutom ökade markberedning signifikant överlevnaden för planterade plantor och naturlig föryngring. Slutligen understryker resultaten behovet av en mångsidig och flexibel skogsskötsel för att säkerställa att föryngringarna kan anpassas till de komplexa och föränderliga utmaningar som klimatförändringar innebär. Tillvägagångssättet som presenteras i denna avhandling är grundat på principerna om resistance, resilience och transition som ligger i linje med de bredare klimatanpassningsstrategier som kan appliceras för att hantera Sveriges skogsföryngringar mitt i en ökande klimatosäkerhet.

Nyckelord: skogsföryngring; klimatförändring; tall; gran; etablering; torka; snytbagge; belagda frön; klimatanpassning.

Prilagajanje obnove gozdov podnebnim spremembam

Znanstveni povzetek

Zaradi hitro spreminjajočega se podnebja je obnova gozdov na Švedskem vse bolj ogrožena, saj so tradicionalne prakse upravljanja vedno manj zanesljive. To doktorsko delo obravnava te izzive s preučevanjem učinkovitosti glavnih metod obnove gozdov na Švedskem v kontekstu klimatskih sprememb. Ekstremna suša leta 2018 služi kot primer pojava, ki naj bi bil v prihodnosti vse pogostejši in je del vseh študij tega doktorskega dela. Obravnavani načini prilagoditve so: mehanske zaščite pred poškodbami velikega rjavega rilčkarja (*Hylobius abietis*), spreminjanje sadilnih položajev, dodajanje organskega gnojila, uporaba prevlečenih semen in uporaba naravne obnove gozda. Rezultati kažejo, da so se mehanske zaščite pred velikimi rjavimi rilčkarji obnesle enako dobro kot prepovedani insekticidi v letu brez suše, kar kaže na možnost njihove uporabe. V sušnem letu je bil ugotovljen sinergijski odziv med sušo in velikimi rjavimi rilčkarji, kar nakazuje na preplet različnih vzrokov škode na sadikah iglavcev. Preživetje posajenih sadik je bilo znatno manjše zaradi suše, vendar ne toliko, če so bile posajene neposredno v mineralno prst in pognojene z arginin-fosfatom. Izguba vlage je pomembno vplivala tudi na prevlečena semena, predvsem zaradi neuspešne pritrditve v prst, sadike s teh semen so dosegle povprečno stopnjo ukoreninjenosti okoli 56 %. Metode mehanske priprave rastišča so bistveno povečale preživetje posajenih in naravno pogozdovanih sadik. Te ugotovitve poudarjajo potrebo po raznolikih in prilagodljivih praksah upravljanja, da se stopnja obnove gozda lahko prilagodi kompleksnim in razvijajočim se izzivom, ki jih predstavljajo podnebne spremembe. Ta pristop, ki temelji na načelih odpornosti, trdoživosti in prilagoditvi v prehodu, se ujema s širšimi strategijami prilagajanja podnebju in ponuja načrt za upravljanje regeneracije gozdov na Švedskem med naraščajočo podnebno negotovostjo.

Ključne besede: obnova gozdov; sprememba podnebja; rdeči bor; navadna smreka; suša; veliki rjavi rilčkar; prevlečena semena; prilagajanje podnebju.

Dedication

This thesis is dedicated to all the wonderful people I have met along the way.

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List of publications

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

I. M. Domevscik, K. Wallertz, K. Hjelm (2024). Effect of Drought and Pine Weevil Damage on Mechanically Protected Norway Spruce Seedlings. Forest Ecology and Management, vol. 566.

II. B. Häggström, M. Domevscik, J. Öhlund, A. Nordin (2021). Survival and growth of Scots pine (Pinus sylvestris) seedlings in north Sweden: effects of planting position and arginine-phosphate addition. Scandinavian Journal of Forest Research, vol. 36 (6), 423-433.

III. M. Domevscik, B. Häggström, H. Lim, J. Öhlund, A. Nordin (2023). Large-scale assessment of artificially coated seeds for forest regeneration across Sweden. New Forests, vol. 54, 255-267.

IV. M. Lula, M. Domevscik, K. Hjelm , M. Andersson, K. Wallertz, U. Nilsson (2024). Recruitment dynamics of naturally regenerated Scots pine under different overstory densities in Southern Sweden (manuscript).

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The contribution of Matej Domevscik (MD) to the papers included in this thesis was as follows:

I. MD assisted with the fieldwork for an established trial. MD was in charge of data and statistical analysis and writing the paper with input from the co-authors.

II. MD planned and carried out the fieldwork together with the main author. MD assisted with data and statistical analysis and contributed to writing the manuscript.

III. MD planned, organised, and carried out the fieldwork for an established field trial. MD was in charge of data and statistical analysis and writing the paper with input from the co-authors.

IV. MD assisted with the fieldwork for an established trial. MD assisted with data and statistical analysis and contributed to writing the manuscript.

Abbreviations

ANOVA	Analysis of variance
AP	Arginine phosphate (organic fertiliser)
CM	Capped mound
MS	Mineral soil
MSP	Mechanical site preparation
RRT	Resistance, resilience, transition (adaptation framework)
SP	SeedPAD (coated seed)
VPD	Vapour pressure deficit

1. Introduction

Forests have long been integral to Scandinavia, in terms of both economic and cultural development. References to tall, shaded conifer forests with a carpet of bilberries below can be found in many works of art, children's stories, and everyday products. Although their role has changed over the years, from slash-and-burn agriculture to carbon capture programmes (Skogsstyrelsen 2020), forests have managed to remain a constant in the landscape even today. This is partly thanks to natural regeneration, an ecophysiological process at the heart of a thriving forest.

However, the enduring presence of forests is not merely a result of regeneration but also a product of conscious and sustained forest regeneration practices, which are the focus of this thesis. Sweden and other Scandinavian countries have a long history of forest use, combined with a long and rich history of forest management (KSLA 2015). Still, due to the heavy exploitation to support the mining, paper and pulp industry, vast stretches of Swedish forest were degraded by the late 19th century (Östlund *et al.* 1997b; Skogsstyrelsen 2020). This started political action towards sustainable use of forests. As a result, Sweden's first Forestry Act, adopted in 1903, enshrined forest regeneration into law (Skogsstyrelsen 2020).

Forests grow slowly, particularly in the boreal region where management plans are measured in decades if not centuries. This makes forestry an inherently traditionalistic field, where management practices done at the time of planting may be considered outdated by the time the trees are cut down. To fully understand the situation today, it is therefore important to also understand the development of forest management methods over time.

1.1 Studying forest regeneration in Scandinavia

Over the past century, clear-cutting has become established as the dominant forest management system in Sweden (Östlund *et al.* 1997a; Berg *et al.* 2008; Lundmark *et al.* 2013, 2021). This has created a need for alternative regeneration strategies, as natural regeneration has not proven sufficient under this regime. Research on systematic regeneration started in the 20th century as clearcut forestry was slowly gaining in importance (Lundmark *et al.* 2021). One of the first major publications on forest management in Sweden to address regeneration in particular was "Skogsskötsel: handledning vid uppdragande, vård och föryngring av skog" (Forest management: guidance on the cultivation, care and regeneration of forests) by Anders Wahlgren (Wahlgren 1914). This work described fundamental regeneration practices and systems such as different planting positions, many of which are still in use today, as it laid the foundation for both forest regeneration management and further research.

In the mid-20th century, research therefore focused on efficient and rational planting (Ebeling 1957) in line with systematic and standardised clear-cutting practices. Around the same time, tree improvement programmes were initiated to select trees with desirable traits (Haapanen *et al.* 2015). Through a system of recurrent selection, breeding populations gradually improved with respect to selected traits such as survival, growth, quality and resilience to pests and frost damage (Haapanen *et al.* 2015; Jansson *et al.* 2017). This process of improvement remains ongoing, with new seed orchards still being established to provide seeds for forest regeneration (Skogsstyrelsen 2020).

In the 1960s, foresters in Finland began to use ploughing for forest regeneration (Nyyssönen 1997), marking the beginning of the development of modern site preparation methods (MSP) (Bärring 1967; Lundmark 1977; Örlander *et al.* 1990). In the 1970s, several studies into the environmental factors affecting seedling establishment and mortality emerged, for instance Söderström (1976) and Persson (1978). Ecophysiological studies of the growth and establishment of seedlings continued into the 1980s (Örlander 1984; Ingestad 1987), with a focus on improving survival and growth. Towards the end of the 20th century, the focus of research shifted as traditional studies striving to optimise planting were complemented by studies of regeneration following natural disturbance dynamics (Attiwill 1994; Fries *et al.* 1997; Angelstam 1998).

In recent years, an important focus of research has been genomic improvements of seedling material (Lenz *et al.* 2020; Capador-Barreto *et al.* 2021), fuelled by the decoding of the Norway spruce (*Picea abies*) genome in 2013 (Nystedt *et al.* 2013). While the genome of the other dominant conifer species, Scots pine (*Pinus sylvestris*), remains to be fully decoded (Pyhäjärvi *et al.* 2020), there are already studies using genotyping-by-sequencing to determine the relatedness and growth of Scots pine (Calleja-Rodriguez *et al.* 2019; Hall *et al.* 2020). Another major topic of recent research has been climate change and its effects on forests (White 2012; Lindner *et al.* 2014; Girona *et al.* 2023; Felton *et al.* 2024a; Laudon *et al.* 2024). This includes studies into various sources of damage to forests under warmer climate conditions (Rasheed *et al.* 2020; Frank 2021), and the impact of extreme drought events on seedlings and trees (Hart *et al.* 2017; Netherer *et al.* 2019; Luoranen *et al.* 2023).

1.2 Current practice and status

Swedish forests are conifer-dominated, with Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) each covering approximately 40% of the forested area (Skogsstyrelsen 2024a). The vast majority of these forests are even-aged, under management regimes which harvest through clear-cutting (Skogsstyrelsen 2020) (Figure 1). Retention forestry, a practice that aims to retain trees that have particularly high biodiversity value, are around cultural remains or close to bodies of water, is widely practiced (Fedrowitz *et al.* 2014; Simonsson *et al.* 2015). After a forest stand is harvested, the ground is usually prepared using mechanical site preparation (MSP) (Örlander *et al.* 1990). The main reasons for using MSP are to reduce competition from surrounding vegetation and to create good planting positions. Mounding and disc trenching are commonly used, both of which invert the top layer of soil, exposing the mineral soil underneath (Örlander *et al.* 1990). After MSP, clearcuts are usually replanted manually with seedlings that have been pregrown in nurseries. Alternatively, forest stands can also be regenerated through direct seeding or natural regeneration, but these methods are less common. After successful regeneration, the forest stand is pre-commercially and commercially thinned to promote the most vital and valuable trees. Trees are harvested once they reach maturity, and this marks the beginning of a new cycle. The turnover or rotation age varies between conifer species and site conditions, from approximately 60 to 110 years (Skogsstyrelsen 2020).

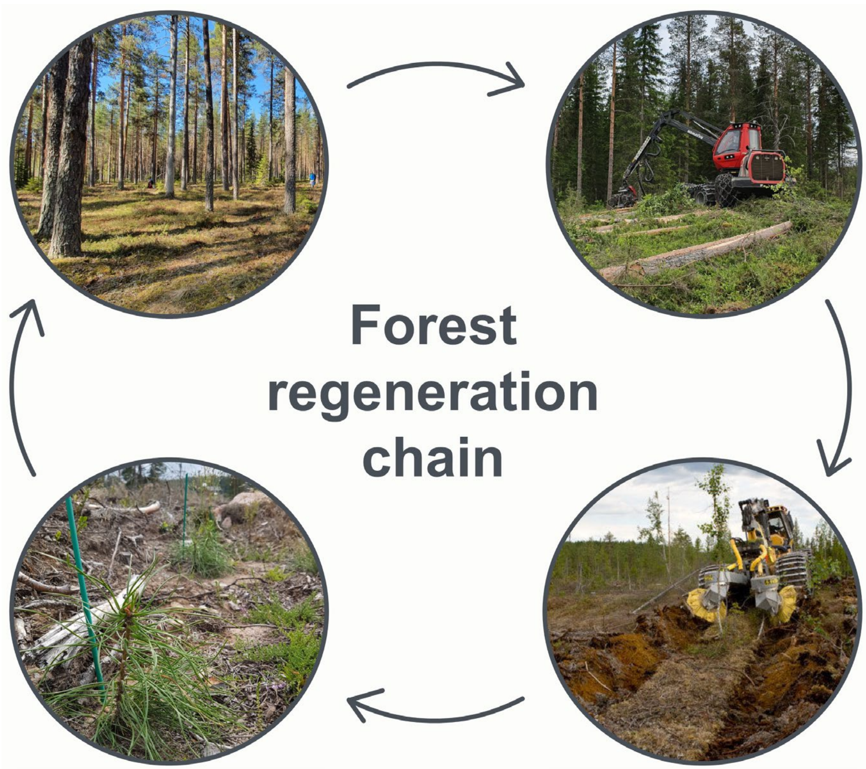

Figure 1. Schematic of the forest regeneration chain currently practiced in Sweden. Clockwise from top right: machine harvest of the forest stand, mechanical site preparation, seedlings planted, mature forest grows. Site preparation picture by Bracke Forest AB, others by Matej Domevscik.

1.2.1 Planting of nursery seedlings

Planting nursery seedlings following MSP is a well-established regeneration method (Skogsstyrelsen 2020), which uses seeds usually collected from seed orchards that are germinated and grown under optimised conditions. Depending on the needs of the site to be planted, the growing period can be adjusted to produce a larger seedling with a more developed root system. Such larger seedlings are commonly used in southern Sweden where competition from surrounding vegetation is a bigger issue than it is in the north (Hallsby 2013). In addition, seedlings are commonly provided with some form of protection to reduce damage by pine weevil (*Hylobius abietis*) (Petersson *et al.* 2004; Sjöström 2020). These treatments can considerably increase the level of investment per seedling and the resource requirements of nursery operations (Aldentun 2002). Nonetheless, in 2022 nursery seedlings were used to regenerate 87% of clearcut areas in Sweden (Skogsstyrelsen 2024a), making planting the most common method for forest regeneration. In 2022, around 422 million nursery seedlings were planted in Sweden (Skogsstyrelsen 2024a).

Once the seedlings have reached a suitable size for the respective planting area (10-30 cm), seedlings are manually planted on clearcuts by a planting team. In general, seedlings are grown in trays with peat-filled containers with a volume of 30 cm^3 or 50 cm^3, ensuring easy storage, transport, and planting. Such seedlings are often referred to as containerised seedlings and may also be freeze-stored to make the logistics before planting easier.

While widely used, seedlings require careful planning and precise timing from germination to final planting. They are typically ordered and produced well in advance to ensure availability for the spring planting season which is usually April-June (Hallsby 2013). Moreover, any delay or mishandling during transport to the clearcuts can severely reduce the survival of nursery seedlings (Mataruga *et al.* 2023). Even with freezer storage, they cannot be stored indefinitely, as they have a limited shelf life and need to be planted within a specific timeframe.

1.2.2 Direct seeding

Direct seeding refers to artificially regenerating a forest stand using seeds produced in seed orchards or collected from forest stands. Not all areas are suitable for this method but, when done well, direct seeding can result in dense stands of trees with well-developed root systems (Wennström 2001). Direct seeding is not widespread under the current Swedish forestry model: in 2022, it was used on just 3% of the total regeneration area in Sweden (Skogsstyrelsen 2024a).

Using seeds grown in seed orchards opens up the possibility of using genetically improved seed material or seeds with different provenances, both of which have been shown to increase survival and growth rates (Persson 1994; Egbäck *et al.* 2017). Direct seeding is usually cheaper per hectare than planting nursery seedlings, but seeds need time to germinate and establish, which may increase the rotation time.

A common challenge with direct seeding is predation of seeds by insects, rodents, and birds. Previous studies have reported mortality rates of 20-60% in Scots pine (Nystrand & Granström 2000; Worthy *et al.* 2006). Covering the seeds immediately after seeding does reportedly reduce predation (Nilson & Hjältén 2003), but this may be hard to implement on a large scale. Another challenge with direct seeding is the inter-annual variation in the quantity of seeds produced in orchards (Prescher *et al.* 2005), which can severely limit the availability of high-quality seeds. In addition, seedlings from direct seeding have been shown to achieve establishment rates of around 20% (Palma & Laurance 2015; Grossnickle & Ivetić 2017), which can result in low restocking rates. Studies show that microsite preparation can help to increase the establishment rate (Winsa & Bergsten 1994; Wennström *et al.* 1999), but this may add to the overall costs of regeneration. On the other hand, a potential solution is the mechanical distribution of seeds directly after site preparation which may reduce costs by reducing the number of actions needed on the clearcut. However, since direct seeding is not currently widely used in Swedish forestry, there are few direct seeding machines in use.

1.2.3 Natural regeneration

In contrast to artificial methods, natural regeneration relies on seed material from existing trees to regenerate the harvested area. While not a common method under the current Swedish forestry model, it is increasingly discussed in connection with biodiversity conservation values (Brang *et al.* 2014; Seedre *et al.* 2018) and in other silvicultural systems related to continuous-cover forestry (CCF) (Koivula *et al.* 2020). Natural regeneration was reportedly used on around 7% of the total regeneration area in Sweden in 2022 (Skogsstyrelsen 2024a).

A commonly used method for natural regeneration of Scots pine is the seed tree method, under which all trees except the selected seed trees are removed through a standard harvest (Karlsson *et al.* 2017). The seed trees are generally large, high-quality trees with high seed dispersal potential, but their selection can depend on the needs of the area. After harvesting, the ground is prepared with MSP to create good establishment conditions (Béland *et al.* 2000; Karlsson & Nilsson 2005; Nilsson *et al.* 2006). Previous research shows that, while seeds germinate over the whole area, the highest number and largest seedlings are found in the prepared areas (Hagner 1962). When the new seedlings reach an average around 30-100 cm in height, depending on the area, the old seed trees are removed to increase space and reduce competition with the new stand.

Another common method for natural regeneration is the shelterwood system, under which large mature trees from the old stand are left in an area to provide seed material and shelter (Karlsson *et al.* 2017). The shelterwood system differs from the seed tree method mainly in the higher density of mature trees that are retained after harvesting. The shelter provided by these mature trees to the regenerating stand below influences site conditions at the stand level. Previous studies have shown reduced variation in soil temperature under shelterwood stands due to changes in air movement, where mature trees create a layer of insulation and reduce wind speed (Béland *et al.* 2000; Langvall 2000; Agestam *et al.* 2003). In comparison, on clearcuts, rapid heat loss during the night can lead to frost damage on seedlings (Örlander *et al.* 1990; Spittlehouse & Stathers 1990).

When selecting areas for natural regeneration, special attention needs to be paid to high wind occurrence in the area as these systems are prone to storm damage (Hånell & Ottosson-Löfvenius 1994). Further, natural regeneration is inherently unable to make use of genetically improved seed material which is a significant focus under the current Swedish forestry model (Simonsen 2013; Skogsstyrelsen 2020). Although additional direct seeding or planting of nursery seedlings is possible under a shelterwood, it is not commonly practiced due to the increased costs involved.

1.3 Impact of future climate on forest regeneration

Climate change is a long-term and constantly evolving process that is influenced by many factors (Karl & Trenberth 2003). While the climate has slowly changed several times in the past (Alley *et al.* 1999) the rapid pace of current changes is concerning. These changes may affect current forest regeneration in unexpected ways and introduce new challenges. To better understand the nature of these changes, several studies have sought to predict the future climate using global climate models (GCM) and downscaling them to regional climate models (RCM) using historical data (Christensen *et al.* 2001; Chen *et al.* 2015; Lind *et al.* 2023). Four changes to Sweden's future climate are consistent across several models: an increase in overall mean temperature (Beniston *et al.* 2007; Lind *et al.* 2023), more intense weather events (Beniston *et al.* 2007; Chen *et al.* 2015; Lind *et al.* 2023), more winter precipitation (Beniston *et al.* 2007; Lind *et al.* 2023), and less summer precipitation in south and central Sweden (May 2008; Chen *et al.* 2015; Spinoni *et al.* 2018; Lind *et al.* 2023). Together, these changes could have a marked impact on the establishment of seedlings.

An effect of higher mean temperatures is a prolongation of the growing season, which is on average already 17 days longer in Sweden today than it was 30 years ago (SMHI 2024). This could increase the abundance and growth of competing vegetation which would significantly influence regeneration (Nilsson *et al.* 1996; Örlander *et al.* 1996; Jobidon *et al.* 2003; Axelsson *et al.* 2014). Moreover, pests that are currently temperature limited, such as insect and fungi, could expand into larger areas (Allen *et al.* 2010). Additionally, for Scandinavia, previous research has also identified a positive warming loop connected to snowmelt, as higher temperatures reduce snow cover, which in turn increases temperature (Lind *et al.* 2023). This may mean that weather conditions during the main planting period in spring will generally be warmer and drier than previously.

Overall, precipitation in Sweden is predicted to increase (Lind *et al.* 2023), although the bulk of this increase is predicted to occur in winter (Beniston *et al.* 2007; Chen *et al.* 2015; Lind *et al.* 2023). During this season, seedlings are dormant and their transpiration demands reduced due to low rates of photosynthesis (Strand *et al.* 2002). Increased precipitation during this time would not contribute to better establishment or growth of seedlings. Meanwhile, precipitation during the summer, when seedlings do grow and establish, is predicted to decrease in south and central Sweden leading to droughts (Chen *et al.* 2015; Spinoni *et al.* 2018; Lind *et al.* 2023). As a majority of seedlings in Sweden are planted in late spring/early summer, this could have major implications for their establishment and growth. A recent example of extreme drought in Sweden occurred in the summer of 2018. Several studies reported increased mortality of both seedlings (Beloiu Schwenke *et al.* 2023; Luoranen *et al.* 2023) and trees (Schuldt *et al.* 2020; Sturm *et al.* 2022) through desiccation and other drought related causes of mortality, such as insect attacks (Senf & Seidl 2021).

1.4 Current forest regeneration under pressure for change

Successful early regeneration is largely a product of microsite conditions and various damage factors during the first few years (Spittlehouse & Stathers 1990). These comprise many different biotic and abiotic factors that interact with one another, resulting in a variation of site conditions across space and time. Hence, site conditions vary significantly both between and within individual regeneration sites (Holmström *et al.* 2019; Nordin *et al.* 2023). Additionally, local weather conditions can fluctuate greatly from year to year and are further intensified by ongoing climate change. Consequently, the complexity of the current situation necessitates an agile approach to regeneration, which may not align with existing practices focused on achieving efficiency through standardization. It is therefore not a surprise that even though Swedish forest regeneration has developed into a highly optimised system, several issues persist. This thesis mainly focuses on three factors of variation with key importance for regeneration outcome: damage by pine weevils, moisture and nutrient acquisition.

1.4.1 Damage by pine weevils

Pine weevils remain a major cause of seedling mortality despite protections applied to seedlings. This destructive forest pest feeds on the bark of conifer seedlings, girdling them and causing mortality rates of up to 80% in unprotected seedlings (Örlander & Nilsson 1999). Historically the problem was managed using chemical insecticides (Nilsson *et al.* 2010). Over recent decades, however, most of these chemicals have been banned in Swedish forestry due to their harmful side effects. Protection is instead done by mechanical means with a coating on the lower part of the seedlings' stems (Nordlander *et al.* 2009, 2011). These coatings are applied before seedlings leave the nursery and aim to protect the bottom of the stem, i.e. the part most vulnerable to girdling. While these protections are promising, many questions connected to their use remain unaddressed. For example, how would damage above the coating affect seedling survival? Moreover, mechanical coatings could restrict the stem or cover the seedlings' needles, thereby limiting growth by reducing photosynthesis (Sjöström 2020). The durability of these coatings in field conditions is also a concern.

Pine weevils exhibit an established pattern of behaviour in which damage to seedlings is highest in the first three years after clear-cutting (Örlander *et al.* 1997; Wallertz *et al.* 2016). While not common, planting nursery seedlings can be delayed for a few years after harvesting, and this has been shown to reduce the impact of pine weevils (Örlander *et al.* 1997). Another successful measure for reducing pine weevil damage is MSP, particularly when it uses methods which expose the mineral soil (Petersson *et al.* 2005; Nordlander *et* *al.* 2011; Wallertz *et al.* 2018). Pine weevils are less inclined to remain on mineral soil for extended periods of time, probably because it provides fewer hiding places than planting spots in organic soil.

1.4.2 Moisture acquisition

Another challenge, integral to the regeneration cycle, is consistent seedling establishment. Large variations between sites in seedling survival have been noted by previous studies (Hjelm *et al.* 2019; Sikström *et al.* 2020; Nordin *et al.* 2023). Research has shown that adequate moisture acquisition directly after planting is a critical first step in seedling establishment (Grossnickle 2005; Luoranen *et al.* 2023) This is particularly true in drought when soil moisture is limited, but such conditions are hard to predict locally (Holmström *et al.* 2019). Current efforts to address regeneration in dry areas are limited, although Scots pine is commonly preferred as it grows better than Norway spruce under drier conditions (Albrektson *et al.* 2012; Baumgarten *et al.* 2019).

One way to change microsite conditions that influence establishment is through mechanical site preparation (MSP) which allows us to modify soil features (Spittlehouse & Stathers 1990). Typically, the MSP creates two planting positions with distinct characteristics (Figure 2). Lower planting positions are created in the depression made by site preparation, directly in the mineral soil (MS). Higher planting positions occur on top of the inverted material and comprise the upper mineral soil layer, a double layer of organic material, and the underlying mineral soil. In line with the definition given by Sutton (1993), these are hereafter referred to as capped mounds (CM).

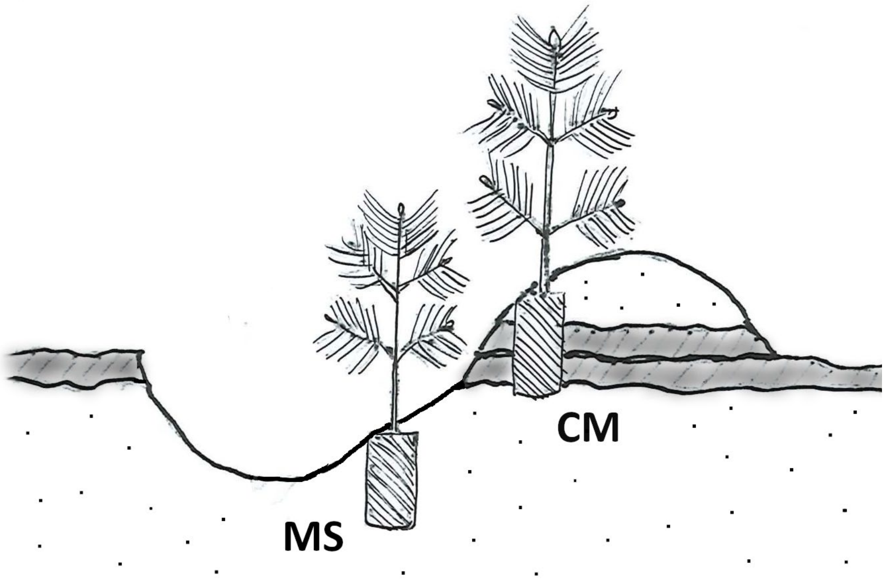

Figure 2. Mineral soil (MS) and capped mound (CM) planting positions. Organic soil layer is represented in darker shade, while mineral soil is white with dots. Drawing by Bodil Häggström.

