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Improving boreal forest regeneration in a variable climate

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Cover: A cross-section of a capped mound where a Scots pine seedling is planted. Photo: Bodil Häggström.

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Errata for
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In Paper II, the first line of page 3 was cut away in the downloadable version of the journal´s PDF that is part of the thesis. This is now corrected by the journal for any future downloads.

Paper II, Page 3	Location: First line is missing Is now: Should be: nitrogen is mainly available to seedlings in its natural organic form i.e., amino acids (Inselsbacher

Improving boreal forest regeneration in a variable climate

Abstract

Regeneration of boreal forests in Sweden mainly involves planting Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) seedlings on clear-cut areas, although there is an increasing interest in planting broadleaves and in applying continuous cover forestry (CCF). Seedling establishment is generally enhanced by mechanical soil preparation. With a warming climate, increases in drought periods and pests can reduce the regeneration success and further consideration of site conditions may be needed during planting. This thesis aims to better adapt boreal forest regeneration practices to local environments. My studies have focused on regeneration with seedlings of Scots pine (Papers I-IV), Norway spruce (Papers II & III) and silver birch (*Betula pendula* Roth.) (Paper II) by analyzing data collected from field experiments from 16 sites in Sweden. Based on this field data, I have evaluated the effects of planting positions (Papers I & III), environmental conditions (Paper I), seedling sizes (Paper III), arginine-phosphate addition (Papers I, II & III), and competition with mature trees (Paper IV). Pine survival was, overall, higher, and less variable over a wide range of site conditions when planted in mineral soil than in capped mounds, especially during dry weather (Paper I). Growth of pine was equal when planted in mineral soil and in capped mounds on most sites studied in Paper I, while growth of pine and spruce in general was lower in mineral soil than in hinge and capped mound positions in Paper III. Damage and mortality by pine weevil on pine and spruce was higher in planting positions where organic material was present (Paper III). Addition of arginine-phosphate enhanced seedling survival and growth on some, but not all sites (Papers I & II), and its effect varied between sites and tree species (Papers I & II) and, for pine, with seedling size (Paper III). For pine seedlings, root isolation and fertilization enhanced growth along the edge of a mature forest (Paper IV), while only root isolation enhanced growth beneath a closed canopy of mature trees (Paper IV). These results emphasize that adapting regeneration practices to the site conditions at the time of planting is a key to success.

Keywords: planting position, growth environment, Norway spruce, Scots pine, silver birch, arginine phosphate, forest regeneration, seedling establishment.

Skogsföryngring i ett varierande klimat – metodanpassning till lokala förhållanden

Sammanfattning

I Sverige föryngras skog efter avverkning oftast med plantor av inhemsk tall eller gran. Intresset ökar dock för plantering med lövträd, som vårtbjörk, samt för hyggesfritt skogsbruk där föryngring sker i konkurrens med större träd. Markberedning förbättrar generellt föryngringsresultaten, som trots detta kan variera kraftigt då standardiserade metoder inte alltid tar full hänsyn till den lokala ståndorten och rådande väderförhållanden. I denna avhandling har jag studerat etablering och tillväxt av tallplantor (Studie I-IV), granplantor (Studie II & III) och björkplantor (Studie II) samt utvärderat effekterna av planteringspunkt (Studie I & III), lokala förhållanden (Studie I), plantstorlek (Studie III), tillförsel av argininfosfat (Studie I-III) och konkurrens med vuxna träd (Studie IV). Överlevnad av tallplantor var över lag högre och varierade mindre när de planterades i mineraljord än på omvända torvor, speciellt vid torra väderförhållanden (Studie I). Tallplantor planterade i mineraljord växte likvärdigt med de planterade i omvända torvor på de flesta lokaler i Studie I, medan tall- och granplantor i Studie III växte sämre i mineraljorden än på omvända torvor av hög kvalitet. Skador och dödlighet orsakad av snytbagge var högre i planteringspunkter med organiskt material i närheten av plantan (Studie III). Tillförsel av argininfosfat ökade överlevnaden på några, men inte alla studerade lokaler (Studie I & II), effekten på tillväxt varierade mellan lokaler och trädslag (Studie I & II) och, för tall, även med plantstorlek (Studie III). Tallplantor i konkurrens med vuxna träd växte bättre om deras rötter isolerades från de vuxna trädens och i hyggeskanter även av kvävetillförsel (Studie IV).

Resultaten framhåller att man kan förbättra resultaten vid skogsföryngring genom att bättre anpassa föryngringsmetoder till lokala förhållanden. Med ett mer variabelt väder under planteringssäsongen, fler och längre torra perioder och ökat tryck av skadegörare kan det alltså vara lämpligt att i högre utsträckning anpassa nuvarande standardiserade föryngringsåtgärder till lokala förhållanden.

Nyckelord: planteringspunkt, tillväxtmiljö, gran, tall, björk, argininfosfat, skogsföryngring, plantetablering.

Contents

List of publications

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

I. **Bodil Häggström***, Matej Domevscik, Jonas Öhlund & Annika 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, 36:6, 423-433, DOI: 10.1080/02827581.2021.1957999

II. **Häggström B.***, Lutter R., Lundmark T., Sjödin F., Nordin A. (2023). Effect of arginine-phosphate addition on early survival and growth of Scots pine, Norway spruce and silver birch. Silva Fennica vol. 57 no. 2 article id 22013. https://doi.org/10.14214/sf.22013

III. **Häggström, B**.*, Hajek, J., Nordin, A., Öhlund, J. Effects of planting position, seedling size and organic N-fertilization on establishment of planted Scots pine and Norway spruce. (manuscript)

IV. **Häggström, B**.*, Gundale, M.J. & Nordin, A. Environmental controls on seedling establishment in a boreal forest: implications for Scots pine regeneration in continuous cover forestry. *Eur J Forest Res* (2023). https://doi.org/10.1007/s10342-023-01609-1

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Papers I, II & IV are reproduced with the permission of the publishers.

The contribution of Bodil Häggström to the papers included in this thesis was as follows:

I. BH is the main author. BH and MD conducted the field survey. BH compiled the data and performed the statistical analyses. In collaboration with the co-authors, BH developed the research questions and wrote the manuscript.

II. BH is the main author. BH participated in the field survey on two of the three study sites covered in the manuscript. BH compiled the data and performed the statistical analyses. In collaboration with the co-authors, BH developed the research questions and wrote the manuscript.

III. BH is the main author. BH participated in the field survey together with HB and JÖ. BH conducted part of the laboratory work. BH compiled the data and performed the statistical analyses. In collaboration with the co-authors, BH developed the research questions and wrote the manuscript.

IV. BH is the main author. BH compiled the data and performed the statistical analyses. In collaboration with the co-authors, BH developed the research questions and wrote the manuscript.

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Abbreviations

AP	Arginine-phosphate
CCF	Continuous cover forestry, i.e., clear-cut free forestry
MSP	Mechanical soil preparation
SI	Site index, i.e., a site productivity measure used in forestry, indicating the average maximum height in meters of dominant and co-dominant trees at a certain age

1. Introduction

Forests are highly dynamic systems in which multiple variables interact with each other and react to external changes, constantly creating new conditions on different scales (Messier et al. 2013). These variables include plants, light, soil conditions, precipitation, fungi, insects, animals etc. As trees also affect their environment, conditions will naturally change as a tree grows. The conditions that are optimal for a seedling to establish in a given position in the landscape will change as the growing tree consumes more water and nutrients as well as casting more shadow. The new conditions may be optimal for various species, such as tree dwelling lichens and microorganisms in the soil that utilize carbon from the tree roots but might not necessarily be optimal for the establishment a new tree seedling (Messier et al. 2013).