The main benefits of planting on CM are an increase in nutrient availability from the organic layer and a reduction in frost damage (Örlander *et al.* 1990). On the other hand, planting on CM can lead to a higher risk of drought, particularly on dry sites (Örlander *et al.* 1990) since they can vary considerably in terms of how they are prepared for subsequent planting (Sutton 1993; Söderbäck 2012). Since planting is mostly done manually, it is up to the planter to decide where exactly to plant. Ideally, seedlings planted on CM should be positioned as shown in Figure 2, with sufficient contact with the underlying mineral soil. This is not always easy, as a planting position classified as optimal from above may have a deep layer of organic matter underneath (Figure 3). Such a barrier can significantly hamper survival and growth, as early contact with moist underlying soil is crucial (Burdett 1990; Grossnickle 2005). On sites with abundant woody debris or organic matter, planting on CM can sometimes result in higher mortality, especially when combined with longer periods of drought.

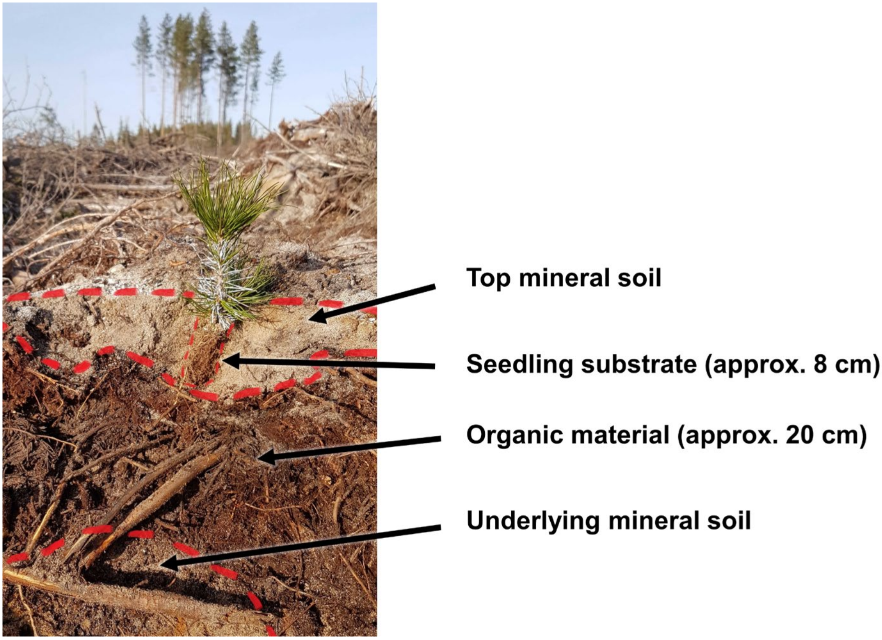

Figure 3. Cross section of a CM planting spot. While this planting position may look suitable from above, a cross-section reveals considerable organic material which restricts the seedling from reaching the moist underlying mineral soil. Picture by Jonas Öhlund.

The main concerns when planting in MS include increased risk of frost damage and waterlogging, which can negatively affect seedling survival. However, the large latitudinal range and diversity of sites in Sweden means that not all sites are affected equally. On dry sites in particular, planting in a high position in mineral soil may still result in higher survival overall. In this regard, because of an average yearly rainfall of around 500-700 mm/m^2 (SMHI 2024), many of the sites in northern Sweden can already be considered dry compared to the south. As the climate changes in the future, the number of dry sites may increase further.

An alternative to securing soil moisture through MSP is focusing on manipulating environmental factors through silvicultural methods. Clearcuts typically experience significant fluctuations in environmental factors such as temperature and soil moisture (Spittlehouse & Stathers 1990; Langvall 2000; Oleskog & Sahlén 2000). Reducing this variation could improve seedlings' ability to respond to other sources of stress. This can be achieved at two different scales. At a large-scale, seedlings can be protected through a shelterwood system, in which mature trees create an insulating layer above the seedlings (Langvall 2000). Stable environmental factors mitigate risks such as frost damage and are essential to the consistent growth and survival of seedlings. Combining shelterwood treatments with MSP has been shown to further facilitate good establishment of naturally regenerated seedlings (Hagner 1962; Béland *et al.* 2000; Karlsson *et al.* 2002; Karlsson & Nilsson 2005).

Alternatively, an example of protection on a small-scale is the use of coated seeds. As the name suggests, coated seeds consist of a single seed embedded in a layer of minerals that protect it from large variations in soil moisture. Ideally, the coating binds to the mineral soil after planting and facilitates capillary water transfer from the moist soil underneath. While the idea of using coated seeds for forest regeneration is not new, so far very few peer-reviewed results have been published. Similar methods of seed distribution have been tried in the past (Wennström 2014), but none have yet been commercially successful or widely adopted.

1.4.3 Nutrient acquisition

Nutrient acquisition is another important process in seedling establishment, and is limited by the presence of nutrients in the soil. Nitrogen is the limiting factor in boreal forests (Tamm 1991; Sponseller *et al.* 2016), which cover most of Sweden except for the very southern region. Just as moisture is crucial for seedling establishment, acquisition of sufficient nutrients is vital for growth. Fertility varies across the landscape but, on poor sites, consistent establishment can be challenging. Slow growth in these areas can extend the early seedling stage during which seedlings are particularly vulnerable to various damage factors such as pine weevils, ungulate browsing, and drought (Örlander *et al.* 1997; Nilsson *et al.* 2019; Luoranen *et al.* 2023). Some MSP methods mix nutrient-rich humus soil into the planting spot, leaving the nutrients available for seedlings. However, other methods remove the humus layer entirely, exposing the mineral soil underneath. Reasons for this can be varied, because of site features or to reduce pine weevil damage, but in this case such planting positions may lack nutrients entirely. In these nutrient-deficient planting positions, addition of nutrients may be required (Nilsson *et al.* 2019, 2024). Fertilisation at the seedling stage is currently being explored experimentally (Gruffman *et al.* 2012; Castro *et al.* 2021; Svensson *et al.* 2023; Nilsson *et al.* 2024), but it is not commonly done in operational forest management. However, there is a growing interest in its practical applications.

1.5 Aim

The aim of this thesis was to investigate the performance of Swedish forest regeneration in the context of climate change, particularly the extreme drought of 2018. Specifically, this work aimed to test performance of a number of methods that could potentially alleviate negative effects of increasing variations in site conditions on survival and growth of conifer seedlings across Sweden. The methods tested were mechanical protection against pine weevils, changing planting positions, addition of organic fertiliser, using coated seeds, and application of natural regeneration. Climate change adaptation potential of these methods was then further discussed, by exploring a framework of resistance, resilience and transition adaptation.

2. Methods

The methods presented here are a summary of those used in the papers included in this thesis, which are referred to throughout. For further details, please see those papers, and the references provided. Paper IV is included in the printed version of the thesis.

2.1 Study sites

A total of 38 sites were used in this thesis. They were established on clearcut or shelterwood areas in Sweden between the latitudes of 56.3°N and 67.1°N, giving a large latitudinal gradient of 1275 km between sites (Figure 4). Paper I included 14 sites (Table 1) established in April-May 2018 and 2019; Paper II included 11 sites (Table 2) established in May-June 2018; Paper III included 12 sites established in May-June 2017 (Table 3); and Paper IV included 1 site established in February 2017 (Table 4). The location, elevation, and number of growing season days for each site were recorded, allowing for comparison between different sites and geographies. Additionally, study-specific data are provided for each experiment.

Annual precipitation varied between sites due to several factors, including latitude, terrain features, distance from the sea, climate type and years. Table 5 shows precipitation during May-August (2017-2019), which is within the growing season for all sites, and is commonly time of early establishment for spring planting season.

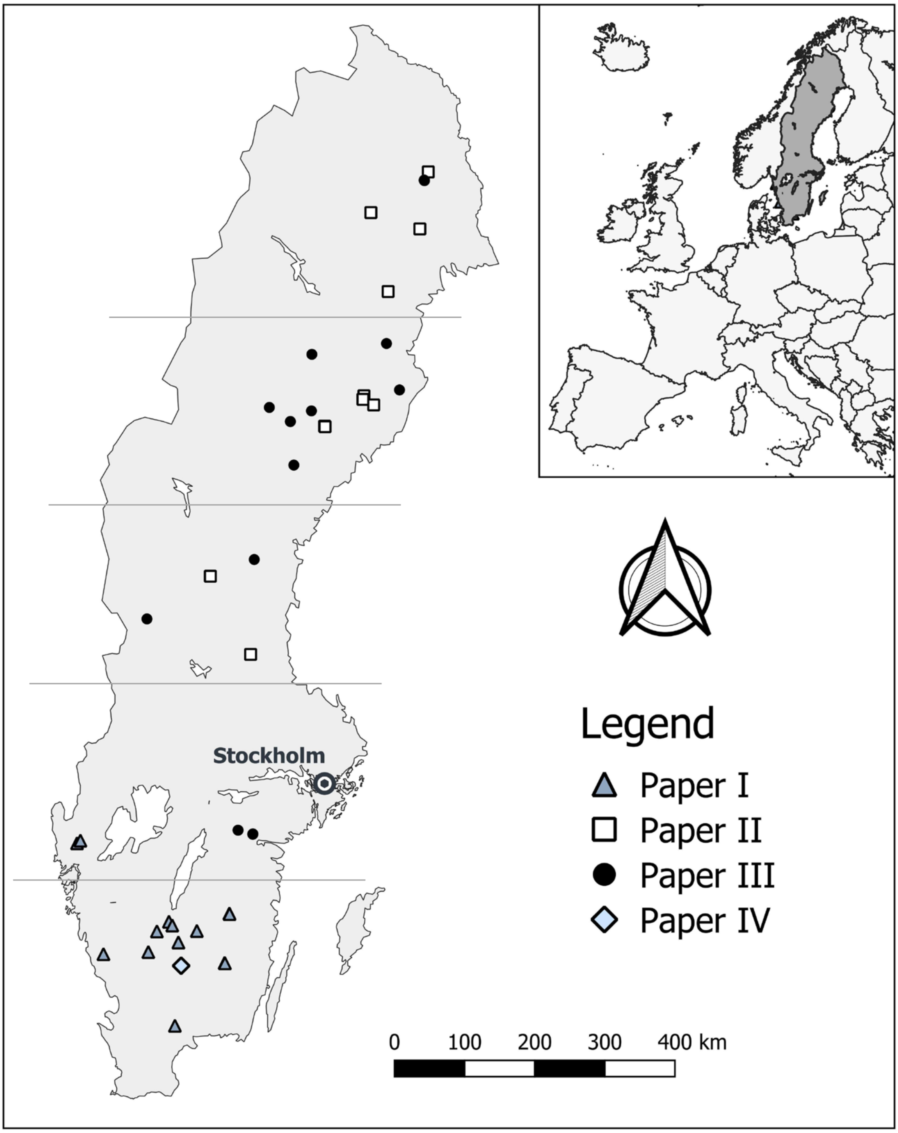

Figure 4. Map of the study sites between latitudes 56.3°N and 67.1°N. Lines represent delineation of sites grouped into clusters used in Table 5. The scale represents distances on the map of Sweden to the left.

Table 1. Site description of the 14 experimental forest clearcut sites included in paper I, arranged from north to south.

Site name	Location (lat/long)	Elevation [m; a.s.l]	Growing season [days]	Planting year	Precipitation GS [mm]	Max VPD GS [kPa]
Sanneskogen	58.63/11.88	149	219	2019	703	2.70
Brattöns gård	58.60/11.80	128	219	2019	646	2.70
Snibben	57.74/15.54	251	194	2018	351	3.87
Norrhult	57.73/15.54	223	194	2018	351	3.87
Månsarp	57.63/14.09	242	218	2018	235	3.73
Kränsberg	57.58/14.17	240	218	2019	474	3.26
Margrevehult	57.51/14.76	224	217	2019	394	3.12
Lilla Öjhult	57.50/13.81	274	218	2019	551	2.94
Siggaskog	57.36/14.32	195	218	2019	590	2.94
Nennesmo	57.23/13.61	163	218	2019	483	2.94
Släne	57.19/12.55	139	226	2018	443	3.91
Kroksjövägen	57.10/15.42	237	218	2018	345	3.51
Björnamossvägen	57.10/15.42	247	218	2018	345	3.51
Kullaskogen	56.30/14.25	117	224	2018	241	3.99

Table 2. Site description of the 11 experimental forest clearcut sites included in paper II, arranged from north to south.

Site name	Location (lat/long)	Elevation [m; a.s.l]	Growing season [days]	Precipitation first 30 days [mm]	Pot size (cm^3)	Number of measured seedlings
Pajala	67.09/22.30	200	130	13	30	288
Jokkmokk	66.64/20.30	260	130	48	50	107
Skajte	66.38/21.82	200	135	43	30	88
Kvällsberget	65.62/20.63	180	140	43	30	64
Hällnäs	64.31/19.64	300	145	44	50	68
Vindeln	64.26/19.61	180	145	45	50	81
Torrbergsknösen	64.18/19.91	180	145	44	50	14
Åselhål 2	63.95/18.44	280	145	24	50	62
Åselhål 1	63.95/18.45	260	145	24	50	42
Strömbacken	62.07/15.09	260	155	36	30/50	284
Källåsen	61.06/16.16	360	165	35	50	109

Table 3. Site description of the 12 experimental forest clearcut sites included in Paper III, arranged from north to south.

Site name	Location (lat/long)	Elevation [m; a.s.l]	Growing season [days]	Topsoil composition	No. of replicated plots	
					SeedPAD unfertilised	SeedPAD fertilised
Rissavägen	66.99/22.13	241	139	Silty till	1	3
Nyback	64.95/20.44	143	170	Coarse till	6	2
Bergsvik	64.88/18.17	268	149	Coarse till	2	
Backmyran	64.35/20.71	175	170	Coarse till	5	7
Varpsjovägen	64.22/16.84	364	145	Coarse till	4	4
Tallsjö	64.14/17.92	319	149	Moist till	5	3
Stormon	64.03/17.44	297	145	Till	6	2
Svanatjarn	63.47/17.49	319	146	Till	4	2
Storulvsjö	62.28/16.3	418	146	Moist till	3	2
Nyhult	61.51/13.4	570	146	Sandy till		2
Lilla Malthult	58.8/15.77	69	194	Sandy till	6	2
Hostdagskärret	58.75/16.13	86	194	Podzol	6	2

Table 4. Site description of the experimental forest site included in Paper IV, including mean values of weather variables and growing season days for the duration of the study period, 2017-2023.

Sites	Location (lat/long)	Elevation [m; a.s.l]	Growing season [days]	Precipitation sum. GS [mm]	Max VPD GS [kPa]	Mean VPD GS [kPa]
Tagel	57.06/14.39	220	214	475	3.13	0.59

Table 5. Sum of precipitation in May-August 2017, 2018, and 2019 for all sites grouped into six clusters. Clusters are arranged from north to south and delineated in Figure 4. Precipitation data were obtained from the SMHI open database using the weather station nearest to sites within each cluster (mean distance to sites 42 km, max distance 137 km).

Cluster name	**Range of latitudes**	**Number of sites**	**∑ precip. 2017 [mm]**	**∑ precip. 2018 [mm]**	**∑ precip. 2019 [mm]**
North Norrland	67.1-65.6	5	266.2	195.1	306.4
South Norrland	64.9-63.5	12	251	154.7	248.2
Mid Sweden	62.3-61.1	4	325.7	239.2	211.9
Southcentral east	58.8	2	187.6	134.4	228.1
Southcentral west	58.6	2	265.5	169.7	356.3
South Sweden	57.8-56.3	13	310.7	166.9	291.1

2.2 Material and data collection

Data for all studies were collected from field measurements, controlled laboratory experiments, network of national observation stations and digital models. During the study period, each site was generally visited at least once per year to record establishment rates, survival, the height or biomass of seedlings, and to collect any reports of damage and general site features. The dataset on field conditions was supplemented with environmental factor data collected by SMHI (Swedish Meteorological and Hydrological Institute), SGU (Geological Survey of Sweden), and Lantmäteriet (The Swedish Mapping, Cadastral and Land Registration Authority). Measurements of field-collected material and controlled experiments were carried out in the soil laboratory of SLU (the Swedish University of Agricultural Sciences) in Umeå.

2.2.1 Paper I

For this study, 14 sites were established in southern Sweden, half in 2018 and half in 2019. Following clear-cutting, each site was planted with 180 containerised Norway spruce seedlings with the aim of planting them in mineral soil. Seedlings sourced from the same nursery and batch were treated with four different mechanical protections (Conniflex, Cambiguard, Ekovax, Hylonox) (Figure 5), a standard insecticide (Merit Forest), or left untreated. Each treatment was replicated 30 times in large blocks and at sufficient distance from surrounding forests to minimise edge effects. Replication was systematic using Latin squares.

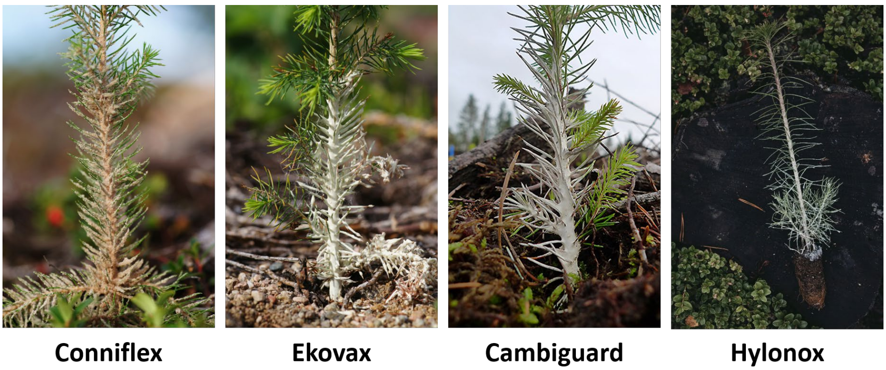

Figure 5. Mechanical protection methods against pine weevils used in Paper I. Pictures by Claes Hellqvist and Karin Hjelm.

Seedlings were monitored for survival, height, and damage over four growing seasons. Survival was visually assessed, while height was measured from soil surface to the top shoot. Damage type and severity were recorded on a scale from slight to lethal. Pine weevil damage, if present, was noted in terms of bark removal area and location on the stem. For mechanically protected seedlings, the coated area was distinguished from the rest of the stem, while for insecticide-treated and untreated seedlings, the lower 10 cm was considered the bottom of the stem. Additionally, the persistence of the coating was visually assessed after the first and second growing seasons.

2.2.2 Paper II

A field experiment was set up in the early summer of 2018 to test the effects of fertilisation and planting position on the survival and growth of Scots pine nursery seedlings. Seedlings were distributed into two treatment groups, one fertilised with one dose of arginine-phosphate (AP) (40 mg N and 22 mg P) and the other unfertilised. Seedlings from both treatment groups were planted in one of the three planting positions: capped mounds (CM), mineral soil (MS), or non-prepared soil.

Two to four parallel blocks were set up at each of 11 sites in Sweden, between the latitudes of 67.09 and 61.06 degrees (see Figure 4). Each block comprised six parallel rows of approximately 20 seedlings, one row for each fertiliser/planting position combination. An exception to this was the northernmost site, Pajala, where 70-100 seedlings were planted per row. On each site the blocks were positioned adjacent to each other in relatively homogenous areas with no expected block effect, hence each site was treated as one plot in the analysis. Seedling material and size (30 cc and 50 cc pots) varied between sites, depending on the site owner (Table 2).

Fieldwork was performed following the second growing season, in August-September 2019. Seedlings next to a marking stick that had green needles were considered to have survived, whereas dead or missing seedlings were recorded as non-surviving. Every second surviving and undamaged seedling in a row, after a random start at the first or second seedling, was also measured for leader shoot length i.e., height between top branches and terminal bud.

2.2.3 Paper III

The coated seeds used in this study were developed by Arevo and SweTree Technologies under the name of SeedPAD (SP). Each SP comprised a single seed of Scots pine covered with a layer of vermiculate mineral and wrapped in dissolvable polysaccharide foil (see Figure 6). The pads were 35 mm in diameter with a thickness of 3.5 mm and were deployed with the seed underneath. When exposed to sufficient water, the polysaccharide foil readily dissolved and the vermiculate formed a seal over the seed, conserving moisture within. The SPs used were either fertilised with one dose of arginine-phosphate (10 mg N and 5.5 mg P) or unfertilised.

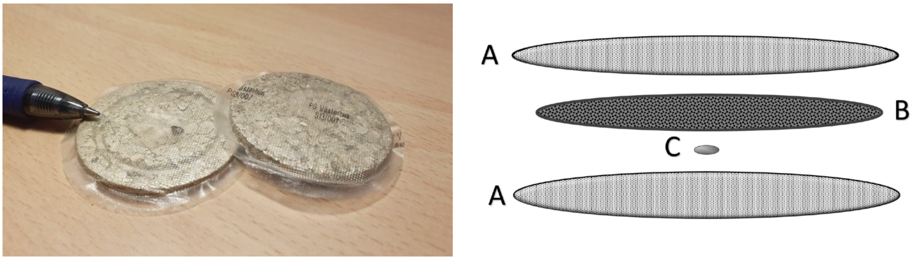

Figure 6. On the right, picture of an unfertilised SeedPAD version 5.0, used since 2016. The pads are deployed with the seed underneath. On the left, diagram of SeedPAD: A – polysaccharide foil, B – layer of vermiculate, C – Scots pine seed.

In May-June 2017, both fertilised and unfertilised SPs were deployed in mineral soil exposed by disc trenching by the landowners, in this instance forest companies. Following commonly used procedures in Swedish forest regeneration, SPs were deployed in two experimental designs: circular and block. Circular plots were either marked as fertilised or unfertilised and contained 35 of the designated SPs in a circle with a radius of 5.64 m (which forms an area of 100 m^2). Block plots comprised two parallel rows of 50 m which were designated either fertilised or unfertilised with an SP deployed at every metre. Each SP in both designs was marked with a marking stick.

Sites were surveyed in late summer 2018 and 2019, recording the survival and growth of seedlings established from the SPs, considering seedlings within 10 cm of the marker stick to be the study seedlings. The growth of living seedlings was measured as the distance from the ground to the top of the shoot, while sticks with dead or missing seedlings were considered non-surviving. In addition, in 2019 five seedlings from each treatment present at each site were carefully excavated for biomass analysis. These seedlings were dried for 24 hours at 60°C (to constant weight), then cut at the stem and the root and shoot parts weighed separately.

A controlled laboratory experiment was set up to investigate the water requirements of SPs, with the aim of identifying factors affecting attachment to the ground. A total of 135 SPs were used, separated into three water addition rates combined with three soil grain sizes. Soil was collected in 2020 from a clearcut in mid Sweden (Storulvsjö) while soil grain sizes were set to best represent field conditions. Water addition rates were determined using local precipitation data averaged for all sites. SPs were placed on soils with grain sizes of 1.7, 5.6 and 10.0 mm diameter to represent fine, medium, and coarse textured soil, respectively. Room temperature water (0.5 ml) was then added to the SPs every 1.5, 3, and 5 minutes for fast, medium, and slow treatments respectively. Attachment was considered successful when the SP could not be easily pushed sidewise from the soil.

2.2.4 Paper IV

The experiments were set up in a Scots pine dominated site during the winters of 2017, 2020, and 2023, following overstory harvest. These stands were further designated as H17, H20 and H23, respectively. Each stand was divided into three overstory treatments: clearcut (0 stems/hectare), seed trees (approx. 100 stems/hectare), and shelterwood (approx. 200 stems/hectare). All areas were also cleared of woody understory vegetation and fenced to prevent browsing by ungulates. MSP was performed immediately after overstory harvest in all stands. For stands H17 and H20, MSP was also performed three years after overstory harvest, in 2020 for H17 and in 2023 for H20.

The experiment employed a split plot design with three or four blocks, each measuring 16 x 8 meters, in each overstory density treatment. MSP was performed with an excavator to create four continuous rows of mineral soil (approximately 0.5 metres wide) in each block, while the soil between the rows remained undisturbed. Sampling plots were then systematically established on areas with and without MSP, totalling 16 and 8 plots per block, respectively. The distance between sampling plots within rows was one metre, and the centres of the specific plots were marked with plastic sticks.

Seedfall was measured using circular seed traps (9.4 cm radius), which were emptied twice per year (June and November) from 2018 to 2020 at H17, from 2020 to 2023 at H20, and in 2023 at H23. Each overstory density treatment had 20, 10, and 6 traps at H17, H20, and H23, respectively. All seeds without wings were counted as Scots pine, as they are difficult to distinguish from Norway spruce seeds when wingless. Seedfall for 2017 was not collected, due to a sampling error.

Seedling recruitment was tracked annually in late autumn at the plot level over three years: 2017-2019 for stand H17 and 2020-2022 for stand H20. Stand H23 included only sampling year 2023. Each sampling plot contained either a small (15 x 15 cm) or large (30 x 30 cm) plastic cross at its centre, aligned with magnetic north to ensure consistency and precise measurements. A small cross was used where the rocky terrain prevented the use of a large cross. Cross axes were marked with scales accurate to 1 cm to record the positions of individual seedlings for identification and long-term monitoring (Figure 7). Seedlings that did not survive to the stage where species identification was possible were registered as Scots pine.

Figure 7. Tracking seedling recruitment: same sampling location on a MSP plot at the clearcut stand harvested in 2017 (H17), beginning with the 2017 inventory (left), followed by 2018 (centre), and 2019 (right).

2.3 Analysis

For all four papers, R-Studio software (R Core Team 2024) was used to analyse the data. Regression analyses in the form of linear models (Paper II), linear mixed-effects models (Paper IV), generalised linear models (Papers II and III), generalised mixed models (Paper I) and generalised binomial mixed models (Paper I) were used throughout the analysis. These were followed by model II and model III ANOVA (analysis of variance) (Papers II and III) and estimated marginal means analysis (Paper I and IV) to interpret the model results.

In Paper I, a generalised mixed model was used to analyse the impact of mechanical protections, coating persistence, planting year, pine weevil damage, and their interactions on seedling height and survival at each survey interval. For survival data, a generalised binomial mixed model was used. The model accounted for site differences by including site as a random variable. To interpret the model outcomes, estimated marginal means from the emmeans R package (Lenth 2023) was used, which included contrast analysis and enabled comparisons between protection methods. Specifically, for ease of interpreting the results, the focus was on comparing mechanical protection methods and insecticide against the untreated control.