Any newly planted or naturally germinated tree seedling needs enough water, light, and nutrients to establish, survive and grow into a mature tree (Margolis & Brand 1990; Grossnickle 2000). The seedling will also be vulnerable to various agents of damage, and in any given environment, the species best adapted to the conditions will thrive while others may perish (Binkley 2021). There are many types of forests, and they all offer a variety of environments, each allowing for different dynamics, species compositions and diversity (Messier et al. 2013). Any given forest regeneration practice can, therefore, have varying effects depending on the environmental conditions of the specific site (Spittlehouse & Stathers 1990). Hence, forest regeneration practices need to be adapted to site conditions.

This thesis is mainly focused on adapting forest regeneration practices to site conditions in boreal forests in Sweden. Boreal forest is the dominant forest type in Sweden, representing the boreal biome which accounts for c. 30 % of the world's forests and covering approximately 14 million km^2 in a broad circumpolar belt, stretching across the northern parts of north America, Europe, and Asia (Gower et al. 2001; Chapin et al. 2011; Thiffault 2019).

Forests in Sweden are mainly managed by rotational forest management, where areas are harvested through clear-cutting practices and replanted with nursery grown seedlings, resulting in a mosaic of even-aged stands in the landscape (SLU 2023). Other ways of managing forest include various continuous cover forestry (CCF) approaches, in which single trees or groups of trees are harvested and mainly replaced by natural regeneration (Pommerening & Murphy 2004). CCF is currently not common in Swedish conditions, but the interest in such management options is increasing. The two most common species used in Swedish boreal forestry are the native conifer species Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) (SLU 2023). There is also a small but increasing interest in planting silver birch (*Betula pendula* Roth), which together with downy birch (*B. pubescens* Herh) are the most common deciduous trees in Swedish forests. Regardless of regeneration method and species, the seedlings face challenges during their establishment phase. Availability of water, nutrients, and light is affected by the local environment, including factors such as abundance of ground vegetation, proximity to mature trees, soil conditions, depth to the water table, weather, and climate conditions (Margolis & Brand 1990; Örlander et al. 1990). Survival and growth are also affected by biotic agents including fungi, insects, and herbivores (Nilsson et al. 2010). Newly planted seedlings are very vulnerable to resource limitations and damage, as the access to soil resources is limited by the small contact surface between their root systems and the surrounding soil (Burdett et al. 1983). The faster a young seedling starts to grow roots, the better its chance of survival and ability to grow and develop into a tree (Grossnickle 2005). Early growth is important also for the seedling to become a part of the future stand; if the seedling grows slower than competing naturally regenerated seedlings, they will likely be removed during pre-commercial thinning which in practice cancels the efforts of planting. Uneven growth of seedlings can also result in dominant seedlings eventually suppressing the surrounding seedlings, resulting in reduced over-all growth of the stand. Hence, the establishment phase is the most important step to successful regeneration (Brand 1991; Grossnickle 2000).

A common aim is to have 1800-2500 vigorous young trees per hectare by the end of the regeneration phase (when the average height in the new stand is approximately 1.3 m), a goal which has been met in between 60 and 80 % of the regeneration areas (Nilsson et al. 2010). The number of approved regenerations has decreased recent years (Skogsstyrelsen 2023a) and recent studies have shown that a large proportion of the planted seedlings is lost during the regeneration phase (Holmström et al. 2019; Gålnander et al. 2020; Ara et al. 2021; Sörensen et al. 2023; Sörensen et al. 2024).