In Paper II, ANOVA was performed on seedling survival and growth data. To investigate survival, survival log-odds (ratio of the probability of survival to probability of death) were used as the response variable, while growth was investigated using leader shoot length. The explanatory factors for both models were site, planting position, and fertilisation treatment. Model III ANOVA was used to detect any interaction between the main factors and followed by model II ANOVA in cases where there was no interaction. In addition, linear models and generalised linear models were used to test which environmental variables had the greatest effect on survival: these included precipitation in the first 30 days after planting, length of growing season and site index.

In Paper III, the establishment rate was assessed using a generalised linear model with a binomial distribution and a logit-link function. Model III ANOVA was applied to detect any interaction between the main factors, and

Model II ANOVA was used where no interaction was found. The effects of site-specific weather variables on the survival of both fertilised and unfertilised SP seedlings were examined. Stepwise selection procedures were employed using Akaike Information Criteria (AIC < 2, $\alpha < 0.05$). For height and biomass responses, a type II ANOVA model without an interaction term between fertilisation and site was performed. The normality of the final residuals for all models was checked visually by plotting them against predictions.

In Paper IV, differences in seedfall across various years and stands were analysed using a two-sample t-test with the assumption of equal variances. Afterwards, seedling recruitment (seedlings/m^2) was compared across different stands and overstory density treatments by fitting a linear mixed-effects model utilising a logarithmic distribution with the lme4 package (Bates *et al.* 2023). In the models, overstory density treatment was a fixed factor and block within a stand was included as a random variable. To interpret the model results, estimated marginal means from the emmeans R package (Lenth, 2023) were used. This included contrast analysis, enabling comparisons between different treatments.

3. Main results

Results presented here are a summary of those from the papers included in this thesis, which are referred to throughout. For further details, please see those papers. Paper IV is included in the printed version of the thesis.

3.1 Paper I

Environmental analysis of the study sites highlighted that the vapour pressure deficit (VPD) was significantly higher in 2018 than in 2019, indicating that the seedlings had probably experienced drought conditions. Maximum VPD values in 2018 ranged from 3.5 to 4 kPa, whereas only two sites surpassed 3 kPa in 2019. Mean VPD for 2018 was also notably higher, showing a 50% increase compared to 2019. Similarly, there was 36% less precipitation in 2018 than in 2019, with 2018 averaging 343 mm and 2019 467 mm. While both were below the norm for the area of 513 mm (1991-2020), precipitation in 2018 was significantly lower, averaged across all sites.

During the drought conditions of 2018, both mechanical protection methods and insecticide had no significant effect on seedling survival. After four seasons, mechanically treated seedlings had a 68% survival rate, while those treated with insecticide and the untreated control showed 72% and 60% survival rates respectively (Figure 8). Notably, only the Cambiguard treatment significantly increased survival to 75% when compared with the untreated control. However, survival rates varied greatly for each treatment across survey occasions, particularly for Conniflex and the untreated group. Coating persistence did not significantly affect survival in 2018.

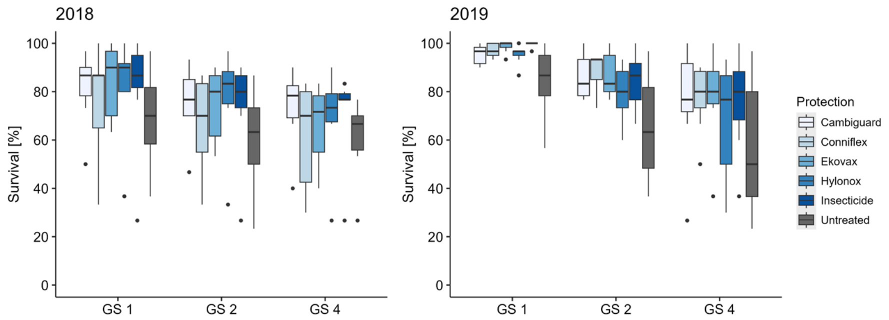

Figure 8. Boxplots of survival of all seedlings during each survey for each of the treatments and both planting years, 2018 and 2019. GS indicates the growing season after which the survey was performed.

In contrast, mechanical protection methods had a significant positive effect on the survival of seedlings planted in 2019. With the exception of Hylonox, all protection treatments resulted in significantly higher seedling survival than the untreated control. Survival rates were more consistent across treatments, particularly after the first and second growing seasons. After four seasons, mechanically treated seedlings, excluding those treated with Hylonox, showed 82% survival, while insecticide-treated and untreated seedlings achieved 81% and 60% survival respectively (Figure 8). Lower coating persistence significantly reduced survival in 2019, particularly for Hylonox-treated seedlings, of which 35% had no protection remaining after two seasons in the field.

Further, a synergistic effect was observed between pine weevil damage and drought. Seedlings in 2019 maintained higher survival rates, even where pine weevil damage levels were severe, than those planted in 2018 (Figure 9A). This trend was also visible when looking at damage to just the bottom of the stem: again, comparable damage levels resulted in lower survival amongst seedlings planted in 2018 than those planted in 2019 (Figure 9B). However, when looking at the top of the stem, seedlings planted in 2019 maintained high survival despite significant pine weevil damage, until very high damage levels were reached (Figure 9C). This trend was not observed in seedlings planted in 2018 where greater pine weevil damage at the top was associated with lower survival rates.

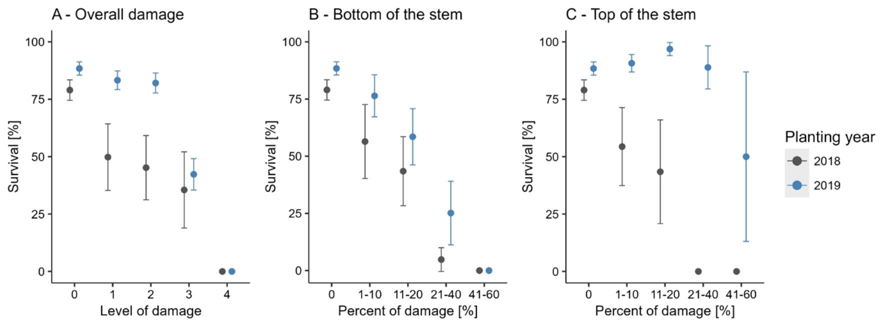

Figure 9. Mean survival of seedlings after two growing seasons in relation to recorded pine weevil damage after one growing season. Figure 9A shows survival at different levels of damage to the whole seedling (0 – no damage, 1 – slight damage, 2 – damage will probably affect growth, 3 – severe damage will affect growth, 4 – lethal damage). Figures 9B and 9C show damage to just the bottom or top of the stem, respectively, expressed in percentage classes representing the proportion of debarked stem. All seedlings with more than 60% damage died. The error bars represent standard errors.

Various factors affecting seedling mortality were recorded in the field, and varied between growing seasons and planting years (Figure 10). The most significant difference was in the first growing season, which was a drought period for seedlings planted in 2018. Some damage factors, such as feeding by pine weevils, are easily identifiable in the field. However, drought damage is much harder to detect as it lacks any specific signs. Since other obvious causes were not observed, it is likely that the difference in mortality observed between the two planting years can be explained by the drought in 2018.

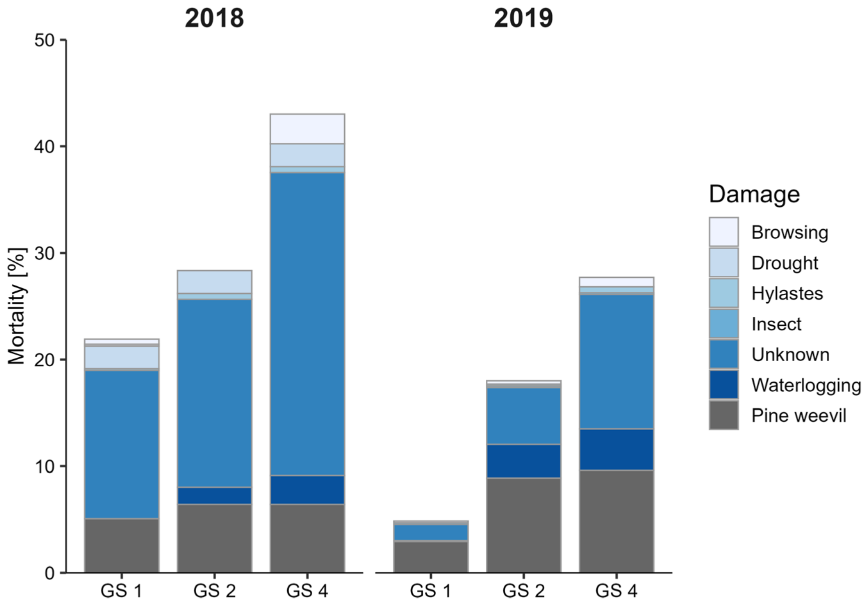

Figure 10. Sources of mortality of all seedlings irrespective of treatment and damage level. The damage bars are cumulative over the growing seasons, showing total damage. Browsing refers to browsing damage by ungulates and insect damage refers to damage by insects other than pine weevil or *Hylastes sp.* GS indicates the growing season after which the survey was performed.

Seedling height did not vary between treatments or planting years, and comparison with the untreated control suggests that neither mechanical protection nor insecticide had any significant effect on it.

3.2 Paper II

Following two growing seasons in the field, the nursery seedlings fertilised with arginine-phosphate exhibited significantly higher survival, 85% compared to 81%, irrespective of site and planting position (Figure 11A,

Table 6). The effect of planting position on seedling survival exhibited an interaction with site, i.e., the positive effect of planting into capped mounds varied between sites (Table 6). Variation in survival between sites was higher for CM than for MS, but this turned out to be highly dependent on precipitation in the first 30 days after planting. Survival of seedlings on CM was significantly higher with more precipitation (Figure 11C), while the opposite was true for seedlings planted in MS (Figure 11B). The latter relationship was weaker, but still significant and explains 25% of the variation in survival, compared to 52% for seedlings planted on CM. In addition, at sites with little precipitation, the differences between survival on CM and in MS were higher, highlighting the greater drought resilience when planting in MS.

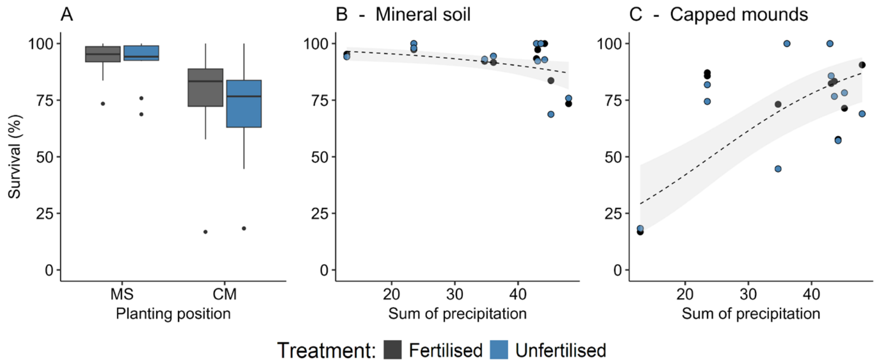

Figure 11. The effect of planting into mineral soil (MS) and capped mounds (CM) on survival (A) of fertilised (AP) and unfertilised nursery seedlings after two growing seasons. The effect of sum of precipitation [mm/m^2] in the first 30 days after planting on survival of seedlings planted into mineral soil (B) and capped mounds (C). The dashed lines represent the predicted curves from logistic regression models for each of the two planting positions. The shaded areas represent the 95% confidence interval for each model. Points indicate mean values for sites with the same precipitation. Grey lines and points denote fertilised seedlings, while blue ones denote unfertilised seedlings.

Table 6. Results from ANOVA analysis of the effects of site, fertilisation treatment (AP), planting position following MSP and the significant interactions between these variables on seedling survival following two growing seasons in the field. Significant effects ($p<0.05$) are highlighted in bold.

	LR Chisq	Df	Pr(>Chisq)
Site	114.17	10	**<0.001**
Treatment	5.01	1	**0.03**
Position	0.00	1	0.99
Site x Position	173.72	10	**<0.001**

Fertilisation had a positive effect on seedling growth, which was larger for MS than CM (Figure 12A, Table 7). In addition, the effect of fertilisation increased with the length of growing season, particularly for the seedlings planted in MS (Figure 12B & 12C).

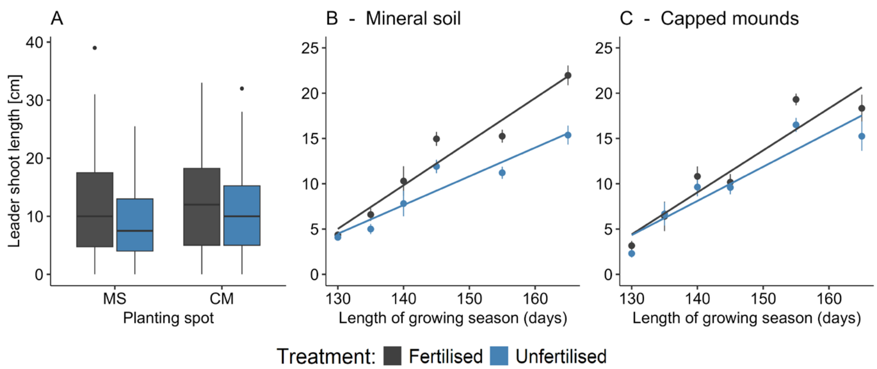

Figure 12. The effect of planting into mineral soil (MS) and capped mounds (CM) on length of leader shoot (A) of fertilised (AP) and unfertilised nursery seedlings after two growing seasons. Linear relationships between leader shoot length and length of growing season (days) for fertilised and unfertilised seedlings planted into mineral soil (B) and capped mounds (C). Points indicate mean values for sites with the same length of growing season and bars indicate standard error. Grey lines and points denote fertilised seedlings, while blue ones denote unfertilised seedlings.

Table 7. Results from ANOVA analysis of the effects of site, fertilisation treatment (AP), planting position following MSP and the significant interactions between these variables on the leader shoot length of seedlings following two growing seasons in the field. Significant effects ($p<0.05$) are highlighted in bold.

	Sum Sq	**Df**	**F value**	**Pr (>F)**
(Intercept)	71407	1	3843.73	**<0.001**
Site	20409	10	109.86	**<0.001**
Treatment	647	1	34.83	**<0.001**
Position	72	1	3.90	**0.049**
Site x Treatment	499	10	2.69	**0.003**
Site x Position	2114	10	11.38	**<0.001**
Treatment x Position	84	1	4.51	**0.034**
Site x Treatment x Position	84	10	0.45	0.919
Residuals	14955	805		

The survival of seedlings planted in positions without MSP was, on average, 58%. There was no significant effect of fertiliser on survival in this planting position (Paper II, Table 4). Instead, there was a negative relationship between survival and length of growing season, i.e., higher seedling survival in areas with shorter growing seasons. Site index was the most important variable explaining growth, with increased growth at higher site index values (Paper II, Figure 5D). A positive fertiliser effect on seedling growth was also found, which was more pronounced on sites with a higher site index, p=0.015 (Paper II, Figure 5D).

3.3 Paper III

Two years after deployment, an average of 54% of the fertilised SeedPADs (SPs) and 58% of the unfertilised SPs had grown into established seedlings (Table 8). Notably, some seedlings established between the first and second year after SP deployment, meaning that survival increased between the two survey years. There was no significant difference in seedling establishment and survival between fertilised and unfertilised SPs in any of the years (Table 9). However, the site had a significant effect on seedling survival in both years, ranging from 87% at Varpsjövägen to 22% at Bäckmyran (Table 9).

Assessing the growth of seedlings across the 12 sites, the addition of fertiliser did not have a significant overall effect on seedling height, biomass, or root-to-shoot ratio (Tables 8 and 9). However, these growth variables varied significantly between the different sites.

Table 8. Mean survival, height and biomass of seedlings established from the SeedPADs. SPs were either fertilised with AP or unfertilised. Surveys were performed in August–September 2018 and 2019. Estimated marginal mean values ± SE.

	Years after deployment	**SeedPAD unfertilised**	**SeedPAD fertilised**
Survival (%)	1	53.4 ± 4.4	46.7 ± 4.9
Survival (%)	2	57.8 ± 4.3	53.7 ± 4.7
Height [cm]	1	6.5 ± 0.3	6.8 ± 0.3
Height [cm]	2	14.6 ± 0.9	14.6 ± 0.9
Total biomass [g]	2	6.5 ± 0.9	5.6. ± 0.9
Shoot biomass [g]	2	5.6 ± 0.8	4.9 ± 0.8
Root biomass [g]	2	0.9 ± 0.1	0.8 ± 0.1
Root: shoot ratio	2	0.2	0.2

Table 9. Results (F- and p-values) from model II ANOVA examining the effect of fertilisation treatment with arginine phosphate, site and their interaction on SeedPAD establishment rate, height, and biomass. Significant effects ($p < 0.05$) are highlighted in bold.

	Years after deployment	Treatment	Site	Interaction
Survival	1	F(1,46)=2.085, p=0.16	F(9,46)=4.505, **p = 0.001**	F(9,46) = 0.823, p = 0.60
Survival	2	F(1,51)=0.089, p=0.77	F(9,51) = 4.155, **p < 0.001**	F(9,51) = 1.169, p = 0.33
Height	1	F(1,9)=0.295, p=0.59	F(9,9) = 13.570, **p < 0.001**	NA
Height	2	F(1,9)=0.0001, p=0.99	F(9,9) = 8.470, **p = 0.002**	NA
Total biomass	2	F(1,9)=0.429, p=0.52	F(11,9) = 36.578, **p < 0.001**	NA
Shoot biomass	2	F(1, 9)=0.405, p=0.54	F(11, 9) = 37.368, **p < 0.001**	NA
Root biomass	2	F(1, 9)=0.574, p=0.46	F(11, 9) = 31.621, **p < 0.001**	NA

Using linear regression modelling of environmental factors collected for all sites, two weather conditions were found to have a significant effect on the survival of SPs. Maximum wind speed and maximum precipitation in the first six weeks after deployment both had a significant effect on the rate of seedling survival. High wind speed decreased survival by 9% and 6%, for fertilised and unfertilised SPs, per additional m/s (Figure 13A). On the other hand, precipitation increased survival of both SP treatments by 11% per additional 10 mm of precipitation (Figure 13B).

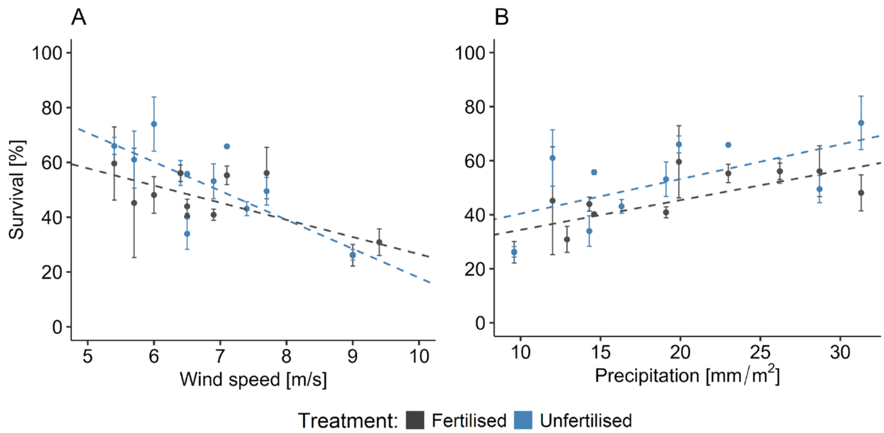

Figure 13. Effect of maximum wind speed (A) and maximum precipitation in a single day (B) within six weeks of SeedPAD (SP) deployment at 12 clearcut forest sites in early summer 2017 on survival of seedlings from unfertilised and fertilised SPs in late summer 2018. The lines represent predicted relationships between the environmental variables and SP survival, as estimated by the linear model. Points indicate mean values for sites with the same precipitation or wind speed and bars indicate standard error. Grey lines and points denote fertilised SPs, while blue ones denote unfertilised SPs.

The results of laboratory testing of SPs indicated that the availability of sufficient moisture plays a key role in proper attachment. Two clear trends can be seen in Figure 14: increasing the speed of water addition reduces the water requirement overall, as does smaller soil grain size. On average, SPs on coarse-grained soil required 34% more water than on fine grained soil. Similarly, the increase in water requirement needed for dissolution between slow and fast water addition within a soil texture type was c. 30%.

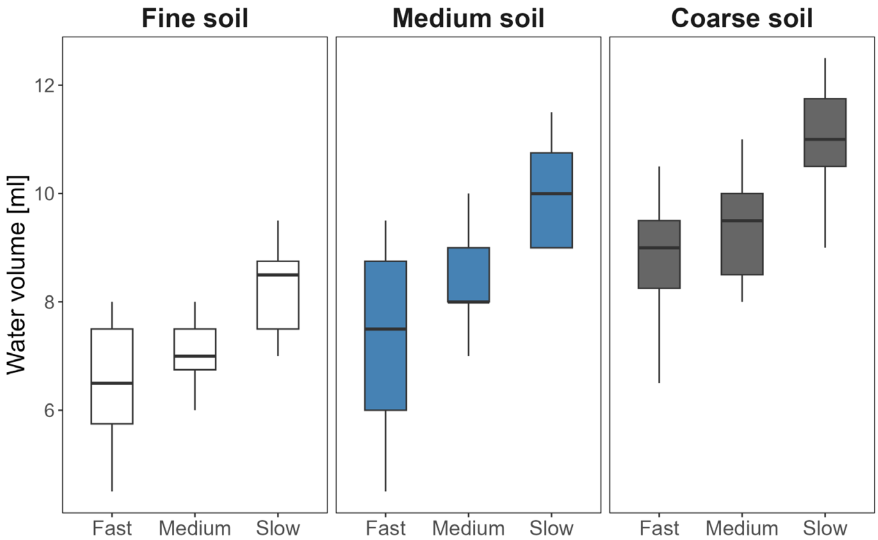

Figure 14. Water volume required for dissolution of SeedPADs (SP), compared across three different soil textures and speeds of water addition. For soil treatments, grain sizes were set to 1.7, 5.6 and 10.0 mm diameter for fine, medium, and coarse soil respectively. For speed of water addition treatments, SPs had water dripped onto them every 1.5, 3, and 5 min for fast, medium, and slow treatments respectively.

3.4 Paper IV

Seedfall differed across stands, overstory density treatments, and years (Figure 15). In 2020, seedfall at H17 (four years post-harvest) was significantly greater than at H20 (one year post-harvest; p-value < 0.001). Similarly, in 2023, seedfall at H20 (four years post-harvest) was significantly higher than at H23 (one year post-harvest; p-value = 0.029).

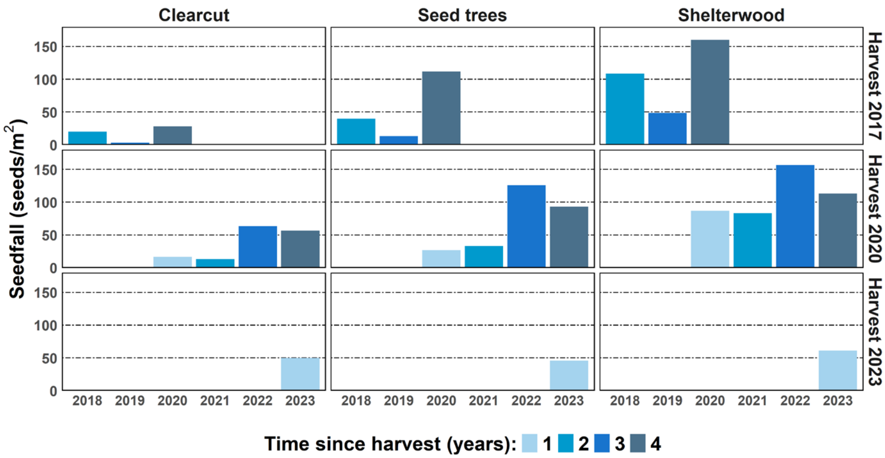

Figure 15. Seedfall (seeds/m^2) during years 2018-2023. The upper, middle and lower rows represent data from stands harvested in 2017, 2020 and 2023, respectively. Due to a sampling error, seedfall of 2017 was not collected.

Mechanical site preparation (MSP) had a strong positive impact on seedling recruitment in the first year following overstory harvest (p-value < 0.0001). Due to the strong effect and lack of seedlings in plots without MSP, recruitment results presented below are only for MSP plots.

In the first year after overstory harvest, seedling recruitment across all three stands was significantly higher under shelterwood treatment (p = 0.039) compared to clearcut areas (Figures 16 and 17). There was also a trend toward higher recruitment under seed trees (p = 0.069) compared to clearcuts. However, three years after overstory harvest at H17 and H20, there was no significant difference in recruitment under seed trees (p-value =

0.364) compared to clearcuts, though a trend was observed for shelterwood treatment (p-value = 0.070). Third-year cohort recruitment was significantly higher under shelterwoods at both H17 and H20 compared to clearcuts ($p = 0.032$) (Figure 16). In comparison, seed trees showed only a trend towards higher recruitment ($p = 0.051$).

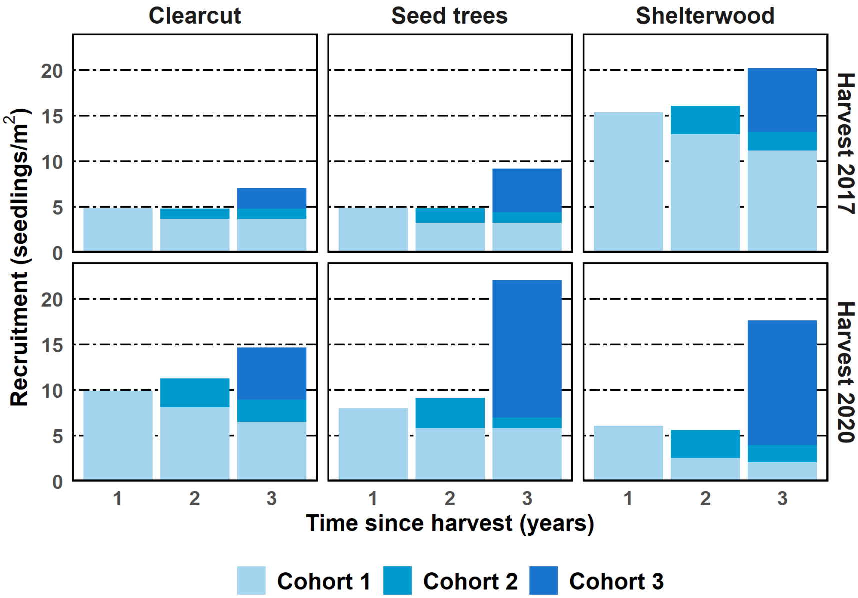

Figure 16. Recruitment of seedlings (per m^2) in MSP plots. The upper and lower rows represent data from stands harvested in 2017 and 2020 (H17 & H20), respectively.

Immediate and delayed MSP were compared using 2020 and 2023 as paired years (H17 delayed with H20 immediate, and H20 delayed with H23 immediate). Three years after overstory harvest, delayed MSP had a significant positive impact on seedling recruitment under shelterwoods in 2020 ($p = 0.005$) compared to immediate MSP. However, this trend was not statistically significant under seed trees in 2020 ($p = 0.332$) or for any of the treatments in 2023 (Figure 17).

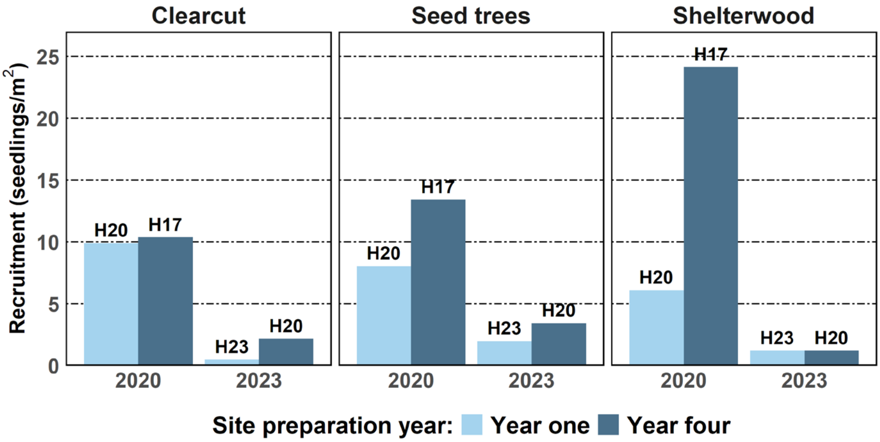

Figure 17. Recruitment of seedlings (per m^2) after immediate and delayed mechanical site preparation for clearcut, seed tree and shelterwood treatments. Years 2020 and 2023 were used as pair years (H17 delayed with H20 immediate and H20 delayed with H23 immediate). Immediate MSP was done in connection with the harvest and delayed MSP was done before the start of the growing season on the fourth year after harvest.

4. Discussion

Forest management in Sweden, with its long history, increasingly faces challenges from the rapidly changing climate. Although climate models predict the general direction of changes in the climate (Lind *et al.* 2023), reliable applications at a local level are not yet possible. This uncertainty challenges traditional forest management, which has largely been carried out in a similar way for many decades and assumes that planted seedlings will reliably grow into high quality forests. Instead, increasingly variable growing conditions may result in regeneration failing, as approaches that worked in the past may now be ill-suited for current and future conditions. Complexity and scale of extreme events, such as the 2018 drought (Schuldt *et al.* 2020; Haberstroh *et al.* 2022), further complicates the adoption of any measures in operational forest management. What is more, current challenges may be exacerbated while new ones emerge, meaning that no single solution is likely to work long-term and on all sites. Instead, we need to adapt our regeneration methods to ensure that seedlings can withstand a variety of conditions, regardless of the future climate.

When discussing adaptations to climate change, it is crucial to also consider the desired outcome (Millar *et al.* 2007; Nagel *et al.* 2017). What is the goal of adaptation and what are we adapting to? While climate adaptation is a wide and complex topic (Spittlehouse & Stewart 2003; Felton *et al.* 2024b), this thesis follows the definitions established by Millar *et al.* 2007 and further developed by Adaptive Silviculture for Climate Change (ASCC) (Nagel *et al.* 2017). This framework categorises adaptation measures into resistance, resilience and transition and aligns them to the scale of change (Figure 18).

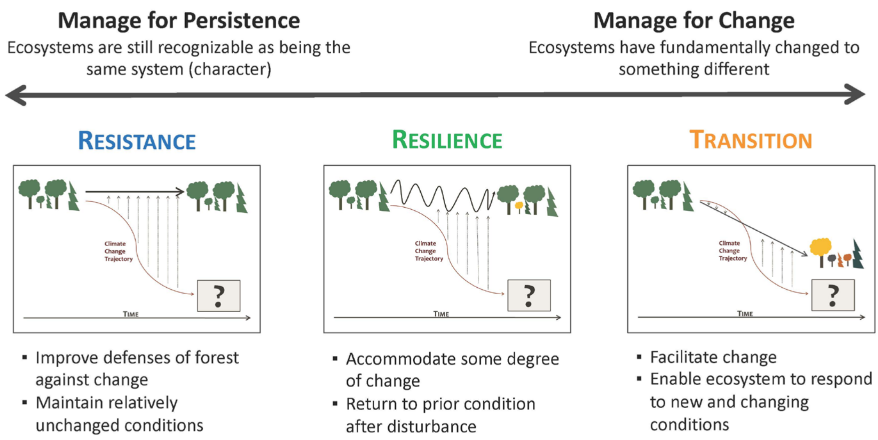

Figure 18. Climate change adaptation flowchart developed by Adaptive Silviculture for Climate Change (ASCC) (Nagel *et al.* 2017) following Millar *et al.* 2007.

Within this framework, resistance adaptation strives to resist the disturbance, aiming to maintain current conditions (Millar *et al.* 2007). While this response requires little initial change, increasingly intense interventions may be required over time to maintain resistance. As growing conditions change, the resistance response may eventually fail altogether. However, in the short term, resistance management can improve seedling response to some environmental stressors such as insects and diseases, thus contributing to better defence overall.

Another option is to manage for resilience, meaning that seedlings have the capacity to withstand the disturbance, and return to their prior condition afterwards (Millar *et al.* 2007). Resilience management has broader applications than resistance management, allowing seedlings to respond to a wider range of conditions as needed. An example of this is site adaptation practices in which the regeneration method and site preparation promote good establishment and growth. Seedlings thus well-established can better adapt to factors like drought by increasing root growth and can return to prior conditions after the drought period has ended. By enhancing seedlings' ability to adapt to and recover from a range of disturbances, resilience management contributes to their long-term survival and growth even while climatic conditions change.

Adaptation through transition is another alternative, in which forest regeneration is managed towards achieving a new state that may be better aligned with future conditions (Millar *et al.* 2007). This approach involves enabling forests to naturally adapt to changing environmental conditions rather than resisting these changes. While forests have historically undergone several transitions, the rapid pace of climate change challenges their natural ability to respond. To assist and accelerate this process, strategies such as assisted species migration (Palmer & Larson 2014), introducing new species (Meason & Mason 2014), enhancing genetic diversity (Schaberg *et al.* 2008), breeding species for resistance (Zas *et al.* 2017) and adjusting harvest management can be used. The regeneration stage in particular provides an ideal opportunity to shape the forest of the future by shifting species composition and management practices. These practices can facilitate a smooth transition to a new state, ensuring forests are better adapted to future conditions.

4.1 Adaptation to pine weevil damage

Seedlings in field conditions often face multiple stressors from different sources (Bansal *et al.* 2013). They resist these stressors until the combined pressure becomes too great, leading to mortality. An example of this is pine weevil damage, which may reduce seedlings' ability to transpire and take up nutrients, while also reducing their vitality and predisposing the seedlings to other sources of damage. In this regard, analysis in Paper I revealed a synergistic effect between pine weevil damage and drought, for seedlings planted during a drought year. However, when pine weevil damage was the primary cause of mortality, the mechanical protections tested in Paper I performed equally as well as insecticides, and better than the untreated control. The lack of any difference in growth between protected and unprotected seedlings suggests that the coatings did not restrict seedling growth, as has previously been suggested (Sjöström 2020). This demonstrates their potential as tools for forest management and effective replacement for banned insecticides.

Still, such interactions between drought and other damage factors are becoming increasingly important and are linked to the rapid pace of climate change. Climate patterns are predicted to be increasingly variable and it is likely that the primary damage factors will vary over time, with drought being important one year but not the next. In contrast, pine weevils are a stable factor, and although their activity may vary, they are a consistent source of damage (Örlander *et al.* 1997). Prioritising resistance management against pine weevils would not only protect seedlings from direct damage but may also enhance their overall response to other stressors, such as drought, when that does occur.

Further, temperature changes due to climate change are likely to expand the range of pine weevils (Nordlander *et al.* 2017), but their activity levels in already-affected areas may not increase. This remains unclear, as we lack evidence on how multiple climate change scenarios might influence pine weevil behaviour. Previous studies indicate that pine weevils are limited by high temperatures (above 30 °C) (Christiansen & Bakke 1968, 1971), but temperatures vary significantly in the landscape, making such predictions hard to apply to practical management. Despite these uncertainties, it is likely that pine weevils will expand northwards (Nordlander *et al.* 2017), suggesting that mechanical protection methods against pine weevil and planting in MS should be considered in northern Sweden as well. Although implementing these methods will significantly increase the cost of regeneration, this issue should be approached from the perspective of the whole regeneration cycle. Investing more at the regeneration stage can lead to fewer problems later on, as early establishment issues tend to persist in the years following regeneration (Wallertz *et al.* 2014).

In the future, as growing conditions change, current pine weevil protection methods might fail altogether as the combined stresses from numerous factors become too great. Resistance to various single stress factors should be considered a short-term solution as, ultimately, we cannot protect seedlings against all individual sources of stress. In this scenario, ever-increasing interventions against pine weevil damage may be needed to ensure high seedling survival. Ultimately, transition adaptation could be considered regarding pine weevil damage. Pine weevils are attracted to freshly cut stumps found on clearcuts, where they lay their eggs and start a new life cycle (Christiansen & Bakke 1968). Adopting continuous cover management that avoids clearcuts, such as shelterwoods or seed tree systems, could reduce the presence of fresh stumps and thus attractiveness to pine weevils (Nordlander *et al.* 2003; Wallertz *et al.* 2005). Further, pine weevils target seedlings but not seeds. Seedlings that grow in field conditions from seeds may be too small to be attacked during the period of high pine weevil presence. While other factors such as the suitability of a site for this type of management should be considered, this approach represents a transition to a new system that could help mitigate pine weevil damage.

Unfortunately, current abundance of pine weevils and their ability to spread across landscapes makes such a transition difficult (Örlander *et al.* 1997). Unless a substantial portion of the forest is managed without clear-cutting, it is unlikely that we will see a significant reduction in pine weevil populations or damage to seedlings. Moreover, this transition could only be adopted gradually over long periods of time, as forest management plans cannot change overnight. Given the rapid pace of climate change, it may be a long-term goal rather than an immediate solution.

4.2 Adaptation to moisture stress

Predicting local drought conditions is challenging, especially in operational forestry and during the establishment of experiments. Preparations for harvest or planting often occur well ahead of time, before the onset of the growing conditions that will ultimately influence establishment. Therefore, the primary objective of the four studies included in this thesis was to investigate various aspects of forest regeneration rather than evaluate seedling performance under drought conditions. However, all four studies coincidentally included the growing season of 2018, a summer marked by extreme drought in Sweden (Hayatgheibi *et al.* 2021; Wolf *et al.* 2023). This situation provided an additional opportunity to examine the effects of drought on nursery seedlings after planting, direct seeding, and natural regeneration, which are the main methods of regeneration used in Swedish forestry today.

In particular, the studies in Paper I and IV allow for investigation into the effect of drought on seedlings because they include a replicate in time. Although these replicates were conducted on different sites due to the specifics of each study, the widespread nature of the drought means that performance can nonetheless be compared. In the study detailed in Paper I, there is clear evidence that drought was the main damage factor in 2018. In the following non-drought year of 2019, pine weevils were the main cause of damage. It is important to note that the seedlings used in Paper I were Norway spruce, whereas the studies in all the other papers used Scots pine. Given that Norway spruce is more sensitive to drought conditions, the seedlings in Paper I were probably more strongly affected by drought, than they would have been if they were Scots pine. Nevertheless, in Paper II we do see significant mortality in Scots pine nursery seedlings planted in 2018.

Paper IV focused on the recruitment of naturally regenerated seedlings in shelterwoods, which is significantly different to planting nursery seedlings on clearcuts. Nonetheless, through replicates in time we see variation in environmental conditions over the study period at all three sites (2017-2023). Two years stand out as drought years: 2018 and to a lesser degree 2023. During these years, reasonable seedfall did not lead to seedling recruitment, probably due to unfavourable establishment conditions. In 2019, recruitment was notably higher despite minimal seedfall. This suggests that seeds from 2018 overwintered and established under conditions that were more favourable. Such delayed establishment could represent a resilience response to drought, in which seeds germinate and establish when environmental conditions become more favourable (Castro *et al.* 2005). This resilience mechanism highlights natural adaptation to drought that has evolved over the species' existence. However, the rapid pace of climate change challenges any species' ability to adapt fast enough. Ultimately, we may see a northward shift of the southern growth limit of Scots pine (Haberstroh *et al.* 2022) but, for now, additional measures for resilience adaptation, such as MSP in shelterwood systems, can help to secure soil water availability.

The benefits of such MSP treatments were evident in Papers II and IV, both of which included non-MSP spots for planted and naturally regenerated seedlings, respectively. In these non-MSP spots, establishment rates were significantly lower as well as growth of nursery seedlings. In Paper IV, MSP served as an important tool for removing competition for space and soil moisture, which would otherwise hinder the establishment of seedlings in shelterwood systems (Castro *et al.* 2005). It may well be that the differences between stands stem from the quality of MSP. Stands H20 and H23 had rockier terrain that may have influenced the quality of MSP, leading to less exposed mineral soil and reduced recruitment in higher overstory densities.

Focusing on types of MSP, the survival of nursery seedlings in Paper II suggests that while seedlings planted on CM are more sensitive to drought, those planted in MS may suffer from high precipitation. However, the negative effect associated with MS explained less of the variation in survival than the positive effect did for CM. This suggests that the negative trend in MS might be better explained by other variables, such as increased frost damage and oxygen deficiency for seedlings planted too deep in the MS position. Nonetheless, the largest difference in survival between the two planting positions was observed on sites with lower precipitation during the initial establishment period. Together with higher survival in MS than CM, this suggests that drought was the most important mortality factor for nursery seedlings in Paper II.

Currently, general planting guidelines in Sweden recommend planting in CM, except in the southern regions (Hallsby 2013; Skogsstyrelsen 2024b). A recent nationwide study by Skogforsk (Forestry Institute of Sweden) found that approximately 55% of seedlings in northern and 40% in central Sweden were planted in CM (Berglund *et al.* 2024). However, given the variability of both this planting spot and future weather conditions, the widespread application of this recommendation may need to be reconsidered. Instead, varied precipitation patterns expected in the future suggest relying solely on rainfall to maintain adequate soil moisture levels may prove insufficient (Nikulin *et al.* 2011; Chen *et al.* 2015). Therefore, the focus should shift towards securing water availability in the ground. In this context, site adaptation of MSP methods could be employed as a resilience strategy to address variable soil moisture conditions, particularly during the early growth phase. Under such management, good initial establishment provides seedlings with a better chance to survive periods of moisture stress and recover after the disturbance has ended.

Similarly to planted seedlings, the variation in survival of coated seeds (SP) in Paper III was largely explained by site-specific factors tied to soil moisture, namely precipitation and wind speed. This indicates that SPs benefit from a heavy precipitation event in the first six weeks after deployment, as seen by the significant positive relationship between maximum precipitation and survival. While the importance of precipitation early in the establishment of nursery seedlings has previously been reported (Burdett *et al.* 1984; Burdett 1990; Grossnickle 2012), proper attachment to the ground is a first step that is unique to the SP. The results indicate that precipitation may have enhanced attachment and, in turn, survival of the emerging seedling, which requires good contact between roots and available soil water early in the growth process (Burdett *et al.* 1984; Grossnickle 2005, 2012). Although the polysaccharide layer was designed to readily dissolve in contact with water and facilitate attachment, local precipitation conditions may have been insufficient for all SPs to attach properly. This is supported by the results of the controlled dissolution experiment, in which up to 12 ml of water was required for an SP to attach properly on coarse soil. SPs not properly attached may stay slightly suspended above the ground and thus lack a direct connection with the soil water. In addition, maximum wind speed had a significant negative effect on the survival of SPs, suggesting a risk of SPs being mechanically removed and/or desiccation of the growing environment for the emerging seedling.

Planting of nursery seedlings currently dominates forest regeneration landscape in Sweden, and considerable efforts are made towards improving seedling production (Wennström *et al.* 2016; Riikonen & Luoranen 2019; Moler *et al.* 2022). While resistance breeding and introduction of new species can serve as a transition adaptation of the current system, there are other possibilities to consider. Variable environmental conditions in the landscape suggest that planting of nursery seedlings may not be suitable for every site, particularly in the variable future. Similar to planting positions, adapting the choice of regeneration method to the needs of the area may produce seedlings more adapted to their local environment. In this regard and in the context of future challenges to forest regeneration, direct seeding and natural regeneration may offer benefits that have previously been overlooked. Unfavourable growing conditions at the time of planting can have severe consequences for nursery seedlings which must be planted soon after leaving the nursery (Hallsby 2013; Mataruga *et al.* 2023). In this respect, seeds are much better suited to wait and establish under more favourable conditions. Another point to consider is the resilience adaptation of seedlings established from seeds versus nursery seedlings. Studies show that, while nursery seedlings may have high root biomass, naturally-established seedlings have a much wider root distribution (Burdett *et al.* 1984; Burdett 1990). Similarly, Örlander 1984 demonstrated higher water potential in Scots pine seedlings established in situ when compared with nursery seedlings for up to four years after planting. During periods of drought, an extensive root system that ensures high water potential can translate into higher survival and growth rates (Grossnickle 2005). Additionally, in conifers, most water loss occurs through transpiration via the needles (Grier & Running 1977). Planted seedlings develop considerable needle foliage in nurseries by the time they are planted, which facilitates quick biomass acquisition through photosynthesis. However, in dry conditions their root systems may struggle to support the aboveground biomass (Grossnickle 2005, 2012). In comparison, the lower needle surface area of naturally established seedlings may result in lower moisture loss. Under drought conditions, such balancing of moisture acquisition through roots, while minimising loses through shoots, may play an important role.

4.3 Adaptation to nutrient availability

The addition of arginine-phosphate (AP) fertiliser to the seed coating had no significant effect on the survival or growth of seedlings emerging from SPs following two years in the field (Paper III). This finding contrasts with a study by Castro *et al.* 2021, performed at one of the sites also included in Paper III (Svanatjarn), who found a 50% increase in survival rate of SPs after one growing season as a result of adding nitrogen fertiliser, either as AP or as mineral ammonium nitrate. However, at this particular site, the addition of AP also increased survival of the SPs included in Paper III by 14% after two growing seasons. The apparent site dependency of the AP effect on seedlings from SPs highlights the interaction between fertilising and other environmental variables. Also, while nutrient availability is important for seedling growth, it may not be as important for early germination, when moisture acquisition is probably more critical. In contrast, for the nursery seedlings included in Paper II, AP addition had a positive effect on survival irrespective of site and planting position.

For seedlings in Paper II, the AP enhanced growth (measured as leader shoot length) was 13% for seedlings positioned on capped mounds (CM) and 29% for those in mineral soil (MS). While the positive effect of AP addition on seedling growth has been shown before (Lim *et al.* 2021; Häggström *et al.* 2023; Luoranen *et al.* 2024), the positive effect of AP on survival of Scots pine seedlings has rarely been reported. This may be because most studies on AP fertilisation do not focus on survival, but on its positive effects through enhancing root growth and increasing mycorrhizal infection of roots. For instance, Gruffman et al. 2012 reported that adding AP had positive effects on the growth of Scots pine seedlings at three sites in northern Sweden but no significant additional impact on their survival over using commercial inorganic fertiliser.

In the study presented in Paper II, the increased survival of nursery seedlings was indeed probably linked to the positive effect of AP fertiliser on root growth and mycorrhizal colonisation (Castro *et al.* 2021; Lim *et al.* 2021). Both have been shown to increase seedlings' water uptake capacity, a crucial factor in their early-stage development (Burdett 1990). In this case, it may be that AP increased the early growth of roots and thus helped nursery seedlings survive the immediate summer drought of 2018. In comparison, SPs (Paper III) experienced drought conditions during the second year after deployment, making it harder to see the effect of drought on survival. In addition, it seems possible that any AP-facilitated survival benefits of SPs may be subordinate to proper attachment.

Considering the context of variable precipitation, fertilisation of nursery seedlings could serve as a resilience adaptation against drought conditions in the future. If drought does occur, AP-facilitated root growth would boost moisture acquisition, helping seedlings to establish and survive (Castro *et al.* 2021; Häggström *et al.* 2023). Meanwhile, in years with growing conditions closer to the average, the fertiliser is easy to apply at nursery or planting stage. While this would increase the overall cost of regeneration, it may be offset by otherwise required additional planting interventions when disturbances occur. However, while fertilisation offers potential, there are several factors to consider in practical application. First, the variation in nutrient requirements between sites, as highlighted by the site dependency illustrated in Paper III. Adapting the selection of nutrients supplied to the plants to their physiological needs is essential to maximising the effectiveness of such adaptations. Second, the timing of fertiliser application is crucial. If applied at the time of planting, fertilisers might promote root growth, improving seedlings' resilience to drought. However, if planting coincides with drought conditions, some fertilisers might exacerbate seedlings' stress by increasing soil salinity (Jacobs & Timmer 2005), potentially leading to root mortality (Jacobs *et al.* 2004). Therefore, finding a balance is essential to avoid the negative impacts of fertilisation under such conditions.

Still, adding fertiliser to ameliorate difficult growing conditions is not an adaptation exclusive to seedlings of established species. Instead, it could also be used in connection with new species that are part of the transition process. Establishment and early growth are commonly times when seedlings are particularly vulnerable (Normark & Sjölin 2015; Nilsson *et al.* 2019; Sukhbaatar *et al.* 2020), which makes it a critical phase in a regeneration process of any species. With the above discussed limitations in mind, fertilisation could still serve as an additional measure during transition adaptation, when adapted to species, sites and environmental conditions.

4.4 Climate-adapted forest regeneration

Regeneration is at a core of any dynamic, thriving forest, but especially one that faces increasing challenges. Through careful forest management, we can ensure that forests remain an integral part of the landscape also in the future. However, the lessons of the past should not be applied in the present without considering the complexities of climate change (Millar *et al.* 2007; Lindner *et al.* 2010, 2014; Bernal *et al.* 2012). Moreover, the scale of any proposed management is crucial. While individual forest stands can be preserved with substantial investment, climate change affects the entire landscape, requiring a large-scale response. Given this, our approach to these challenges should be holistic. The regeneration cycle is a continuous process, not a series of stages, and requires a long-term perspective: investing more at certain stages can provide greater benefits in the long run. In this regard, good initial establishment is a key component in survival and growth, as demonstrated by studies in Papers II and III.

In climate-adapted forest regeneration, RRT framework (resistance, resilience, transition) (Nagel *et al.* 2017) can serve as a guide to adaptation in an increasingly complex system. While it may sometimes be hard to clearly define each approach in a specific case, due to the multitude of disturbances, this framework still provides valuable guidelines for forest management. Moreover, while the different approaches within RRT may seem mutually exclusive, they can be used alongside each other. Site-specific adaptation is key, where relevant issues are identified and appropriate approaches selected. Ideally, regeneration methods should use resistance management to address current damage, while incorporating resilience or transition management for the long-term perspective. Examples of this would be mechanical protections against pine weevils on fertilised seedlings bred for drier conditions or on seedlings of new species. By employing multiple approaches simultaneously, we can better account for the unpredictability and variability of future conditions. At the same time, there will be situations where not all damage sources can be addressed. In those cases, it is important to address the most significant stressor, as this could improve the response to other sources of stress.

Climate-adapted forest regeneration also consists of ever expanding toolbox of management approaches that try to tackle one or several challenges to forest regeneration. Ideally, site adaptation is the first step in choosing appropriate management, followed by flexible and agile implementation. An example of this approach are coated seeds (SP) used in Paper III. With an average survival rate of c. 56%, it is clear that SP seeds can successfully germinate and develop into vital seedlings under field conditions. Covering seeds with a protective vermiculate layer can minimise the variations in temperature and moisture found on the surface of mineral soil. They however suffer from problems with initial attachment that can be counteracted by watering them. A possible solution for small-scale private forest owners, who may be more flexible in their operations than forestry companies, is to perform SP deployment right before a large, forecasted precipitation event. Such adaptable, short notice operations may be feasible because SPs are easier to handle, transport, and store than nursery seedlings. Seeds within the pads remain dormant until they are exposed to sufficient water, thus it is possible to exert greater control over the start of germination. This storability of SPs could also decrease waste in planting operations, which can occur if seedlings are not planted within a given time frame after leaving the nursery (Mataruga *et al.* 2023). For large planting operations however, the small and uniform form of SPs, coupled with the fact that they do not need to be dug in, creates the potential for large-scale mechanisation of their deployment. The volume of water required for watering each SP is small where such watering is targeted. This scalable approach could also have other advantages, such as mitigating the impact of future labour shortages and reducing silvicultural costs when deployed at scale.

5. Conclusions

Forest management in Sweden is rooted in traditional practices, but the variability of future climate conditions makes it clear that what has worked in the past may no longer be effective. The research outlined in this thesis emphasises the need for adaptive strategies in forest regeneration, particularly in the face of climate change. In this regard, the RRT (resistance, resilience, transition) framework offers a comprehensive approach to addressing these challenges. While resistance strategies may offer short-term solutions, particularly against specific threats like pine weevil damage, they are not sufficient on their own. Resilience and transition strategies are also crucial for ensuring that forest regeneration methods remain viable as the climate continues to change.

The studies conducted in this thesis also highlight the importance of initial establishment in ensuring the long-term survival and growth of conifer seedlings. Investments in this early stage, such as using mechanical site preparation, mechanical protections against pine weevils, and fertilisation, can yield significant benefits by enhancing seedlings' response to various stressors like drought and insect damage. However, these strategies must be tailored to specific site conditions and integrated within broader management goals to be fully effective.

Successful climate-adapted forest regeneration requires a holistic approach that balances short and long-term objectives. The integration of resistance, resilience, and transition strategies, adapted to local conditions, will be key to sustaining thriving forest in Sweden in the face of an uncertain climate future.

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Popular science summary

One of the most vulnerable periods in the lives of trees is their establishment as seedlings. In those first few years, trees can easily die due to a number of factors. Soil features, weather variables and pests are among the most important ones. While many studies have been done on this topic over the years, climate change is quickly diminishing our understanding of the system as well as the tools available. New solutions are therefore urgently needed to adapt forest regeneration to the changed environment of the future. With this goal in mind, the studies in this thesis tested several such adaptations: mechanical protections against pine weevil damage, changes in planting positions, the addition of organic fertiliser, the use of coated seeds, and natural regeneration. The overall goal of these solutions is to ensure good establishment of seedlings and therefore successful forest regeneration.

The results emphasise the need for diverse and flexible management in order to help forest regeneration adapt to the changing climate. This approach, based on resistance, resilience, and transition adaptation, aligns with broader climate adaptation strategies and provides guidance for Swedish forest regeneration in the future. Only by managing our forests in a way that they consistently grow back, can we preserve the carbon-sink role of forests and the many other values they provide.

Populärvetenskaplig sammanfattning

En av de mest sårbara perioderna i trädens liv är deras etablering som plantor. Under de första åren kan plantor lätt dö på grund av ett antal orsaker. Faktorer kopplade till markegenskaper, vädervariabler och skadedjur utgör de största hoten. Trots att många studier har gjorts inom detta ämne genom åren, minskar klimatförändringarna snabbt vår förståelse för hur systemet fungerar, såväl som våra tillgängliga verktyg. Nya lösningar behövs därför akut för att anpassa skogsföryngringarna till framtidens förändrade miljö och klimat. Med detta mål i åtanke undersökte studierna i denna avhandling flera sådana anpassningar: mekaniska skydd mot skador från snytbagge, förändringar i val av planteringspunkter, tillsats av organisk gödning, användning av belagda frön och naturlig föryngring. Det övergripande målet med dessa metoder är att säkerställa en god plantetablering och därmed säkerställa en lyckad föryngring.

Resultaten betonar behovet av mångsidig och flexibel skötsel för att hjälpa skogsföryngringarna att anpassa sig till det förändrade klimatet. Detta tillvägagångssätt, baserat på resistance, resilience och transition, ligger i linje med bredare klimatanpassningsstrategier och ger vägledning för svensk skogsföryngring i framtiden. Endast genom att sköta våra skogar på ett hållbart sätt och garantera deras återväxt kan vi säkerställa deras roll som kolsänka och bevara de många andra värden som skogen ger.

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Effect of drought and pine weevil damage on mechanically protected Norway spruce seedlings

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Picea abies

ABSTRACT

Pine weevils (*Hylobius abietis* L.) pose a significant threat to conifer seedlings by feeding on the bark, thus damaging or killing seedlings. Historically, insecticides were used to suppress such damage, but were slowly phased out in Sweden due to environmental and health concerns. This study aimed to assess field performance of an alternative protection method: mechanical coating applied to the stem of planted Norway spruce (*Picea abies*) seedlings. Field trials were conducted on 14 sites in south Sweden, using four different types of mechanical protection (Cambiguard, Conniflex, Ekovax, Hylonox), standard insecticide (Merit Forest), and ambient control. Seven sites were established in the drought year of 2018 and seven more in 2019. This allowed for additional investigation of the effect of drought on seedling establishment and possible interaction with pine weevil damage. Seedlings were surveyed for survival and height after the first, second and fourth growing season. Results show drought as the main source of damage for seedlings planted in 2018, with no significant effect of insecticide or mechanical protection on survival of seedlings. However, mechanical protections performed equally well as insecticide and positively increased survival by 30 %, compared to untreated, four growing seasons after planting for seedlings planted in 2019. Seedling height was not significantly affected by planting year or any of the treatments, suggesting no adverse effects of coating application. However, a synergistic effect between pine weevil damage and drought was observed, where even low levels of pine weevil damage resulted in high mortality for seedlings planted in 2018, compared to those planted in 2019. Additionally, for seedlings planted in 2019, damage to the top of the stem did not result in significant mortality, until high damage levels were reached (40 % and above). The opposite was found for seedlings planted in a 2018 drought year, where both damage to the top and the bottom of the stem followed a linear response. In conclusion, we show that investigated mechanical protection methods can be considered a viable replacement for insecticides, but our results also highlight the importance of considering multiple environmental stressors such as drought and pest damage on seedling establishment.

1. Introduction

Pine weevils (*Hylobius abietis* L.) are a considerable source of damage to conifer seedlings in large parts of Europe (Day and Leather, 1997). They feed on the bark, eventually girdling the seedling and preventing the transport of water, which may lead to mortality. The problem is widespread in southern Sweden (Örlander and Nilsson, 1999; von Sydow, 1997; Wallertz et al., 2016) and southern Norway (Holt Hanssen and Sundheim Fløistad, 2018) where mortality of up to 60 % has been reported for unprotected seedlings. Since around 440 million seedlings are planted in Sweden annually (Skogsstyrelsen, 2024), such losses represent a significant economic setback.

Pest damage to conifer seedlings, including that by pine weevils, has historically been suppressed using chemical insecticides (Giurca and von Stedingk, 2014). Over the past few decades however, insecticides have been largely banned for use in forestry due to negative effects both on natural environment and on work environment (Giurca and von Stedingk, 2014). Nevertheless, the problem of pine weevil damage remains, and novel methods of protection are urgently needed. In recent years, mechanical protection by coating the lower part of the seedlings' stem has emerged as an alternative to chemical solutions (Nordlander et al., 2011, 2009). However, there are still many unanswered questions to be

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resolved regarding the use of these alternatives. One consideration is that mechanical coatings would constrict the stem or cover the needles of the seedlings, thus limiting growth through reduced photosynthesis, which has been shown in a greenhouse experiment (Sjöström, 2020). Their persistence in field conditions is another factor, as pine weevil exhibit an established pattern of seasonal damage over a longer period of time. The majority of pine weevil damage to seedlings occurs in the first three years after clearcutting (von Sydow, 1997; Wallertz et al., 2016), and coatings would thus have to be long lasting, covering a period of several years.

Further, pine weevils, among other insects, are not the only factor affecting seedling survival and growth (Bergquist and Örlander, 1998; Grossnickle, 2012; Jobidon et al., 2003; Langvall et al., 2001; Wallertz et al., 2018). Environmental factors such as microclimate, planting spot and weather patterns play an important role in seedling establishment, which has been widely studied over the past decades (Grossnickle, 2012; Häggström et al., 2021; Holmström et al., 2019; Nilsson and Örlander, 1995; Nordin et al., 2023; Sikström et al., 2020; Wallertz et al., 2018). With a changing climate (Christensen et al., 2001; Christensen and Christensen, 2007; May, 2008), some parts of this collective knowledge should be reconsidered, as growing conditions may have changed from when many of these silvicultural concepts were first established. Several climate models predict a warmer climate with increasingly long and severe droughts in the future, especially summers, which will surely affect forests as well (Allen et al., 2010; Krikken et al., 2019; Lindner et al., 2010; Reich and Oleksyn, 2008). The consequences of these altered growing circumstances are still poorly understood, as are our tools to adapt to them. A recent case of such a drought year was the summer of 2018, which has been widely reported as having detrimental impact on seedling survival and growth (Beloiu Schwenke et al., 2023; Lindroth et al., 2021; Schuldt et al., 2020; Sturm et al., 2022).

In multi-damage scenarios, like seedling establishment on clearcuts, interaction between different damage factors should be considered. An example of a well-studied system is the effect of drought on spruce bark beetle (*Ips typographus*) damage to mature trees (Hart et al., 2017; Netherer et al., 2022, 2021, 2019; Williams et al., 2013). Research shows that spruce bark beetles actively select trees that have previously been drought stressed, leading to great outbreaks of insect damage following a drought (Hart et al., 2017; Netherer et al., 2019). The mechanism behind selection are the weaker tree defenses, such as reduced production of monoterpenes and resin, as drought puts an additional stress on trees (Kaiser et al., 2013; Netherer et al., 2022). Such multi damage responses have been less studied in pine weevils, with most studies utilizing an artificial or semi-artificial experimental setup (Lavallée et al., 1994; Rasheed et al., 2020; Selander and Immonen, 1992; Suárez-Vidal et al., 2019). For example, Selander & Immonen (1992) reported that pine weevils selected drought stressed seedlings when enclosed in cages for 20 hours. Similarly, Suarez-Vidal et al. (2019) reported 75 % higher pine weevil damage on moderately drought stressed seedlings when enclosed together for 4 days, compared to pine weevil damage on both low and high drought stressed seedlings. However, it is also important to consider that pine weevils themselves are affected by drought and other environmental conditions. While greenhouse experiments may focus on the scale of responses to pine weevil damage, overall survival of seedlings in field conditions is still of value, as it may directly contribute to forest management decisions.

Even though many studies have been done on pine weevils with the aim of understanding and reducing the problem (Barredo et al., 2015; Nordlander et al., 2017; Örlander et al., 1997; Petersson et al., 2004; von Sydow, 1997; Wallertz et al., 2016, 2014; Zas et al., 2020), some knowledge gaps remain. For example, field observations have shown that if a seedling is damaged and girdled underneath the lowest branch, it will most likely die. However, if only the upper portion of the stem is damaged, the seedling has the potential to survive and maintain adequate transportation of water and nutrients despite the injury. This type of damage would correspond to damage from ungulate browsing, where seedlings can tolerate some damage to shoots, but still survive (Kupferschmid, 2017). However, to our knowledge, the effect of location of pine weevil damage on seedling survival has not yet been investigated in a replicated field trial. Additionally, only a few studies have examined multi-damage scenarios involving pine weevils (Lavallée et al., 1994; Rasheed et al., 2020; Selander and Immonen, 1992; Suárez-Vidal et al., 2019).

The aim of this study was to assess performance of mechanical pine weevil protection on survival and growth of planted conifer seedlings in field conditions. Owing to chance drought conditions at the start of the experiment, we expanded the aim to include assessing the impact of drought on seedlings as well as interaction between drought and pine weevil damage. We hypothesized that mechanical protection would perform equally well as insecticide, but better than untreated control. Further, we hypothesized that the damage between the two factors is synergistic, where the combined stress of drought and pine weevil damage increases overall mortality more than the sum of its parts. Additionally, we hypothesized that the damage to the bottom of the stem would have a higher impact on overall seedling survival compared to damage to the top of the stem.

2. Methods

To test field performance of mechanical protection on seedlings, seven study sites were established in south Sweden in 2018, with seven more sites established in 2019 (Fig. 1). Following a standard clearcutting procedure, 180 Norway spruce (*Picea abies*) seedlings were planted on each site, striving to plant in mineral soil. Containerized seedlings from the same nursery and batch were coated with mechanical protections, which were applied to the stem of the seedling before leaving the nursery (Fig. 2). In total four different mechanical protections were tested: Conniflex (Svenska Skogsplantor), Cambiguard (Södra Forest), Ekovax (Norsk Wax AS) and Hylonox (Organox AB), standard commercially available insecticide (Merit Forest, Bayer AB) and untreated. Each treatment was replicated 30 times in one large block (approximately 30 $\times$30 m) on each site, sufficiently away from the surrounding forest to avoid edge effect. Replication was systematic using Latin squares, where each treatment occurred once in each row and each column of a block.

Seedlings on each site were surveyed for survival, height, and damage for four years: immediately after planting, after one growing season, after two growing seasons, and after four growing seasons. Survival was assessed visually by characterizing seedlings as vigorous and with green needles, while height (in mm) was measured from soil surface to and including top shoot. Whenever damage was recorded, type and severity of damage was noted, whenever possible (1 = slight damage – less importance, 2 = damaged – may affect growth, 3 = severely damaged – will affect growth, 4 = probably lethal damage). If pine weevil damage was found, area of removed bark in percentage classes and location of damage (top or bottom of stem) were noted. For mechanically protected seedlings bottom was the coated area, while top was considered above the coating. For insecticide treated and untreated control, bottom was 10 cm measured from the soil, while top was above the 10 cm mark. Additionally, persistence of coating was assessed visually after the first and second growing seasons and sorted into following classes: intact (entire coating left), coating partially removed (pine weevil can damage the seedling), coating significantly removed (pine weevil can girdle and kill the seedling), no coating left.

Environmental variables, especially relating to drought conditions, were collected from SMHI open database (Swedish Meteorological and Hydrological Institute) (SMHI, 2024). These included temperature and relative humidity used to calculate vapor pressure deficit (VPD) for our sites. Additionally, we used temperature data to establish growing seasons for each site, i.e., when daily mean temperatures reached above 5 °C, roughly April-November. For each site, data from the closest weather observation station was selected, resulting in mean distance to

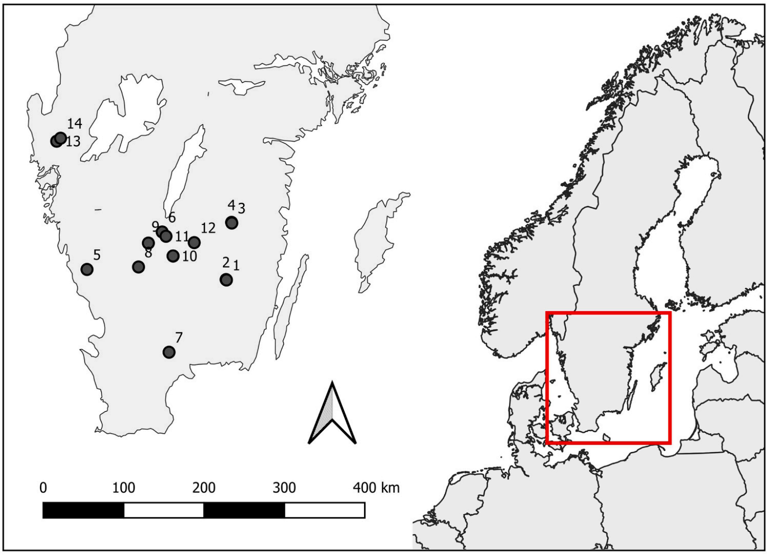

Fig. 1. Map of the 14 study sites between latitudes of 58° and 56°. The red rectangle indicates the zoomed view on the left. Scale indicates distances of the left map.

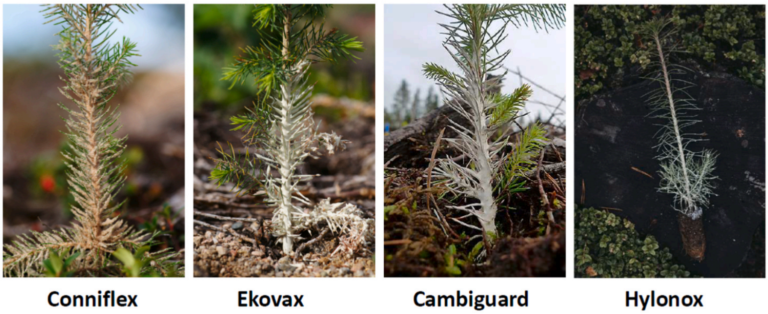

Fig. 2. Pictures of the mechanical protection coatings used in the study (photos: Claes Hellqvist and Karin Hjelm, SLU).

sites of 34.2 km. Some sites were close together and shared weather observation station, resulting in five different stations for sites 1–7 and four stations for sites 8–14. For precipitation data, more stations were available, resulting in an average distance to sites of 15.7 km, where five stations were selected for sites 1–7 and seven for 8–15.

Generalized mixed model in R (R core team, 2024) was used to determine the effect of mechanical protections, persistence of coatings, planting year, pine weevil damage and their interaction on seedling height and survival for each survey. For survival data, generalized binomial mixed model was used instead. To account for the impact of site differences, site was included as a random variable in the final model. To interpret model results, estimated marginal means in the emmeans R package were used (Lenth, 2022). This included contrast analysis, i.e., comparisons between protection methods. For easier interpretation of results, we focused on comparison of mechanical protection methods and insecticide against untreated control.

3. Results

Environmental variable calculations for the sites showed higher maximum and mean VPD (vapor pressure deficit) in 2018 compared to 2019 (Table 1), indicating that seedlings planted in 2018 may have experienced drought conditions. Maximum VPD values were between 3.5 and 4 kPa for 2018, whereas only two sites reached above 3 kPa in 2019. Additionally, mean VPD for 2018 was 50 % higher compared to 2019. There was also a 36 % decrease in precipitation during 2018 compared to 2019 for the same sites. The normal precipitation value for the area (1991–2020) of 513.29 mm indicates that while 2019 was still below average in terms of precipitation with 466.97 mm, 2018 was even lower with 343.26 mm, averaged for all sites.

During the drought conditions of 2018, except for Cambiguard, we found no significant effect of mechanical protection methods, or insecticide on survival of seedlings (Fig. 3). After four seasons in the field, average survival of mechanically treated seedlings was 68 %, while insecticide treated and untreated control had 72 % and 60 % survival, respectively. Only one treatment, Cambiguard, had a positive effect and significantly increased survival of seedlings four seasons after planting to 75 %, compared to untreated control (Table 2). For other treatments, we saw large variations in survival for every survey, especially Conniflex and untreated. Persistence of coating was not found to be a significant

Table 1
List of sites used in the study with vapor pressure deficit (VPD) (kPa) and growing season precipitation (Sum precip.) (mm) values for 2018 and 2019. Sites 1–7 were planted in 2018, while sites 8–14 were planted in 2019. Bold numbers are values during the first growing season when seedlings were planted on those sites. The normal value (1991–2020) of precipitation in the area was 513.29 mm during the growing season, roughly April-November (SMHI, 2024).

		2018			2019		
	Site	**Max VPD**	**Mean VPD**	**Sum precip.**	**Max VPD**	**Mean VPD**	**Sum precip.**
1	Kroksjövägen	**3.51**	**0.59**	**345**	2.73	0.29	347
2	Björnamossvägen	**3.51**	**0.59**	**345**	2.73	0.29	347
3	Norrhult	**3.87**	**0.70**	**351**	3.51	0.57	325
4	Snibben	**3.87**	**0.70**	**351**	3.51	0.57	325
5	Släne	**3.91**	**0.41**	**443**	2.80	0.28	674
6	Månsarp	**3.73**	**0.47**	**235**	3.26	0.36	337
7	Kullaskogen	**3.99**	**0.48**	**241**	3.34	0.36	342
8	Nennesmo	3.63	0.66	293	**2.94**	**0.42**	**483**
9	Lilla Öjhult	3.63	0.66	344	**2.94**	**0.42**	**551**
10	Siggaskog	3.63	0.66	321	**2.94**	**0.42**	**590**
11	Kränsberg	3.73	0.47	342	**3.26**	**0.36**	**474**
12	Margrevehult	3.99	0.63	309	**3.12**	**0.41**	**394**
13	Brattöns gård	3.31	0.48	470	**2.70**	**0.31**	**646**
14	Sanneskogen	3.31	0.48	417	**2.70**	**0.31**	**703**
	Mean value	3.69	0.57	343	3.04	0.38	467

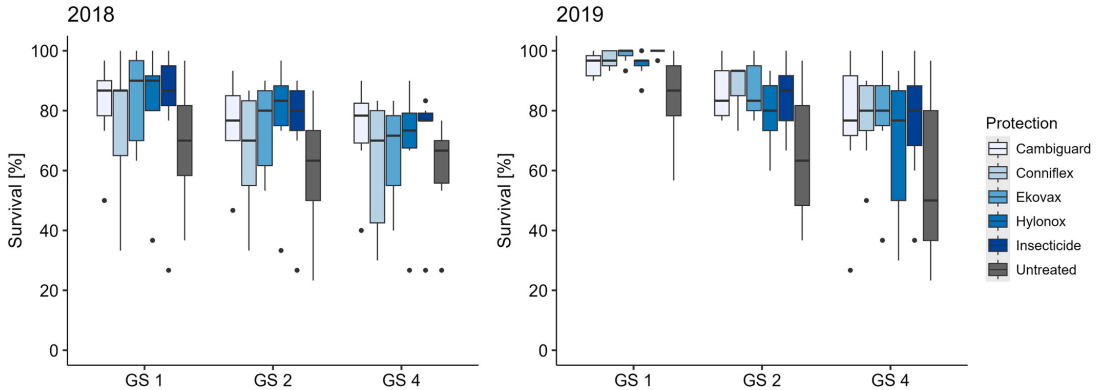

Fig. 3. Boxplots of survival of all seedlings during each survey for each of the treatments and both planting years, 2018 and 2019. GS indicates the growing season after which the survey was performed.

Table 2
Probability of seedling survival after four growing seasons in the field for each treatment method and both planting years. SE stands for standard error. P-values reported are from contrasts comparison in estimated marginal means analysis, where every treatment was compared against untreated. Significant p-values are highlighted in bold.

	2018			2019		
Treatment	**Survival**	**SE**	**p-value**	**Survival**	**SE**	**p-value**
Cambiguard	0.745	0.065	**0.030**	0.809	0.074	**0.0001**
Conniflex	0.622	0.078	0.982	0.828	0.069	**<0.0001**
Ekovax	0.672	0.074	0.562	0.823	0.071	**<0.0001**
Hylonox	0.696	0.070	0.281	0.722	0.096	0.0732
Insecticide	0.715	0.067	0.137	0.809	0.074	**0.0001**
Untreated	0.604	0.079	/	0.600	0.113	/

factor affecting survival in 2018.

In contrast, there was a positive significant effect of mechanical protection methods on survival for seedlings planted in 2019 (Fig. 3). Mechanical protection increased survival of seedlings and performed significantly better when compared to untreated control (Table 2). One exception was Hylonox, where the difference was not significant, but there was still a tendency towards higher survival than untreated control (p=0.073). There was also a lower variation in survival among treatments, especially after the first and second growing season, when mortality of the treated seedlings was relatively low. After four seasons in the field, average survival of mechanically treated seedlings, excluding Hylonox, was 82 %, while insecticide treated and untreated control had 81 % and 60 % survival, respectively. Persistence of coating was found as a significant factor affecting survival in 2019, but only for Hylonox treatment, where 35 % of all Hylonox treated seedlings planted in 2019 had no protection left after two seasons in the field. In comparison, the proportion of seedlings with no protection left for other treatments were 2 %, 5 % and 1 % for Cambiguard, Conniflex, and Ekovax, respectively.

Further, focusing on seedlings with signs of pine weevil damage, a synergistic effect was observed between pine weevil damage and drought, i.e., similar levels of pine weevil damage resulted in higher mortality in the following season for seedlings planted during the drought year of 2018 (Fig. 4A). Already at first level of damage (slight) after the first planting season, seedlings planted in 2018 had an average survival of 49 % after two growing seasons, while those planted in 2019 had a survival of 83 % at the same damage level. Moreover, seedlings planted in 2019 were able to maintain survival above 80 % until severe level of damage was reached, while seedlings planted in 2018 showed a gradual decrease in survival with increasing levels of damage. Additionally, there was greater variability in survival for the seedlings

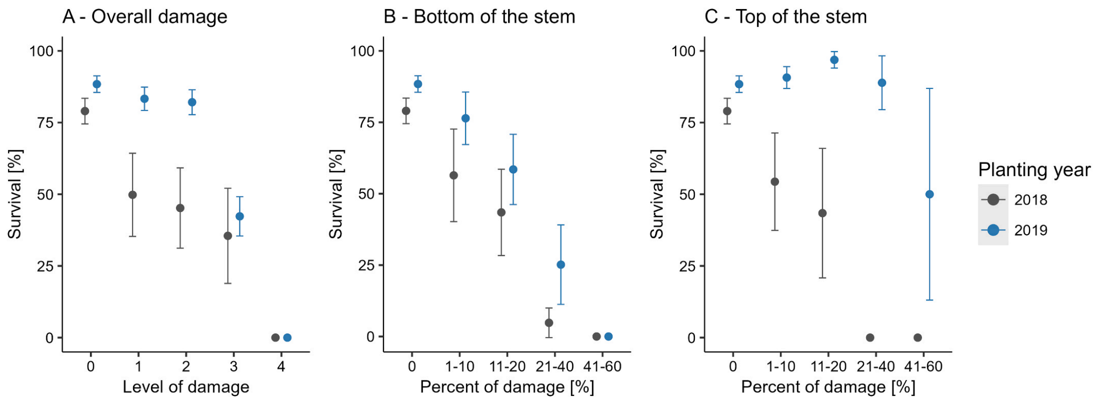

Fig. 4. Mean survival of seedlings after two growing seasons in relation to recorded pine weevil damage after one growing season. Fig. 4A shows survival in different levels of damage to whole seedling (0 – no damage, 1- slight damage, 2- damage will probably affect growth, 3- severe damage will affect growth, 4 – lethal damage). Figs. 4B and 4C show damage only to the bottom or top of the stem, respectively, expressed in percentage classes representing proportion of debarked stem. All seedlings with damage higher than 60 % died. The error bars represent standard errors.

planted in 2018 compared to those planted in 2019.

When looking at damage only to the bottom or top of the stem, similar differences were found between the two planting years (Fig. 4B & 4 C), i.e., similar damage level resulted in higher mortality to seedlings planted in 2018. Damage at the bottom of the stem shows a similar pattern to overall damage, decreasing survival with increasing damage for both planting years. However, when the damage occurred at the top of the stem, until considerable levels of damage were reached (41 % of debarked area and above), seedlings planted in 2019 had a relatively high survival of around 90 %. In comparison, damage at the top of the stem for seedlings planted in 2018 had a gradually decreasing survival, following a similar pattern as damage at the bottom of the stem.

Several damage factors affecting mortality were recorded in our study, which differed between growing seasons and planting years (Fig. 5). The greatest difference between the two planting years was for mortality during the first growing season, which was the drought season for seedlings planted in 2018. This may explain differences in mortality between the two planting years since the source of damage for the majority of damaged seedlings was unknown. While some of the damage factors were easy to identify in field conditions, like areas of pine weevil

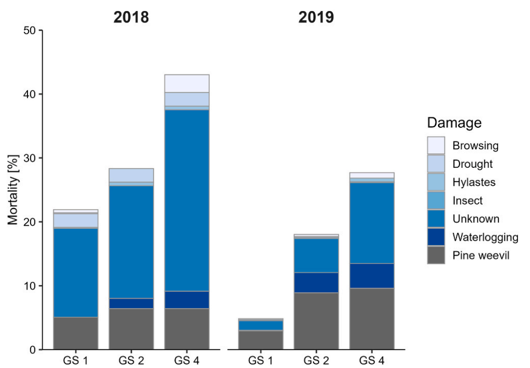

Fig. 5. Sources of mortality of all seedlings irrespective of treatment and damage level. The damage bars are cumulative over the years, presenting total damage. Browsing label refers to browsing damage by ungulates and insect damage label refers to damage by insects other than pine weevil or *Hylastes sp.* GS indicates the growing season after which the survey was performed.

feeding, drought damage has few specific signs and is thus hard to pinpoint. Therefore, it may be that a significant portion of the unknown damage was due to drought, especially during the growing season of 2018. Moreover, after the first growing season, we recorded lower rates of pine weevil attack for the 2018 seedlings, where 13 % of seedlings showed signs of debarking, while the percentage was 20 % for seedlings planted in 2019. Despite this difference, mortality attributed to pine weevil damage in the first growing season was slightly higher for seedlings planted in 2018, suggesting synergistic effects between drought and pine weevil damage.

There was no difference in height of seedlings between different treatment methods or planting years (Fig. 6). Additionally, estimated marginal means comparison of different methods revealed no difference in height of all seedlings treated with any mechanical protection method or insecticide compared to untreated control.

4. Discussion

Our analysis of site factors using climate data from SMHI, alongside other studies (Lindroth et al., 2021; Schuldt et al., 2020; Sturm et al., 2022), suggests that the summer of 2018 was indeed an exceptionally dry year, which had a detrimental effect on planted seedlings (Luoranen et al., 2023). This can be observed both in high VPD values as well as in the amount of precipitation during the growing season. While precipitation during the growing season of 2019 was also below average, when considering normal precipitation values for the area, it was closer than that of 2018. The detrimental impact on seedlings is also evident Fig. 5, which shows greater overall mortality in the 2018 dataset. The majority of damage was noted as unknown, which, when coupled with site factor analysis, could suggest drought related damage, otherwise difficult to pinpoint. Additionally the effect of drought is seen in Fig. 3, as the overall lower survival with higher variation for the 2018 dataset, compared to 2019.

Although one of the main goals of the study was to test field performance of mechanical protection methods on Norway spruce seedlings against pine weevil damage, coincidentally, the experiment was started during a year with an exceptional drought (Lindroth et al., 2021; Schuldt et al., 2020). This allowed for additional investigation into performance of protection methods under drought conditions as well as multi-damage scenario of seedling establishment. Our results are in line with other studies showing that drought significantly influences survival of seedlings (Grossnickle, 2012; Luoranen et al., 2023), where additional stress

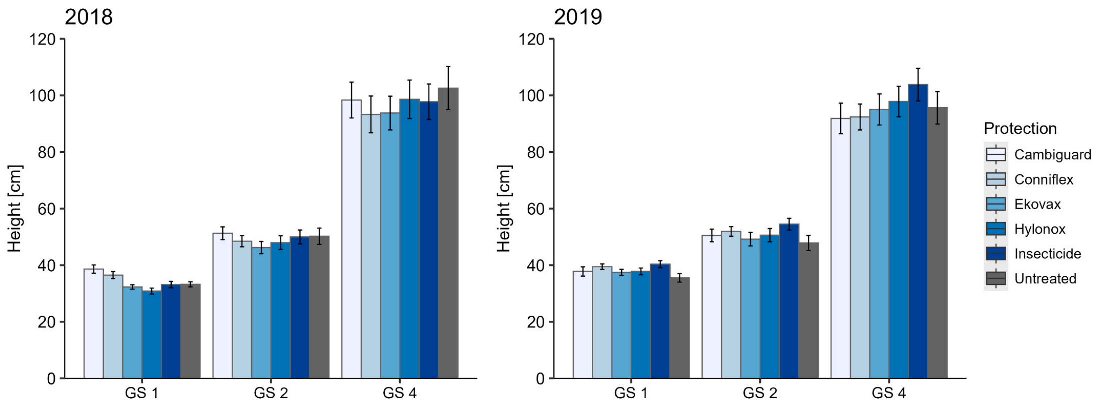

Fig. 6. Mean height of all seedlings during each survey for each of the treatments and both planting years, 2018 and 2019. The error bars represent standard errors. GS indicates the growing season after which the survey was performed.

may predispose seedlings to mortality from other damage factors (Grossnickle, 2012). This aspect is also highly relevant for the future with predictions of more frequent and severe droughts (Beniston et al., 2007; Chen et al., 2015; Spinoni et al., 2018), which may significantly impact seedling survival. For seedlings planted in the drought year of 2018, only one protection method, Cambiguard, performed significantly better than untreated. This was somewhat expected, as neither mechanical protection nor insecticide are designed to protect seedlings from desiccation or other drought related damages. Moreover, Cambiguard performed similarly to other mechanical protection methods for seedlings planted in 2019, suggesting other causes may have contributed to survival of seedlings coated with Cambiguard in 2018. However, for seedlings planted during a non-drought year, mechanical protections performed equally well as insecticide, and significantly better than untreated, indicating their potential as replacements for insecticide. This was further highlighted by the fact that insecticide did not protect seedlings significantly better than untreated when seedlings were planted during a drought year, indicating that drought was a more important factor than pine weevils in this case.

An important finding to emerge from our analysis is the persistence in the application of protective coating, which should be the focus of further development. It is important that protective coatings last sufficiently long to provide protection, as shown in the example of Hylonox. While its coating application was not significantly different from other methods for the 2018 dataset, Hylonox in the 2019 dataset had a significantly higher proportion of seedlings with no coating coverage after two seasons. While there may be other factors involved, lower amount of coating left on the seedlings could result in higher rates of pine weevil attack and help explain lower survival of seedlings treated with Hylonox in the 2019 dataset.

It is also important to consider interaction between drought and pine weevils not only in terms of seedling damage. Previous studies on pine weevils in controlled environments showed reduced feeding behavior and egg laying at air temperatures above 30 °C (Christiansen and Bakke, 1971, 1968). Unfortunately, direct effects of drought in field conditions remain a knowledge gap, since due to their sheer numbers, abundance studies are difficult to implement (Örlander et al., 1997; von Sydow, 1997). Still, it is reasonable to assume that pine weevils themselves were affected by high soil surface temperatures during the summer of 2018, potentially leading to reduced activity and feeding behavior. In our study, drought occurred in the first growing season for the 2018 dataset, which is at the beginning of a longer period of pine weevil damage, previously shown to decrease after three years (Örlander et al., 1997). Still, we wanted to focus on the first growing season, as it is the most important period of seedling establishment (Grossnickle, 2005). Fig. 5 shows comparatively little additional mortality between the first and second growing season for the 2018 dataset, with the majority of mortality occurring in the first growing season. The situation is opposite in the 2019 dataset, most likely owing to the lack of drought in the first growing season of 2019.

While pine weevil activity may have been lower in 2018, as suggested by different recorded attack rates, we still recorded significant damages and seedling mortality attributed to pine weevil damage (Fig. 5). Comparing pine weevil damage between the two planting years (Fig. 4), we saw that seedlings planted in 2019 had a higher survival than those planted in 2018 for the same damage classes, until damage became severe. It is impossible to completely separate the effect of drought and pine weevil damage in field conditions, however, it seems that the combined effect of both factors contributed to an overall lower survival. This is in line with previous research in greenhouse conditions, where seedlings were exposed to pine weevils and varying levels of drought, under controlled conditions. Suarez-Vidal et al. (2019) showed a non-linear seedling response to drought, where medium stress resulted in highest damage, later linked to lower production of defensive compounds (Suárez-Vidal et al., 2019). In varied field conditions, it may be that our study seedlings also experienced different levels of drought stress and were subsequently attacked at different rates. For example, highly drought stressed seedlings would have reduced cambium thickness, thus potentially leading to reduced attack rates. In our investigation, however, we chose to focus on evaluating overall survival rates of seedlings within the context of a regeneration process, rather than investigation into distinctions in drought stress susceptibility. Moreover, analysis of seedling height data shows no impact of drought on growth of seedlings, suggesting little gradation of drought damage. It seems that drought stress in 2018 was severe enough to push the majority of already stressed seedlings into mortality, regardless of any additional damage by pine weevils.

Location of pine weevil attack on seedlings has long been thought to play a role in overall mortality, but studies testing this in field conditions have been lacking. Logically, damage further down the stem would restrict the seedling more, as a higher portion of the stem would be deprived of water transport. Our results are in line with this, as we saw a linear response of survival to pine weevil damage on the bottom of the stem, but not the top, for seedlings planted in 2019 (Fig. 4). Contrastingly, seedlings with pine weevil damage to the top of the stem were able to retain high survival (above 80 %), until high levels of damage were reached. The situation is different for seedlings planted in 2018, where we do not see this higher tolerance for damage at the top of the steam, but instead, a response similar to when the damage occurred at the bottom of the stem. This may indicate that during a non-drought year, damage to the bottom of the stem is indeed the deciding factor of the overall survival. During a drought year, however, location of pine weevil damage to seedlings is of lesser importance to their survival, as the drought itself is either the dominant damage factor or significantly predisposes seedlings to mortality by pine weevil. Under drought conditions, careful selection of planting spots and other drought-mitigating methods could become even more important to ensure adequate seedling survival (Häggström et al., 2021; Nordin et al., 2022).

There was no effect of protection methods on measured height of seedlings, suggesting that concerns of coating constricting seedling growth or reducing transpiration and needle leaf area were unfounded, which was previously shown in a greenhouse experiment (Sjöström, 2020). Interestingly, there were also no differences between the two planting years, suggesting that seedlings that established well and survived in 2018 were no different in terms of height growth from seedlings planted in a non-drought year. This is in line with other research that suggests proper initial establishment is a key factor in survival of seedlings in field conditions (Burdett, 1990; Grossnickle, 2012, 2005; Häggström et al., 2021; Nordin et al., 2023).

5. Conclusions

We show that mechanical protection methods against pine weevil tested in this study perform well in protecting conifer seedlings when planted during a non-drought year. They increased survival of seedlings and performed similarly to insecticide treated and better than untreated seedlings. A similar height growth among all treatments indicate that no physiological restrictions could be connected to mechanical protections. Additionally, we show high survival of seedlings with pine weevil damage at the top of the stem, until high damage levels were reached. In comparison, when the seedlings were planted in a drought year, additional drought stress increased overall mortality and reduced the importance of mechanical protection. Under these conditions, the combined stress of pine weevil damage and drought significantly decreased survival, regardless of the location of damage on the stem. The findings presented here highlight the interplay between different environmental stressors on survival of seedlings in field conditions. They emphasize the necessity of tailored management strategies adapted to specific planting conditions to optimize seedling survival.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Survival and growth of Scots pine (*Pinus sylvestris)* seedlings in north Sweden: effects of planting position and arginine phosphate addition

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ABSTRACT

Forest regeneration by tree planting on harvested sites in the boreal forests of northern Europe is frequently preceded by site preparation to increase survival and growth of the seedlings. We studied whether a small addition of arginine phosphate (AP treatment) at the time of planting would further enhance the seedlings' early performance. Following two growth seasons, we investigated survival and growth of Scots pine (*Pinus sylvestris)* seedlings on 11 locations between latitudes 61.1°N and 67.1°N in the boreal forest of northern Sweden. The planting positions of seedlings were on capped mounds and bare mineral soil following mechanical site preparation, and in non-prepared soil. We found that seedling survival following site preparation increased with AP treatment. On capped mounds, seedling survival was more variable and appeared more dependent on precipitation during the first month after planting than seedlings positioned in the mineral soil. The positive effect of AP treatment on seedling growth differed between sites and was more pronounced on sites with longer growing seasons. AP treatment had no significant effect on survival of seedlings planted in non-prepared soil, while the positive effect on growth was more pronounced at sites with higher fertility using this planting position.

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Introduction

Forestry practice in the Nordic countries involves the planting of tree seedlings on harvested forest sites. The environment on such clear-cuts is challenging for the seedlings. To improve their survival and growth, mechanical site preparation is used. Mounding and disc trenching are the two most common mechanical site preparation methods used in Sweden. Elevated planting positions are produced as isolated mounds in rows when mounding by excavator is carried out, while elongated continuous berms are produced by disc trenching. When successfully completed, the resulting elevated planting areas following both mounding and disc trenching consist of an inverted humus layer positioned on underlying intact humus and topped by mineral soil. The terminology used regarding mineral mounds on inverted organic matter may vary depending on method, country where the method is practiced and author (Sutton 1993). Here, we use the term "capped mound" for both isolated mounds and continuous berms, where "capped" implies a mineral soil cover over a mound of organic matter (Sutton 1993) and thus accurately describes the resulting elevated planting positions produced by both disc trenching and mounding. Capped mounds are the recommended planting positions in Swedish forestry (Skogsstyrelsen 2020), mainly because nutrients released during decomposition of the embedded organic material are beneficial to seedling growth. Furthermore, the raised position is warmer and less exposed to frost damage and flooding than a lower one (Örlander et al. 1990; Langvall et al. 2001; Burton et al. 2000). On the other hand, capped mounds can suffer from low soil moisture conditions because the organic layer within them reduces capillary water flow from below (Örlander et al. 1990, 1998; Burton et al. 2000; de Chantal et al. 2003). Also, variation in soil type, the occurrence of large rocks, stumps and logging residues on the clear-cut site can cause a large variation in the quality of the capped mounds, even within a single site (Sutton 1993; Larsson 2011; Söderbäck 2012; Sundström 2021). Mechanical site preparation is generally carried out the year before planting to allow the capped mounds to be compacted by snow. Nevertheless, if there are many branches, rocks or dense ground vegetation embedded within the capped mound, the contact with underlying soil and access to capillary water can yet be compromised (Örlander et al. 1990; Grossnickle 2005). Thus, an individual quality assessment is made for every capped mound at the time of planting. It is generally recommended to plant deep, preferably through the organic layer (Örlander et al. 1990). However, it is not a trivial matter to judge whether a capped mound provides a suitable planting position or not. It is not always possible to assess the depth of the mineral cover of a capped mound externally and it may not always be practically possible to position

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Figure 1. A cross section of a capped mound that would be classified as optimal when looking from above ground. The cross section reveals that the planting position is not optimal for the seedling to reach capillary water. Dashed lines mark the top surface of the capped mound, top and bottom of the organic layer and the outline of the seedling substrate. The seedling substrate barely reaches through the top mineral layer and is far above the underlying mineral soil. This specific capped mound was not from a trial site included in this study, but the aim of this figure is to provide an example of how the interior of a capped mound might look.

the seedling correctly i.e. through the organic layer so that the roots reach the mineral soil to access capillary water (Figure 1). Sometimes the depth of planting can be limited by physical obstacles beneath the surface, such as a twigs or rocks, or by seedling size. The most common seedling stock types planted in northern Sweden are grown in containers with a cell size of 30 or 50 cm^3. Pine seedlings grown in these containers are often no more than 10 cm tall when planted. If planted too deep, these seedlings would have a very low proportion of the shoot above ground which could, potentially, negatively affect growth (Johansson et al. 2015).

Climate change scenarios predict both increased temperature and precipitation in Sweden (Strandberg et al. 2015). Despite the increase in precipitation, a reduction in water availability is expected in many areas of Sweden during the summer due to increased evaporation (Eklund et al. 2015). With increasing evaporation, there will be an increasing risk of seedling desiccation and water stress-induced mortality. Seedlings planted in capped mounds are particularly susceptible in such scenarios, since low soil moisture conditions decreases water uptake ability of seedlings more in capped mounds than in pure mineral positions (Örlander 1986). At present, the recommendation when planting during dry weather conditions in south Sweden is that seedlings should be planted at a relatively high position in the mineral soil exposed by the soil scarification, while in north Sweden the recommendation is to plant in the capped mound regardless of weather conditions (Skogsstyrelsen 2020). However, planting in mineral soil can potentially lead to reduced growth due to the low nutrient availability. Nitrogen availability is often limited in boreal forests, where most of the plant-available nitrogen is found in the humus layer (Tamm 1991; Grossnickle 2000; Bhatti et al. 2005).

The addition of a long-term release nitrogen source at the time of planting could potentially compensate for the lower nitrogen availability in the mineral soil (Brand 1991; Thiffault & Jobidon 2006). Fertilizers based on inorganic nitrogen, such as ammonium and nitrate, are the most common commercially available ones, but nitrogen is naturally mainly available to plants in organic form i.e. amino acids in boreal forests (Inselsbacher & Näsholm 2012). The amino acid arginine is synthesized by coniferous trees and also many vascular plants to enable internal storage of nitrogen in foliage or other plant parts (Nordin et al. 2001). Arginine has the highest nitrogen content of the amino acids (Cánovas et al. 2007). In *Pinus sylvestris* L., arginine is the dominant constituent of the amino acid nitrogen pool in needles, twigs and bark, and a major constituent, along with glutamine, in the wood (Nordin et al. 2001). When nitrogen uptake exceeds levels the trees can utilize for growth, the arginine levels increase in needles and wood (Edfast et al. 1996; Nordin et al. 2001). This storage is then utilized by plant metabolic processes to provide nitrogen required for early season growth (Canton et al. 2005). Also, in forest soils, amino acids act as an organic nitrogen source accessed by plant roots (Öhlund and Näsholm 2001; Gruffman et al. 2013). In soil, arginine is a strong cation and has a very high binding capacity to soil particles (Inselsbacher et al. 2011). Consequently, arginine nitrogen does not leach from forest soils even when applied in relatively high doses (e.g.

Hedwall et al. 2018). Hence, an environmentally friendly and commercially available fertilizer based on arginine has been developed: arGrow® (Arevo AB, Umeå, Sweden). In arGrow®, the arginine is crystallized with phosphate and granulated to form a slow-release fertilizer. So far, most studies of fertilization with arginine have been in tree seedling nurseries and have shown that conifer seedlings treated with arginine develop a higher mean dry weight, a higher root-to-shoot ratio as well as a larger proportion of root tips colonized by mycorrhiza, compared to seedlings treated with inorganic nitrogen fertilizers (Öhlund and Näsholm 2002; Gruffman et al. 2012).

The aim of this study was to evaluate the effects of adding arginine phosphate (arGrow®) on the field performance of *P. sylvestris* seedlings in different planting positions. We used a large field trial, across 11 clear-cut forest sites between latitudes of 61.1°N and 67.1°N in northern Sweden. The experiment was carried out on multiple commercial forestry sites which offered a wide range of environmental conditions to mimic "real life" conditions. This approach exploits the different combinations of environmental variables present at each site. Some variables are related to natural variation, such as geographical location, soil type and climate, while others are related to silviculture practices, such as site preparation method and site preparation performance along with seedling features such as stock type, seed source, seedling size and nursery regime. Many of these variables and their combinations can potentially affect seedling performance in the field (Burdett 1990; Margolis & Brand 1990; Grossnickle 2012). However, this broad span of site conditions is also the strength of this study since the main goal was to achieve results that were practically applicable to a great range of commercial site conditions rather than to controlled experimental conditions.

The effect of arginine phosphate treatment (AP treatment) was evaluated for seedlings planted in capped mounds, the adjacent exposed mineral soil and in non-prepared soil. Many previous studies have pointed out that seedling performance in non-prepared soil is normally significantly lower than that in scarified soil, but the practice may still be interesting on sites with particularly sensitive ground vegetation, such as reindeer lichens. Also, seedling performance data were correlated with weather (precipitation), climate (length of growing season) and site fertility conditions (site index). The effects of these variables on seedling growth and survival in different planting positions and treatment combinations were evaluated.

The main objectives of this study were (i) to evaluate the effect of arginine phosphate (AP) treatment at the time of planting on seedling performance in different planting positions over multiple sites in northern Sweden; (ii) to evaluate the effect of climate variation across sites on seedling performance in the different planting position and treatment combinations and (iii) to evaluate the potential of arginine phosphate as a tool to compensate for the lower nutrient availability in mineral soil as compared to capped mounds, where nutrients are available from decomposing organic material.

To address these objectives, we formulated the following hypotheses:

1. AP treatment at the time of planting will positively affect survival. We expected that the positive effect of arginine phosphate on root growth and mycorrhizal colonization (Öhlund and Näsholm 2002; Gruffman et al. 2012) would enhance survival since extension of the root system can increase the water uptake capacity of seedlings (Bréda et al. 2006; Brunner et al. 2015).
2. Low precipitation during the seedling establishment period will affect survival negatively, particularly for seedlings positioned on capped mounds. We expected that seedlings on capped mounds would exhibit a higher dependence on precipitation in comparison to seedlings in bare mineral soil. This would be due the restricted access to capillary water from below compared to the more direct access to capillary water in mineral soil (Örlander et al. 1990, 1998; Burton et al. 2000; de Chantal et al. 2003).
3. AP treatment will enhance seedling growth. We expected that the positive effect of arginine phosphate on root growth and mycorrhizal colonization (Öhlund and Näsholm 2002; Gruffman et al. 2012) as well as the direct access to nitrogen would enhance shoot growth.
4. AP treatment of seedlings planted in bare mineral soil will exhibit similar growth in this position to that in capped mounds. We expect that the direct access to nitrogen through the long-term release nitrogen source (Brand 1991; Thiffault and Jobidon 2006) will facilitate increased growth in the otherwise nitrogen-limited environment (Tamm 1991; Grossnickle 2000; Bhatti et al. 2005).
5. Seedlings will perform better after mechanical site preparation than in non-prepared soil. Site preparation is known to enhance seedling performance by improving micro-site conditions to favor establishment of the newly planted seedlings, such as increased temperature, decreased competition from ground vegetation and decreased damage from pine weevil (Örlander et al. 1990).

Material and methods

Field experiment design

A field experiment to evaluate the effect of arginine phosphate (AP) treatment on Scots pine (*Pinus sylvestris* L.) seedlings in different planting positions was set up during spring and early summer in 2018. The seedlings were split into two treatment groups: (a) treated with AP: one dose of granular arginine phosphate (arGrow® Granulat, Arevo AB, Umeå, Sweden) was added to the bottom of the planting hole together with each seedling at the time of planting; (b) untreated: no nutrients added. One dose of arGrow® Granulat contains 40 mg N and 22 mg P, the active substance being L-arginine phosphate ($C_6H_{17}N_4O_6P$). The seedlings in each treatment group were planted in three different positions: (i) capped mound i.e. turned-over humus tilt with a mineral soil cover on top of intact humus (Figure 1), (ii) mineral soil i.e. bare mineral soil adjacent to the capped mound where the topsoil had been removed, and (iii) non-prepared soil i.e. undisturbed intact humus where no topsoil or vegetation had been removed. Planting positions

Table 1. Sites A–K are listed from south to north with latitude (Lat.), longitude (Long.), and altitude (Alt., meters above sea level). Volume (vol.) refers to the cell size of the growing containers, which is the volume the seedlings' roots were restrained in at the time of planting.

Site	Lat. (° N)	Long. (° E)	Alt. (m.a.s.l.)	Vol. (cm^3)	Method	Precipitation first 30 days (mm)	Growing season (days)	SI	No. leader shoot length measured
A	61.06	16.16	360	50	DT	35	165	T24	109
B1	62.07	15.09	260	30	DT	36	155	T20	66
B2	62.07	15.09	260	50	DT	36	155	T20	144
C	63.95	18.45	260	50	M	24	145	T22	62
D	63.95	18.44	280	50	DT	24	145	T20	42
E	64.18	19.91	180	50	DT	44	145	T22	14
F	64.26	19.61	180	50	DT	45	145	T21	81
G	64.31	19.64	300	50	DT	44	145	T22	68
H	65.62	20.63	180	30	M	43	140	T19	64
I	66.38	21.82	200	30	DT	43	135	T19	88
J	66.64	20.30	260	50	M	48	130	T16	107
K	67.09	22.30	200	30	DT	13	130	T18	288

Method refers to which mechanical site preparation method was used for each site, disc trenching (DT) or mounding (M). Environment parameters: Total precipitation during the first 30 days after planting in 2018 (SMHI, 2019), length of growing season in days (SMHI 2020) and site index (SI). The "T" in site index indicates pine sites in Swedish site index classification (Hägglund & Lundmark 1987). No. leader shoot length measured = the total number of seedlings measured for each site. Site B include seedlings grown in both containers with cell volume 30 cm^3 (B1) and 50 cm^3 (B2) and is therefore divided into two subsets.

(i) and (ii) were both created during mechanical site preparation carried out in 2017. The mechanical site preparation methods were disc trenching at eight sites and mounding at three sites (Table 1). Planting was carried out by experienced planters. Planting in capped mounds was only carried out where the capped mounds had appropriate mineral soil cover, so when the planting position was classified as "good".

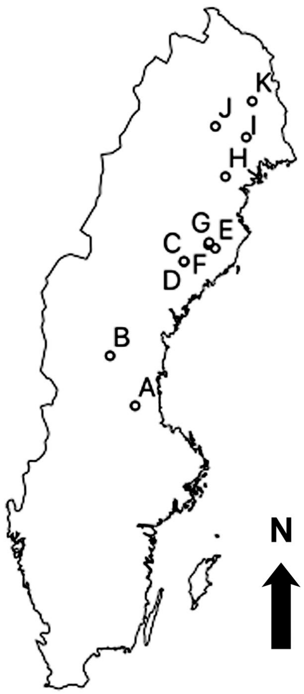

Figure 2. Distribution of sites within the boreal forest area of northern Sweden between latitudes 61.1°N and 67.1 °N.

The experimental plots were spread over multiple sites in Sweden between latitudes 61.1°N and 67.1°N (Figure 2). The soil moisture class was dry on all sites except site C which was mesic. Soil types varied between silty, sandy and coarse till, where larger particle sizes (i.e. gravel and bigger rocks) were present in the soil at all sites. Each site represented a combination of many different environmental variables resulting from a combination of natural variation and silvicultural practices (Table 1). In this study, precipitation during the first 30 days after planting, length of growing season and site index were the variables that showed the most significant correlation to survival and/or growth performance and were therefore the variables chosen to represent site variation (Table 1). Site index (SI) represents the productivity of the sites and is the estimated height of dominant trees at 100 years based on the productivity of the former stand.

At each site, 2–4 rows of seedlings with each planting position and treatment combination were planted on areas with relatively homogeneous terrain. For each track made by either mounding or disc trenching, all three planting positions were used i.e. capped mound and mineral soil positions in the track and non-prepared soil between tracks. The rows were arranged adjacent to each other, so three rows with AP-treated seedlings (one for each planting position), and the next three adjacent rows with untreated seedlings for each planting position, repeated 2–4 times. Due to lack of good planting positions in capped mounds on many sites, varying numbers of seedlings were planted in each position and treatment combination for each site. For details of numbers of planted seedlings, please refer to the supplementary material (Table 7).

Seedling material

Seedlings of *P. sylvestris* from different nurseries were used on different sites/groups of sites depending on the provenance and site owner. Each site was planted with seedlings grown in containers with either 30 cm^3 or 50 cm^3 cells, except for one site (B) which was planted with both sizes (Table 1). For further seedling material details, please refer to the supplementary material (Table 6).

Climate variables

Precipitation data were retrieved from the nearest available Swedish Meteorological and Hydrological Institute (SMHI) weather station (mean distance 18.5 km, maximum distance 30 km) database for each site (SMHI 2019). The length of growing season is the normal value based on 1961–1990 data, where the start of growing season is defined by the first day of the year when the diurnal mean temperature has been above 5°C for four consecutive days, and the end is the last day of the last four days period when the diurnal mean temperature has been below 5°C (SMHI 2020). Precise data for the length of growing season for the new normal period based on data from 1991 to 2020 are not yet available. However, the length of growing season has generally increased all over northern Sweden since 1990 (SMHI 2020) and so we expect that to be true for all the sites included in this study. Therefore we assume that the internal relations between the sites regarding length of growing season have not changed dramatically and that we thereby can relate site-dependent differences in growth and survival to the currently available data.

Inventory methods

A field inventory was carried out at the end of the second growing season during August and September 2019. All seedlings with any green needles were classified as living, seedlings with no green needles, and missing seedlings were classified as dead. Cause of death was not determined since this was not an aim of the study, but the majority of the dead seedlings were ones that were missing. For seedling growth, we used the current year (2019) leader shoot length to represent performance in the field since planting. The leader shoot length was measured from the top branches to the top of the terminal bud. The leader shoot of every second live and undamaged seedling was measured, randomly starting at the first or second seedling in each row. The majority of damaged seedlings lacked dominant leader shoot, often resulting in "brushy" seedlings with multiple leader shoots. The cause was not always possible to determine, but in many cases the leader shoot was removed by browsing. In northern Sweden, browsing by moose in late winter is a common cause of damage to young pine trees (Söderbäck 2012; Bergqvist et al. 2014). Leader shoot damage can also be caused by harsh winter conditions, such as temperature drops during low snow-cover, and have also been found to increase with low precipitation the first weeks after planting (Luoranen et al. 2018). At sites where many seedlings were damaged or dead in any of the planting positions and treatment combinations, all the remaining undamaged seedlings were measured from that combination.

There was a large variation in the number of measurement replicates taken from the 2019 inventory, with a total of 1207 seedlings being measured (Table 1). Varying numbers of seedlings planted at all sites and in all planting positions, variations in survival rates and numbers of damaged seedlings together with part-harvests of entire blocks for other purposes than this study in 2018 at several sites contributed to this.

Data selection and structure

Site C is not included in the analyses of seedlings planted in non-prepared soil since no seedlings were planted in this position at this site. Site A is excluded from the growth variable statistics for non-prepared soil because there were very few measurements due to low survival numbers. Site E was not included in the growth measurement analysis since a high number of damaged seedlings resulted in a very low number of available seedlings to measure in all planting positions. At site B, which was planted with two different seedling sizes, survival analyses only include seedlings of the larger size due to missing survival data for the smaller sized seedlings. However, measurement data include both seedling sizes separated in two datasets for this site.

Seedlings planted in mineral soil and capped mounds were analyzed in the same dataset since the main interest of this study was to compare the performance of seedlings in these two planting positions. Performance of seedlings in non-prepared soil is naturally affected by competition from other vegetation to a greater degree than the seedlings in mechanically prepared soil. Seedlings planted in non-prepared soil were, therefore, analyzed separately to avoid interference with the very different growing environment in the comparison to the mechanically-prepared planting positions.

Analysis methods

We tested the effects of the factors planting position and arginine phosphate treatment as well as the interaction between these factors. Therefore, we chose to use factorial ANOVA since this method can be used to find whether there is any significant effect of each factor and whether there is interaction between them (McDonald 2014; Mangiafico 2015). To account for any difference in effects of planting position and arginine phosphate treatment between sites, we used "site" as a third factor. R-studio (version 1.3.1093) software was used for all statistical analyses (R Core Team 2019). Analysis of variance (ANOVA) was performed for survival and growth using the R car-package (Fox and Weisberg 2019). Generalized linear models (GLM) were used to analyze survival, using survival log-odds (ratio of the probability of survival to probability of death) as the response variable. Growth was analyzed with linear models using leader shoot length as the response variable. To detect whether there were any interactions between the main factors, model III ANOVA was used as this model is recommended for unbalanced designs (Logan 2011; Walker 2018). In cases where no interaction between factors was detected, a follow-up model II ANOVA was carried out since model II is considered more powerful when no interaction is found (Langsrud 2003). The confidence level used in all analyses was 0.95. In the case of interaction between site and any of the other factors, the effect of site was further explored by fitting models separately for each of the levels in the other factors (Logan 2011). Each site represents many different environmental variables, such as amount of precipitation, temperature sum, length of growing season, site index etc. Each of these variables were tested to find which one represented the site effect best.

Generalized linear models were used to illustrate the relationship between (i) survival and precipitation during the first 30 days after planting in capped mounds and mineral soil and (ii) survival in non-prepared soil and length of growing season. Linear models were used to analyze site variation in growth in relation to (i) length of growing season for seedlings planted in capped mounds and mineral soil and (ii) site index for seedlings planted in non-prepared soil.

Results

Seedling survival in capped mounds and mineral soil

Treatment with arginine phosphate (AP treatment) at the time of planting had a significant positive effect on seedling survival after two seasons in the field, that is, the positive effect of AP treatment on seedling survival occurred independently of site and planting position (Figure 3(A), Table 2). The positive effect of AP treatment on survival appeared to be larger when the seedlings were planted on the capped mounds than when planted in the mineral soil (Figure 3(A)). The effect of planting position on seedling survival depended on the site as there was a significant interaction between the two variables (Figure 3(A), Table 2). Survival, averaged over all

Table 2. Results from ANOVA analysis of the effects of site, arginine phosphate (AP) treatment, planting position following mechanical soil preparation and the significant interactions between these variables on seedling survival following two growing seasons in the field.

	LR Chisq	Df	Pr (>Chisq)
Site	114.17	10	**<0.001**
Treatment	5.01	1	**0.03**
Position	0.00	1	0.99
Site x Position	173.72	10	**<0.001**

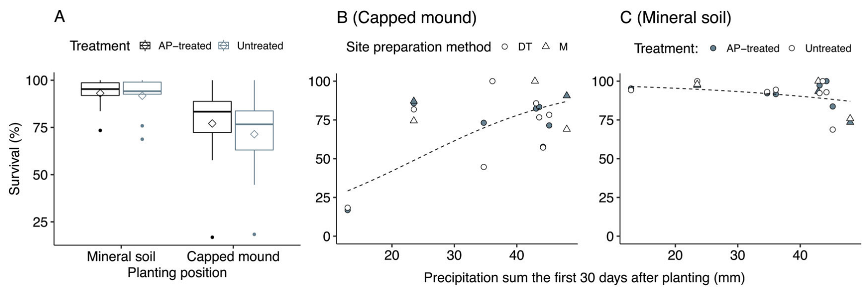

Figure 3. (A) Box and whisker plots of the observed proportional survival range of seedlings planted in mineral soil and on capped mounds with (black) or without (gray) arginine phosphate (AP) treatment across eleven study sites along a north-south gradient in northern Sweden. The diamonds indicate mean values for each position and treatment. The horizontal line in the boxes indicates the median survival value, that is, the value that is in the middle of all observed values. The boxes indicate the range between the lower quartile and upper quartile of the observed values i.e. ~50% of the values for each group are distributed within the boxes. The whiskers (vertical lines) above/below boxes indicate the maximum and minimum values that are not extreme values. Unconnected points outside the boxes represent extreme values that are outside 1.5 times the interquartile range above the upper quartile and below the lower quartile i.e. potential outliers. (B) Proportional survival in relation to precipitation during the first 30 days after planting in capped mounds and (C) mineral soil. Each site is represented by two survival values, one for AP-treated seedlings and one for untreated seedlings. Triangles mark out sites prepared by mounding and circles mark out disc trenched sites. The dashed lines represent the predicted curves from logistic regression models for each of the two planting positions. The gray areas represent the 95% confidence interval for each model.

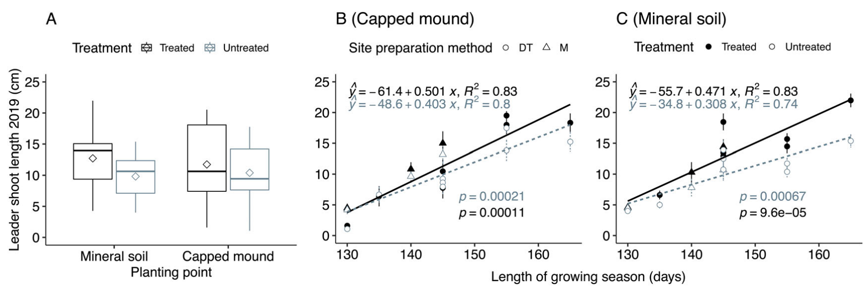

Figure 4. (A) Box and whisker plots of the range of observed mean leader shoot length values of seedlings planted in mineral soil and on capped mounds with (black) or without (gray) arginine phosphate (AP) treatment across eleven study sites along a north-south gradient in northern Sweden. The diamonds indicate mean values for each position and treatment. The horizontal line in the boxes indicates the median of the leader shoot length mean values i.e. the value that is in the middle of all observed values. The boxes indicate the range between the lower quartile and upper quartile of the observed values i.e. ~50% of the values for each group are distributed within the boxes. The whiskers (vertical lines) above/below boxes indicate the maximum and minimum values. (B) Linear relationships between leader shoot length and length of growing season for AP-treated (black text and line) and untreated seedlings (gray text and dashed line) in capped mounds and (C) mineral soil. Points indicate mean values for AP-treated (filled) and untreated (unfilled) seedlings for each site and bars indicate standard error. Triangles mark out sites prepared by mounding and circles mark out disc trenched sites.

Table 3. Results from ANOVA analysis of the effects of site, arginine phosphate (AP) treatment, planting position following mechanical soil preparation and the significant interactions between these variables on the leader shoot length of seedlings following two growing seasons in the field.

	Sum Sq	Df	F value	Pr (>*F*)
(Intercept)	71407	1	3843.73	<0.001
Site	20409	10	109.86	<0.001
Treatment	647	1	34.83	<0.001
Position	72	1	3.90	0.049
Site x Treatment	499	10	2.69	0.003
Site x Position	2114	10	11.38	<0.001
Treatment x Position	84	1	4.51	0.034
Site x Treatment x Position	84	10	0.45	0.919
Residuals	14955	805		

sites, was 71% for untreated and 77% for AP-treated seedlings in capped mounds and 92% for untreated and 93% for AP-treated seedlings in mineral soil. There was also less variation in survival between sites for seedlings in the mineral soil compared to seedlings on capped mounds (Figure 3(A)). Further analysis of the significant interaction between planting position and site revealed that the probability of survival for seedlings positioned on capped mounds increased significantly (p-value = <0.001) with the amount of precipitation at the different sites during the first 30 days following planting (Figure 3(C)), while this relationship was weaker but significantly negative (p-value = 0.01) for the seedlings positioned in mineral soil (Figure 3(B)). The models explained 52% of the variation in survival of seedlings planted in capped mounds and 25% of the variation in of seedlings planted in mineral soil.

Seedling growth in capped mounds and mineral soil

The length of leader shoot varied significantly between sites as well as positions and treatments, with significant pair-wise interaction between the three factors (Figure 4(A), Table 3). Further investigation of the site effect revealed that the length of growing season explained the main part of the site difference (Figure 4(B, C)). The positive effect of AP treatment increased with the length of the growing season, particularly for seedlings planted in the mineral soil (Figure 4(B, C)).

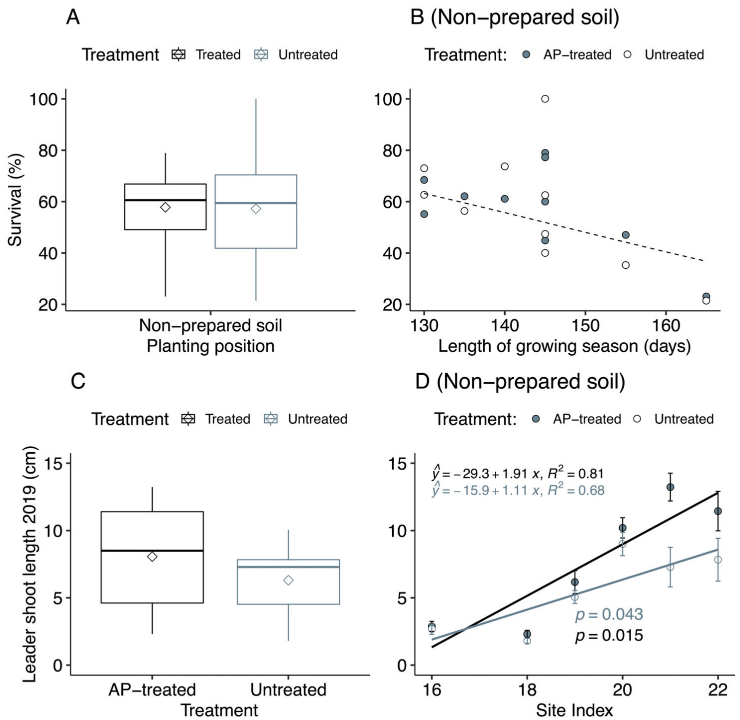

Figure 5. (A) Mean survival of seedlings planted in non-prepared soil with (black) or without (gray) arginine phosphate (AP) treatment across eleven study sites along a north-south gradient in northern Sweden. The diamonds indicate mean survival values for each position and treatment in (A) and mean leader shoot length mean values in (C). The horizontal lines in the boxes indicate the median survival value in (A) and mean leader shoot length mean values in (C) i.e. the value that is in the middle of the observed values for each treatment. The boxes indicate the range between the lower quartile and upper quartile of the observed values i.e. ∼50% of the values for each group are distributed within the boxes. The whiskers (vertical lines) above/below boxes indicate the maximum and minimum values. (B) Probability of survival in relation to length of growing season in non-prepared soil. Each site is represented by two survival values, one for AP-treated seedlings and one for untreated seedlings. The dashed lines represent the predicted curves from the logistic regression model. The gray areas represent the 95% confidence interval. (C) Mean leader shoot length of seedlings planted in non-prepared soil with (black) or without (gray) AP treatment. (D) Linear relationships between leader shoot length and site index for AP-treated and untreated seedlings in non-prepared soil. Points indicate mean values for sites with same site index and bars indicate standard error.

Table 4. Results from ANOVA analysis of the effects of site and arginine phosphate (AP) treatment on survival in non-prepared soil following two growing seasons in the field.

	LR Chisq	Df	Pr (>Chisq)
Treatment	0.03	1	0.87
Site	21.80	9	**0.01**

Table 5. Results from ANOVA analysis of the effects of site, arginine phosphate (AP) treatment and the significant interactions between these variables on leader shoot length in non-prepared soil following two growing seasons in the field.

	Sum Sq	Df	*F* value	Pr (>*F*)
(Intercept)	7372.7	1	1006.58	<0.001
Site	2781.2	8	47.46	<0.001
Treatment	109.6	1	14.96	<0.001
Site x Treatment	148.1	8	2.53	0.01
Residuals	1809.2	247		

Seedling survival and growth in non-prepared soil

In a separate analysis, we investigated the effects of AP treatment on survival and growth of seedlings planted in non-prepared soil. We found that seedling survival was, on average across all sites, 58% in non-prepared soil (Figures 3 and 5(A)). AP treatment had no significant effect on seedling survival (Figure 5(A), Table 4). Instead, we found a significantly negative influence (p-value = 0.01) on seedling survival of the length of growing season i.e. the shorter the growing season, the higher the seedling survival (Figure 5(B)).

There was a positive effect of AP treatment on seedling growth in non-prepared soil, but with a significant interaction between AP treatment and site (Figure 5(C), Table 5). The site index was the most important site variable, affecting growth in non-prepared soil, with the effect of AP treatment being more pronounced at sites with a higher site index (Figure 5(D)).

Discussion

Methods to improve the field performance of planting further are always being looked for as soil scarification and planting are the most expensive forestry investments made by a forest owner. In this study, we have demonstrated that treating pine seedlings with arginine phosphate (AP) at the time of planting can improve both seedling survival and growth. The effect of AP treatment on growth appears to increase with length of growing season for seedlings planted in capped mounds and mineral soil, and with increased site index for seedlings planted in non-prepared soil. We also demonstrated that survival is more variable between sites for seedlings planted in capped mounds than in mineral soil, and that any growth benefits of planting in capped mounds depends strongly on local site conditions. In addition, our results indicated that the mortality of seedlings planted in non-prepared soil increases with a longer growing season.

Supporting our first hypothesis, AP treatment had a positive effect on seedling survival in capped mounds and mineral soil across our 11 study sites along a north-to-south gradient over six latitudes in north Sweden. This positive effect of AP treatment on survival contrasts with findings by other studies of negative effects of nutrient addition when planting conifers, where inorganic N-P-K fertilizers were used (Simpson and Vyse 1995; Rose and Ketchum 2003; Thiffault and Jobidon 2006). The contrasting results may be related to the type of fertilizer used as well as to the dosages, which in the cited studies were 40–175 times higher than in our study. A high fertilizer salt concentration can harm root development which, in turn, negatively affects water uptake (Jacobs et al. 2004). The improvement of survival given by AP treatment could potentially be related to a positive effect of arginine phosphate on root growth and mycorrhiza colonization (Öhlund and Näsholm 2002; Gruffman et al. 2012). Both increased root growth and increased mycorrhiza colonization have been shown to increase the water uptake capacity for seedlings by extension of the absorbing surface of the root system (Bréda et al. 2006; Brunner et al. 2015).

Increased precipitation when the seedlings were establishing had a positive effect on the survival of seedlings positioned on capped mounds, which in part corroborated our second hypothesis. At sites with low precipitation, the differences in survival between seedlings planted in mineral soil and seedlings planted on capped mounds appeared to be larger than at sites with more abundant precipitation i.e. there was an indication that seedlings planted in mineral soil were more resistant to dry weather following planting than seedlings planted on capped mounds (Figure 3(B)). The effect of increased precipitation was negative for seedlings in mineral soil and hence this hypothesis was not corroborated for this planting position. The opposite trends of the curves suggest that seedlings planted in mineral soil are less sensitive to extreme drought, while seedlings planted on capped mounds seem less sensitive to high rates of precipitation. However, survival rates on sites with high precipitation are not exclusively higher for seedlings planted capped mounds. The relationship between reducing survival and increasing precipitation in mineral soil may be due to other unrelated effects, such as frost damage. The largest difference in seedling survival between planting positions was found at sites with lower precipitation during the establishment period. This finding emphasizes the difference between the two planting positions in respect of the risk to planted seedlings when exposed to drought. This variation in drought sensitivity depending on planting position might be one of the reasons why a large variation in survival between sites has been seen in other studies of forest regeneration in the Nordic countries (Hjelm et al. 2019; Sikstrom et al. 2020). The mortality of *P. sylvestris* seedlings has also been found to be strongly related to the number of dry days during the month the seedlings were planted (Sukhbaatar et al. 2020) and seedling mortality is associated with drought stress, even on sites where soil moisture is only low on rare occasions (Burton et al. 2000). The positive relationship between survival and precipitation during the first month explained approximately 50% of the variation in survival for seedlings planted in capped mounds in our model. This reflects that even if precipitation is important, it is not the only variable that affects survival. As Sikstrom et al. (2020) also emphasized, there are multiple causes behind this variation, such as other climatic factors, the mechanical site preparation that has a strong influence on the quality of the available planting area, plant material, handling of the seedlings and how well the seedlings were planted. In this trial, the planting was carried out by experienced planters and only planting positions regarded as good quality were used. The interior quality of the capped mounds was not specifically assessed since this would have been a destructive operation. However, the amount of logging residue could serve as an indicator for general quality of the capped mounds at a site. Smaller amounts of logging residues reduce the risk of a large amount of rough organic material becoming trapped within the capped mounds, thus giving better contact to the mineral soil below where the seedling can utilize capillary rising water. Site B was the only site where both seedling survival and growth were significantly better in capped mounds than in mineral soil. This site was not unique in relation to the combination of other site features, nor at either extreme of the climate variables listed, but it did have relatively smaller amounts of logging residues compared to sites with lower survival based on photographic evidence of the sites. Thereby, the quality of the capped mounds might have been higher at this particular site.

Our third hypothesis was that AP treatment would enhance seedling growth independent of seedling positioning, since increased N uptake is known to have a positive correlation with leader shoot growth in the following year (Grossnickle 2000; Nilsson 2020). We used the length of the leader shoot as an indicator for growth, but it should be noted that the AP treatment is primarily intended to improve the growth of roots and mycorrhiza (Gruffman et al. 2012) and, therefore, shoot length would be a secondary effect of the treatment. This hypothesis could not be confirmed as a general statement since the positive effect of AP treatment on leader shoot growth depended both on site conditions and planting position. However, our results indicated that the positive effect of AP treatment increased with a longer growing season for seedlings planted in capped mounds and in mineral soil. A stronger response to AP treatment was exhibited in mineral soil than in capped mounds. For seedlings planted in non-prepared soil, the site index rather than length of growing season explained the variation in seedling growth, and the growth promoting effect of AP treatment was more pronounced at more fertile sites with higher site indices. This might, as with the positive effect of AP treatment on survival in capped mounds and mineral soil, be related to better root growth and increased mycorrhiza colonization (Öhlund and Näsholm 2002; Gruffman et al. 2012) which would give seedlings planted in non-prepared soil an advantage over competing vegetation, thereby giving these seedlings a chance to benefit from the more fertile site.

We also hypothesized that AP treatment would compensate for the lower nutrient availability in bare mineral soil compared to capped mounds. This hypothesis could not be confirmed because our results indicated that the difference in performance between the two planting positions was highly dependent on site variables, in particular the effect of precipitation during the establishment period on survival, and the length of growing season on growth. Additionally, at most sites, both AP-treated and untreated seedlings planted in mineral soil grew equally well as, or even better than, seedlings planted in tilts. Only at one site (B) did seedlings grow significantly better when positioned in capped mounds. The expectations were that seedlings planted in capped mounds in general would grow better than in mineral soil and that the AP treatment would be needed for the seedlings in mineral soil to grow equally well. One reason behind the somewhat unexpected outcome could be that the summer of 2018 was exceptionally dry, and drought affects both survival and growth negatively (Burdett 1990; Örlander et al. 1990; Bréda et al. 2006; Luoranen et al. 2018). The lack of general superior growth in capped mounds is, however, not unique to our study. In a study by Hjelm et al. (2019), no significant difference in tree volumes was found after 30 years between trees planted in the mineral soil close to the berm after disc trenching and trees planted in capped mounds after mounding.

Our fifth and final hypothesis was corroborated, as survival and growth were both lower in non-prepared soil than in the planting positions resulting from mechanical site preparation. Survival was, on average, only 58% compared to the average survival observed in the mechanically prepared planting positions of 71 and 77% (untreated and AP-treated respectively) in capped mounds and 92 and 93% (untreated and AP-treated respectively) in mineral soil. In contrast to seedlings planted in the mechanically-prepared planting positions, AP treatment had no significant effect on survival in non-prepared soil. Furthermore, survival decreased with length of growing season in non-prepared soil. The negative correlation between survival and length of growing season in non-prepared soil could be seen as an indicator of increased competition from vegetation over the longer the growing season, and might also relate to lower pressure from pine weevil (*Hylobius abietis* L.) at more northly sites and further from the coast i.e. sites with shorter growing seasons (Björklund et al. 2014; Johansson et al. 2015). Both these factors are known to have a negative impact on seedling field performance (Örlander et al. 1990; Nordlander et al. 2011). Pine weevil is a very common cause of damage to planted seedlings in their first years in the field in Scandinavia, and mechanical site preparation is known to reduce the impact significantly (Örlander and Nilsson 1999; Petersson et al. 2005; Nordlander et al. 2011; Wallertz et al. 2018).

Our interpretation of the results is that the initial boost from AP treatment provides an advantage at establishment that is beneficial for survival of seedlings planted in mechanically-prepared planting positions but not in non-prepared soil. For second year growth, AP-treated seedlings seem to be able to utilize more favorable growing conditions i.e. a longer growing season for seedlings planted in capped mounds and mineral soil and a higher site index for seedlings planted in non-prepared soil.

The results presented here apply to sites with dry to mesic moisture classes on silty to coarse till, planted in spring/early summer. This study covers only initial establishment and early growth of the seedlings, and both the high variation in mortality and lack of general superior growth in capped mounds in our study could probably be a consequence of the very dry summer of 2018 and growth patterns might change over time. However, differences found between treatments at an early stage have been found to persist in the following years in other studies (Burton et al. 2000; Thiffault and Jobidon 2006) and a successful establishment is crucial for continued development of the newly planted seedlings (Brand 1991; Grossnickle 2000).

In this study, we have shown that AP treatment can enhance the establishment and early performance of planted Scots pine seedlings. Our results also indicated that seedlings planted in mineral soil are less sensitive to varying environmental conditions compared to seedlings planted in capped mounds. With the expectations of increasingly dry conditions in summer, we argue that the choice of main planting position for Scots pine needs to be adapted to site conditions.

Scots pine is most frequently planted on dry sites due to a relatively high drought hardiness compared to other species and is, therefore, the species that is most vulnerable to drought-induced damage. Variation in precipitation between years is generally large. Hence, there is always a risk of insufficient rainfall in the first weeks after planting for the seedlings to establish well on a certain site. Any site that is not classified as moist due to a near-surface groundwater supply could therefore be defined as potentially drought prone. According to our results, the preferred planting position of Scots pine at drought-prone sites is arguably an elevated position in mineral soil, as this is a safer choice regarding early survival. This argument is in line with other studies and reports that have concluded that planting in capped mounds should be avoided on drought-prone sites (e.g. Lammi (2006) and references therein).

Conclusion

A small addition of arginine phosphate at time of planting had a generally positive effect on the survival of *P. sylvestris* seedlings positioned both on capped mounds and in mineral soil following mechanical site preparation. In a year with low precipitation and high summer temperatures, like 2018, mineral soil appears to be the most appropriate planting position also in north Sweden. This result was supported by the positive relationship between survival and precipitation during the first 30 days following planting for seedlings positioned on capped mounds. The drawback of the mineral soil as a planting position is the low nutrient availability as, in contrast to the capped mounds, there is no decomposition of organic material supporting the establishing seedling with easily accessible nutrients. In this study, seedling growth in the mineral soil and on capped mounds did, however, not differ, but the AP treatment had a stronger positive effect on the growth of seedlings in mineral soil. Also, this positive growth effect increased with the length of the growing season. AP treatment had no significant effect on survival for seedlings planted in soils with no site preparation prior to planting and seedling survival using this planting method decreased as the length of the growing season increased. This negative correlation in part counteracted the positive effect of AP treatment on seedling growth that varied with the site index, that is, the more fertile the site, the more pronounced was the positive effect of AP treatment on seedling growth for seedlings planted in non-prepared soil.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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III

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Large-scale assessment of artificially coated seeds for forest regeneration across Sweden

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Abstract

We report the results of two years' field performance of Scots pine (*Pinus sylvestris*) seedlings regenerated using artificially coated seeds. The coated seeds were used for regeneration on 12 clearcut sites, covering a 1000 km latitudinal gradient across Sweden. The coating was either combined with arginine-phosphate fertilizer (10 mg N per seed) or had no additions. Interactions with environmental variables associated with sites were also assessed. Coated seeds were deployed in May–June 2017 and surveyed in August–September of 2018 and 2019. After two years, the mean establishment rate of seedlings from coated seeds was 56 ± 4% across the 12 sites. The fertilizer addition did not affect survival, and the biomass response to fertilizer varied significantly between sites. Maximum precipitation and wind speed during the first six weeks after deployment were correlated with seedling survival, regardless of fertilization treatment. Establishment increased with increasing precipitation and decreased with increasing wind speed. This highlights the importance of initial weather conditions for the seeds' establishment. Our data suggest that Scots pine regeneration using coated seeds can be practiced in boreal forests, but also that the method is sensitive to the weather conditions at the time of deployment of the seeds.

Keywords Scots pine · Coated seeds · Forest regeneration · Seeding · SeedPAD · Boreal forest

Introduction

In boreal forests, new forest stands have long been artificially regenerated after harvest using nursery-grown conifer seedlings (Nilsson et al. 2010). Currently in Sweden, approximately 80% of the clearcut area, i.e. c. 160,000 hectares per year, is regenerated by this method (Bergquist et al. 2016). This method normally results in 70–80% survival

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of the planted seedlings over the first three years in the field, although it varies greatly with sites, tree species, methods of mechanical site preparation and protection against pests e.g., pine weevil (*Hylobius abietis*) (von Sydow 1997; Holmström et al. 2019; Sikström et al. 2020). However, the use of nursery-grown seedlings is very expensive due to high production costs, as well as the need for planting by hand in a standardized manner that has proved challenging to mechanize (Larsson and Danell 2001; Mattsson and Bergsten 2003; Karlsson and Nilsson 2005).

The development of alternative methods using seeds reduces cost and simplifies mechanization, but their use has been limited due to the generally low establishment success of bare seeds on clearcuts, combined with limited availability of seeds from orchards (Grossnickle and Ivetić 2017). It has, therefore, been of a great interest to forest managers to find ways to enhance the survival and establishment of seedlings following direct seeding. Microsite preparation methods like the use of pyramidal indentations (Winsa and Bergsten 1994; Wennström et al. 1999), covering seeds in substrate (Nilson and Hjältén 2003) and seedbed preparation (Oleskog and Sahlén 2000), have all been shown to increase seedling establishment rates following direct seeding. Such methods may, however, increase silvicultural costs as they require additional investments in site preparation. As an alternative, different techniques have been developed over the years that focus on better protection of seeds from external damage by herbivores, for example (Bellot et al. 2002; Barton et al. 2015; Ceccon et al. 2016) and to improve the germination conditions for seeds (Brofas and Varelides 2000; Becker 2001; Oliveira et al. 2012). A recent product that was developed specifically for use in Nordic boreal forests, LandPuck, features conifer seeds embedded in compressed peat (Wennström 2014). However, so far, large scale field trials to assess the outcomes of forest regeneration have been lacking.

Artificially coating seeds for the delivery of nutrients, protectants, and to ensure growth is a well-developed practice for agricultural crops and horticultural species (Pedrini et al. 2017; Rocha et al. 2019). Such coatings have recently been adapted to the needs of Scots pine (*Pinus sylvestris*) seeds, in particular for boreal forest regeneration. This involves coating seeds with a thin layer of vermiculite wrapped in polysaccharide foil. The foil, made from biodegradable sugars, dissolves quickly when in contact with water, thus attaching and immobilizing the coated seed. The vermiculite forms a cap that traps capillary water transported from the ground, keeping the seed within moist. Previous studies have highlighted the importance of water availability when establishing seedlings from coated seeds, as the success rate largely depends on sufficient moisture retention for the seed to germinate (Winsa 2016). One of the main benefits of this method is the reduced cost because it avoids expensive nursery pre-growing; in addition, deployment can be very speedy (4000–8000 coated seeds/day/planter, compared to 2000–3000 nursery seedlings/day/planter), which offers economic as well as logistic benefits.

One of the major goals in a coated seed-based forest regeneration system is to show a success rate comparable to that of nursery grown seedlings, due to the restricted supply of seeds from orchards. Key factors that determine seedlings' field performance are nutrition and root-shoot ratio of seedlings (Grossnickle 2012). Application of conventional fertilizer (ammonium-nitrate based) enhances the nutrition status of seedlings, but it can also reduce the root-to-shoot ratio (Axelsson and Axelsson 1986). Alternatively, the application of nitrogen fertilizer based on the amino acid arginine has been found to enhance the nutrition of seedlings, promote root development and increase subsequent seedling growth (Cambui et al. 2011; Gruffman et al. 2012; Lim et al. 2021). Thus, applying such a fertilizer directly to the coating may facilitate seedling establishment as well as enhancing growth rates.

In this study, we assess the performance of seeds with a coating including arginine-phosphate fertilizer on 12 clearcuts situated along a south-to-north gradient ranging from latitudes 59°N to 67°N in Sweden. For two consecutive years, we monitored establishment rates and the growth of seedlings grown from coated seeds at the 12 sites. We further examine the effects of site-associated variables to identify environmental factors influencing establishment success of the seedlings. We also tested the effects of some of these variables in a controlled laboratory setting.

Our aim was to examine geographically large-scale field performance of seedlings regenerated from coated seeds and assess whether the performance can be augmented by addition of organic nitrogen fertilizer. We hypothesized that (1) addition of the fertilizer enhances both establishment and early growth of seedlings from coated seeds, and (2) environmental factors affect the seedling establishment.

Materials and methods

The coated seeds were produced by Arevo and SweTree Technologies under the name SeedPAD (afterwards SP). SP consists of a single seed of Scots pine (*Pinus sylvestris*) covered in vermiculite and wrapped in polysaccharide foil with a diameter of 35 mm and thickness of 3.5 mm (Fig. 1). In contact with water, the polysaccharide dissolves, attaching the vermiculite to the underlying mineral layer, thus immobilizing and protecting the seed. The SPs used in the following experiment were either fertilized or unfertilized. Fertilized SPs included the commercial fertilizer arGrow in the coating of vermiculite material, i.e., the fertilizer adds 10 mg nitrogen in the chemical form of the amino acid arginine and 5.5 mg phosphorus as phosphate to each SP.

Both fertilized and unfertilized SPs were deployed in May–June of 2017 to 12 clearcut forest sites across Sweden between the latitudes of 59°N and 67°N (Fig. 2, Table 1). The sites were chosen because of their dry characteristics, locations where Scots pine is commonly planted. Considering the large latitudinal gradient, deployment time had to be adapted to local growing conditions. Therefore, southern sites were planted during May and northern sites during June after the snow melted and at the onset of growing season. Before deployment, mechanical site preparation was performed on all sites in the form of disc trenching. This is a standard scarification process which involves making long furrows and exposing the mineral soil underneath. The SPs were deployed on the exposed mineral soil and marked with sticks next to the deployed pads. Deployment, scarification and marking were performed by forest landowners, i.e., forest companies or private forest owners who were members of a private forest owners' association. Orchard seeds used in the SPs

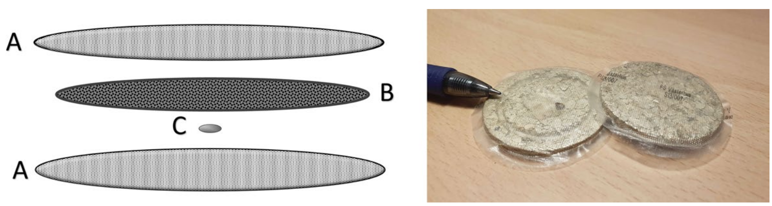

Fig. 1 Left**:** diagram of SeedPAD composition: A—polysaccharide foil, B—layer of vermiculite, C—*P. sylvestris* seed. Right: two unfertilized SeedPADs version 5.0, used since 2016. The pads are deployed with the seed underneath

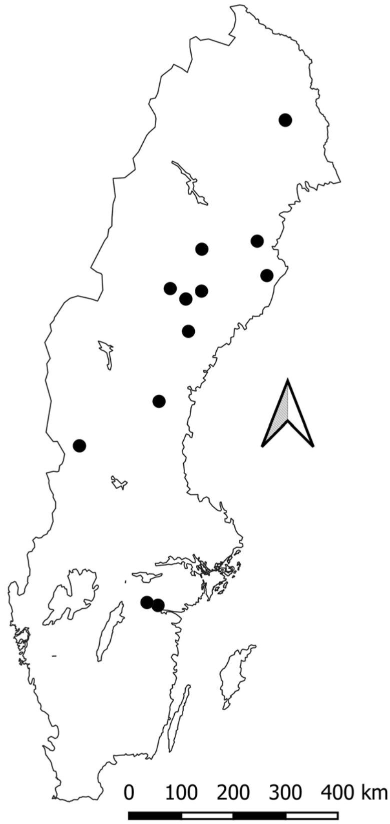

Fig. 2 Map of the 12 study sites between 59°N and 67°N in Sweden

were proprietary to each company and had an average of 98% germination capacity percentage. Non-research parts of clearcuts were regenerated with nursery-grown seedlings.

On each of the 12 regenerated clearcut sites, survey plots were established in the form of circles or rectangles (both 100 m^2) with the location completely randomized (Table 1). Plots were sufficiently away from clearcut edges (> ~ 20 m) to avoid edge effects and thus did not include a buffer zone. Within each of the circular survey plots either 35 fertilized or 35 unfertilized SPs were placed directly on the mineral soil that had been cleared of entire organic dominated layer by the process of soil scarification. The rectangular plots consisted of two parallel 50 m rows, one with 50 fertilized SPs and one with 50 unfertilized SPs deployed directly on the mineral soil. At the sites where both types of plots were established, we had enough buffer area between circular and rectangular plots, and therefore, we used both plot types as similar replicates at each site in the subsequent analyses.

Establishment rate and growth of the seedlings were recorded for each of the two regeneration methods in late August and September of 2018 and 2019. Seedlings were recorded as surviving when there was a live and vigorous seedling next to a marker stick. Growth was measured as distance from the ground to the top of the shoot. Scots pine seedlings growing within a radius of 10 cm around marker sticks were counted as originating from our SPs to account for the possible slight movement of seeds due to precipitation. Marker sticks with either dead (characterized as dried out with brown needles) or missing plants

Table 1 Description of the 12 experimental forest clearcut sites listed from north to south. Mean annual precipitation across the sites was in the range 500–700 mm (2010–2019). Sites with plot type "both" contained plots of both circular and rectangular type

Site name	Location (lat/long)	Elevation [m; a.s.l]	Growing season [days]	Topsoil composition	Plot type	No. of replicated plots	
						SeedPAD unfertilized	SeedPAD fertilized
Rissavägen	66.99/22.13	241	139	Silty till	Both	1	3
Nyback	64.95/20.44	143	170	Coarse till	Both	6	2
Bergsvik	64.88/18.17	268	149	Coarse till	Circular	2	
Backmyran	64.35/20.71	175	170	Coarse till	Both	5	7*
Varpsjovägen	64.22/16.84	364	145	Coarse till	Rectangular	4	4
Tallsjö	64.14/17.92	319	149	Moist till	Rectangular	5	3
Stormon	64.03/17.44	297	145	Till	Rectangular	6	2
Svanatjarn	63.47/17.49	319	146	Till	Both	4	2
Storulvsjö	62.28/16.3	418	146	Moist till	Rectangular	3	2
Nyhult	61.51/13.4	570	146	Sandy till	Circular		2
Lilla Malthult	58.8/15.77	69	194	Sandy till	Both	6*	2
Hostdagskärret	58.75/16.13	86	194	Podzol	Rectangular	6	2

*Due to a sampling error in the 2018 survey, three fertilized plots at Backmyran and two unfertilized plots at Lilla Malthut had to be excluded from the analysis

within the 10 cm radius were recoded as non-surviving. The establishment rate was estimated at the plot scale, as the number of live seedlings per the total number deployed SeedPADs. In addition, in 2019 five seedlings from each treatment plot within each clearcut were carefully excavated and taken for biomass estimation. These samples were dried for 24 h at 60 °C (to a constant weight) cut at the stem base and then the root and shoot parts weighed separately. Based on the harvested samples, we developed allometric equations for roots and shoots using height as a predict variable for each treatment at each site. In contrast to establishment rate, height was recorded on randomly chosen 20 seedlings across all plots for each treatment in each site. Thus, the fertilization effect within a site was not assessed on height or biomass due to non-plot-replication, therefore we only assessed the effect of fertilization across sites.

To assess the cross-site response of establishment rate to fertilization, we recorded environmental factors for each of the 12 sites; type of vegetation present on the clearcut according to National Inventory of Landscapes in Sweden—NILS (Ståhl et al. 2011) and topsoil composition, using visual assessment. Climate data were downloaded from the open database of the Swedish Meteorological and Hydrological Institute. We used data on daily precipitation, temperature, wind, topsoil type, and dates of the onset and end of the vegetation period (a daily mean air temperature ≥ 5 °C) from the nearest available climate monitoring station for each site (mean distance between sampling site and climate station was 32 km and the maximum distance was 46 km). Because we considered that weather conditions around the time of seed deployment and during the growing season after germination, are important factors, we extracted weather data for the first six weeks after deployment in 2017, and during the growing season in 2018 and 2019.

For all the statistical analyses we used R-Studio software (R Core Team 2019). We analyzed response of establishment rate, separate from height and biomass, because the sampling unit of the former is a replicated plot while the latter has no replication at a plot scale. For establishment rate, we assessed the response using a generalized linear model following binomial distribution with logit-link function. After finding no significant effect of the plot shape (circular or rectangular) or its interaction with site, we set fertilizer-treatment, site and their interaction as independent variables, and establishment rate as response variables. For this analysis we used the 10 sites with both fertilizer-treated plots and control plots at each site. Due to an unbalanced dataset (unequal numbers of observations for each treatment), we employed a type III ANOVA model using the car package in R, investigating the effect of fertilizer addition while considering the interaction with site. After concluding that there was no interaction, we employed type II ANOVA. Next, we examined the effects of site-specific weather variables on seedling survival in control plots and fertilized plots, using a generalized linear model across all 12 sites. In order to examine the causality, stepwise selection procedures were employed, based at a level of $\alpha < 0.05$, and the new model was checked with Akaike Information Criteria (AIC) against the previous one. When values of AIC differed by less than 2, the model with fewer degrees of freedom was selected. After several steps this results in a final model including only significant variables. For the response of height and biomass, we performed a type II ANOVA model, without interaction term between fertilization and site. The normality of all models' final residuals were checked visually by plotting them against predictions.

Since precipitation during the first six weeks following deployment of the SPs showed a significant positive effect on seedling establishment, we performed a follow up experiment in a controlled laboratory environment to investigate the relationship between water addition and SP attachment to the ground. The aim was to examine how much water was required for dissolution of the coating and to attach SPs to the ground. We used 135 SPs in total, separated into three different water addition rates combined with three different soil types. The soil used was collected in February 2020 from a forest clearcut site in mid-Sweden and dried in the lab, then sifted to give three different grain sizes. Water addition rates were determined based on local precipitation data averaged for all sites. The grain sizes were set to 1.7, 5.6 and 10.0 mm diameter for fine, medium, and coarse soil, respectively. SPs were placed on a pile of each soil type and room temperature water was dripped onto them using a pipette. At each step, 0.5 ml of water was dripped directly onto the SPs every 1.5, 3 and 5 min for fast, medium, and slow water addition rates, respectively. Dissolution was considered successful when the SP was firmly attached to the ground and could not easily be pushed sideways from the soil without breaking apart.

Results

Two years after forest regeneration, on average 54% of the deployed fertilized SeedPADs (SPs) and 58% of the unfertilized SPs had developed into established seedlings (Table 2). Notably, some seedlings had also established between the first and the second year following the SP deployment, i.e., the establishment rates had increased between the two survey years (Table 2). There was no significant difference in seedling establishment and survival between fertilized and unfertilized SPs for any of the years (Table 3). The effect of site on seedling establishment rate was significant in both years, i.e., it ranged between 87% (at Varpsjövägen) and 22% (at Bäckmyran) (Table 3).

Table 2 Average establishment rate, height and biomass of seedlings established from the SeedPADs. Surveys were performed in August–September 2018 and 2019. Estimated marginal mean values ± SE

	Years after deployment	SeedPAD unfertilized	SeedPAD fertilized
Establishment rate	1	53.4 ± 4.4	46.7 ± 4.9
Establishment rate	2	57.8 ± 4.3	53.7 ± 4.7
Height [cm]	1	6.5 ± 0.3	6.8 ± 0.3
Height [cm]	2	14.6 ± 0.9	14.6 ± 0.9
Total biomass [g]	2	6.5 ± 0.9	5.6 ± 0.9
Shoot biomass [g]	2	5.6 ± 0.8	4.9 ± 0.8
Root biomass [g]	2	0.9 ± 0.1	0.8 ± 0.1
Root: shoot ratio	2	0.2 ± 0.0	0.2 ± 0.0

Table 3 Results (F- and *p*-values) from model II ANOVA examining the effect of fertilization treatment (AP), site and their interaction on SeedPAD establishment rate, height and biomass. Significant effects ($p < 0.05$) are highlighted in bold

	Years after deployment	Treatment	Site	Interaction
Establishment rate	1	F(1,46) = 2.085, *p* = 0.16	F(9,46) = 4.505, ***p* < 0.001**	F(9,46) = 0.823, *p* = 0.60
Establishment rate	2	F(1,51) = 0.089, *p* = 0.77	F(9,51) = 4.155, ***p* < 0.001**	F(9,51) = 1.169, *p* = 0.33
Height	1	F(1,9) = 0.295, *p* = 0.59	F(9,9) = 13.570, ***p* < 0.001**	NA
Height	2	F(1,9) = 0.0001, *p* = 0.99	F(9,9) = 8.470, ***p* = 0.002**	NA
Total biomass	2	F(1,9) = 0.429, *p* = 0.52	F(11,9) = 36.578, ***p* < 0.001**	NA
Shoot biomass	2	F(1, 9) = 0.405, *p* = 0.54	F(11, 9) = 37.368, ***p* < 0.001**	NA
Root biomass	2	F(1, 9) = 0.574, *p* = 0.46	F(11, 9) = 31.621, ***p* < 0.001**	NA

Analyzing the seedlings' growth across the 12 sites, the addition of fertilizer had no significant overall effect on seedling height, biomass or root-to-shoot ratio (Tables 2 and 3) whereas these growth variables varied significantly between the sites (Fig. S1).

To elucidate the factors responsible for the large spatial variation across sites, we considered site-specific weather variables, and found that maximum wind speed and maximum precipitation within the first six weeks after SP deployment had significant effects on the seedling establishment (Fig. 3). High windspeeds following SP deployment had a negative effect on seedling survival recorded at the time of our survey one year later (Fig. 3a). Large precipitation events following deployment, on the other hand, had a positive effect (Fig. 3b).

Our SP dissolution experiment, designed to test water requirements of SPs in a controlled laboratory setting, further highlighted the key role of precipitation for successful forest regeneration with SPs. The results showed two clear trends: increasing the speed

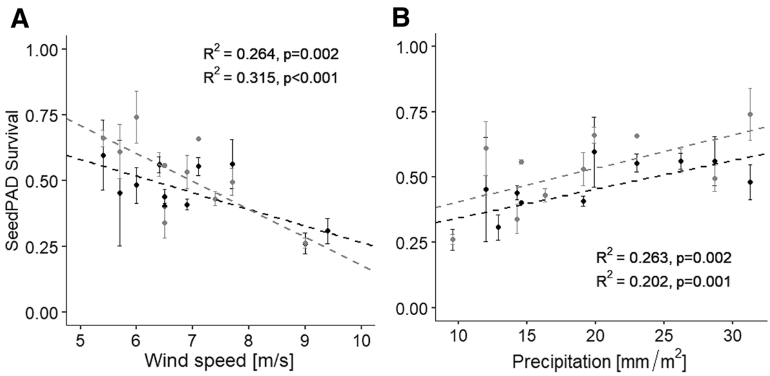

Fig. 3 Effect of maximum wind speed (**A**) and maximum precipitation on a single day (**B**) within six weeks of SeedPAD (SP) deployment in early summer 2017 in 12 clearcut forest sites on establishment of seedlings from unfertilized and fertilized SPs in late summer 2018. Black lines and circles denote fertilized SPs, while gray lines and circles denote unfertilized ones

of water addition resulted in dissolution with less water, while for soils with smaller grain size a smaller volume of water was sufficient for SP dissolution (Fig. 4). On average, SPs on coarse grained soil required 34% more water for dissolution than on fine grained soil. Similarly, the difference between water requirements of fast and slow water application within each soil treatment increased by 27%, 38% and 26% for fine, medium, and coarse soil, respectively.

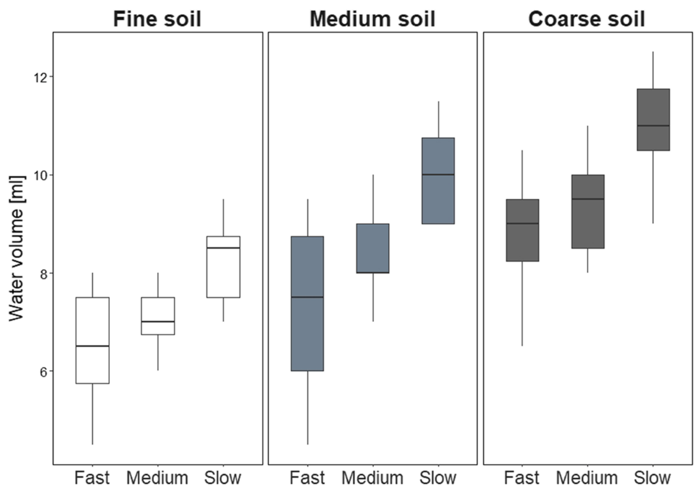

Fig. 4 Water volume required for dissolution of SeedPADs (SP), compared across three different soil textures and speeds of water addition. For soil treatments, grain sizes were set to 1.7, 5.6 and 10.0 mm diameter for fine, medium, and coarse soil, respectively. For speed of treatments, SPs had water dripped onto them every 1.5, 3 and 5 min for fast, medium, and slow treatments, respectively

Discussion

One regeneration goal when using the SeedPADs (SPs) is to achieve comparable results to planting nursery-grown seedlings. The average establishment rate of seedlings from SPs across sites was c. 56 ± 4.5%. Direct comparisons to other regeneration methods were not undertaken in this study, but other studies report establishment rates of conventional direct seeding at c. 20% (Grossnickle and Ivetić 2017), while establishment rates of nursery grown seedlings are reported at c. 76% (Holmström et al. 2019; Sikström et al. 2020). The SP method dramatically increased the seedling establishment rate compared to direct seeding, yet it was c. 35% lower than when planting nursery-grown seedlings. To overcome this deficit, one possible solution could be to deploy a higher number of SeedPADs per hectare. However, increasing seedling density to compensate for lower survival can lead to overstocking, as shown by Ilintsev et al. (2021), which may require additional early tending. Regarding SPs, this remains to be tested over a longer period e.g., following up on SP seedling performance several years into the future, which was beyond the scope of this study. However, it is reasonable to assume that SPs may be exposed to a higher risk of mortality over a longer period than nursery grown seedlings on a clear-cut, as their smaller size makes them more susceptible to damage (Johansson et al. 2015).

The variation in establishment rate in our study was largely explained by site-specific factors, i.e., precipitation and wind speed six weeks after SP deployment, indicating the importance of soil moisture for adhesion of SPs to soils. Indeed, our controlled lab experiment confirmed the importance of the timing and speed of water supply for SP adhesion (Fig. 4). Other factors that may have influenced establishment rates include damage by pine weevil, browsing damage by ungulates and seed predation by rodents and birds, as previously reported in other forest regeneration trials (Heikkilä and Härkönen 1996; Castro et al. 1999; Nilson and Hjältén 2003; Huggard and Arsenault 2009; Bergqvist et al. 2012). Visual inspection of the study plants during two survey seasons revealed no effect of pine weevil or browsing damage, but this may be due to the small size of the study plants. Seed predation, on the other hand, may have occurred prior to the first survey year and seedlings were thus recorded as non-surviving. However, the vermiculite layer may offer protection against seed predation since the seed is completely covered. This suggestion is supported by Nilsson and Hjältén (2003) who showed that covering seeds in substrate following direct seeding reduced seed predation, especially by bank voles (*Clethrionomys glareolus*).

The positive effect of precipitation on SP establishment indicates that initial local weather conditions after SP deployment are crucial for seedling establishment and further development. While it is recommended that *P. sylvestris* seedlings be planted in early summer (Luoranen and Rikala 2013), during this time, precipitation in northern Sweden is relatively low (average 53.1 mm in May–June, 2010–2019) (SMHI 2019). Therefore, at least in this area, we can expect the majority of seedlings from SPs to struggle with early germination. The importance of good contact between roots and available soil water is well documented for the first growing season (Burdett 1990; Grossnickle 2005), and a late start can lead to reduced growth and uneven stand development. To further validate this result, we conducted the dissolution experiment. Here we showed that SPs do, indeed, require a considerable amount of water to properly dissolve, attach and maintain moist conditions close to the seed. We found that water requirements for dissolution were lower on fine soils, owing to a closer contact between the pad with the soil. Further, faster water addition also reduced the total water requirement for dissolution, which confirms the benefit of intense precipitation, as shown by our analysis of field deployed SPs (Fig. 3). Note that our short-term laboratory experiment did not allow for comparable evaporation from the soil media as under clearcut conditions in the field and, therefore, SPs in situ may have required even more water to attach properly, due to evaporation. In relation to this, our model did, indeed, show wind speed as having a negative impact on establishment. The highest recorded wind speed was relatively low (9.6 m/s = 34.6 km/h) thus a reasonable explanation would be the drying effect of wind, as sites with the highest wind speeds were also driest, based on topsoil composition. In this sense, high wind speeds would slow down the process of attachment and germination through removal of moisture from the pads.

Fertilization of SeedPADs with arginine-phosphate had no significant effects on seedling establishment rates. This is in contrast to a recent study by Castro et al. 2021, performed at one of the sites included in the present study (Svanatjarn), who found a 50% increase in establishment rate after one growing season as a result of adding nitrogen-based fertilizer, either in the form of arginine phosphate or mineral ammonium nitrate. However, at this particular site we also recorded increased seedling establishment of arginine fertilized SPs, amounting to 14% after two growing seasons. The apparent site dependency of the arginine-phosphate effect on the seedlings from SPs highlights the interaction between fertilizer application and other environmental variables. Further, while nutrient availability is important for seedling growth, it may not be as important during the early germination process, when water availability is a more important factor. Other studies on the effects of arginine-phosphate additions on survival of nursery grown seedlings in the field have demonstrated both positive effects (Häggström et al. 2021) and no effects (Gruffman et al. 2012).

In comparison to other similar methods of alternative direct seeding (see review by Grossnickle and Ivetić 2017), SPs achieved comparable results to seed shelter methods, where authors report field survival of 54–70% in several species of chestnut four years after planting (Barton et al. 2015). However, a notable downside to seed shelters is the required involvement on planting, which can diminish the cost advantage of direct seeding over nursery seedlings. In this way, simply placing the SPs directly on the mineral soil may avoid such costly involvement while retaining the increased survival benefits.

In conclusion, using SeedPADs significantly augments the establishment of seeds and may have the potential to be used as an alternative method to nursery grown seedlings for forest regeneration, especially in areas with heavy precipitation events in early summer or when combined with manual watering directly after deployment. The method may benefit from further development in relation to SP dissolution and attachment to the ground, to ensure sufficiently moist conditions for successful seed germination and seedling establishment.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11056-022-09920-2.

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Author contributions AN, JÖ and MD contributed to the study conception and design. Material preparation and data collection were performed by MD and BH, analysis was undertaken by MD, BH and HL. The manuscript was written by MD with contributions from all other authors. All authors read and approved the final version of the manuscript.

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Availability of data and material The data that support the findings of this study are available from the corresponding author upon request.

Code availability Not applicable.

Declarations

Conflicts of interest The authors declare no conflict of interest.

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Forest regeneration in Sweden is increasingly challenged by the rapidly changing climate, making traditional management practices less reliable. This thesis examined performance of main regeneration methods across Sweden in the context of variable growing conditions. Adaptations to these conditions were then tested, including mechanical protections against pine weevils, changing of planting positions, addition of organic fertilizer, using coated seeds and applying natural regeneration. Finally, results were put into context of resilience, resistance and transition, with the aim of climate adaptation.

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