To increase the rate of successful establishment, mechanical soil preparation (MSP) is generally undertaken on planting sites (Skogsstyrelsen 2023b). The most common methods in Sweden are mounding and disc-trenching. These methods produce patches or furrows lower than the original ground level where the mineral soil is exposed. The removed top organic material (humus and ground vegetation) is turned upside down adjacent to the patch/pit (mounding) or furrow (disc-trenching) and is ideally capped by a layer of mineral soil. The resulting mounds or ridges are both referred to as capped mounds in this thesis. The disturbance of the soil allows a temporary reduction in vegetative competition and promotes an increase in soil temperature which is positive for root growth (Örlander et al. 1990; Sutton 1993; Löf et al. 2012). In addition, planting in positions surrounded by exposed mineral soil decreases the risk of damage from pine weevil (*Hylobius abietis* L.), which is one of the major threats to small seedlings (Örlander & Nilsson 1999; Kindvall et al. 2000; Thorsen et al. 2001; Björklund et al. 2003; Petersson & Örlander 2003; Petersson et al. 2005; Wallertz et al. 2005; Nilsson et al. 2010; Luoranen et al. 2017; Wallertz et al. 2018). The capped mound is often considered the best planting position due to the higher nutrient availability from decomposing organic material within, and with the elevation above ground level resulting in a higher temperature and decreased risk of oxygen deficiency at moist sites. However, a higher position can be hazardous during dry weather and on dry sites, where the capped mound can become too dry for the seedling to survive because the organic layer in the mound restricts capillary water flow from below (Örlander et al. 1990).

In the first report from a countrywide forest regeneration inventory study ("Föryngringskollen" = "The regeneration control", coordinated by the Forestry Research Institute of Sweden), on average only ~1500 out of the expected 2000-2500 planted seedlings/ha were found (dead + alive) during the year following planting (Berglund et al. 2022; Öhlund et al. 2023). Among the found seedlings, mortality was higher in capped mounds than in mineral soil positions and survival was lowest in northern Sweden where on average only 1250 seedlings/ha were found alive (Öhlund et al. 2023).

A safer choice of planting position in relation to water availability on dry sites and in dry conditions is directly in the exposed mineral soil in the patches and furrows adjacent to the capped mounds, where capillary water flow from below is not restricted by any organic layer. However, the lower nutrient availability in the mineral soil position compared to the capped mounds could lead to reduced growth.

A potential tool to compensate for reduced growth in the lower planting position, and to aid early establishment in general, is to add slow-release nitrogen fertilizer at the time of planting (Burdett et al. 1984; Brand 1991; Jacobs et al. 2005; Thiffault & Jobidon 2006). An organic slow-release nitrogen fertilizer based on arginine phosphate has recently become available for this purpose, with limited but increasing use in commercial forestry. Liquid fertilizer with arginine as the nitrogen source has shown positive effects on root growth in previous nursey studies (Öhlund & Näsholm 2002; Gruffman et al. 2012).

Due to the rise in temperature, situations with high evaporation which can be associated with low soil moisture scenarios during the growing season are likely to become more common in many areas in Sweden (Eklund et al. 2015). Such scenarios have negative consequences for tree growth and mortality (Aldea et al. 2023). This is part of a global issue for future forests, where there is an increasing tendency for tree mortality across the world, with elevated temperatures and water stress being common casual factors (Allen et al. 2010; DeSoto et al. 2020; Senf et al. 2020; Hartmann et al. 2022; Urli et al. 2023). Together with increasing periods of low precipitation during early summer when most seedlings are planted, as observed in recent years, the newly planted seedlings will become increasingly exposed to the risk of drought. This also makes seedlings planted in capped mounds on dry sites even more vulnerable. In addition, it is predicted that pests that benefit from a warmer climate will increase in areas where they may previously have been rare. Clearly, it is becoming increasingly important to adapt forest regeneration practices to local site conditions.

This thesis is based on four papers in which I investigated the effect on early establishment and growth of the following regeneration practices in field studies: the effect of planting position and arginine phosphate on pine in multiple sites representing a wide range of field conditions (Paper I), the effect or arginine phosphate on pine, spruce, and birch in three field case studies (Paper II), the effect of planting position- and quality, arginine phosphate addition and seedling size on pine and spruce in a field case study (Paper III). I also studied the effect of root isolation and nitrogen fertilization on pine in relation to the vicinity of mature trees (Paper IV).

1.1 Aim and research questions

The aim of this thesis is to better adapt boreal forest regeneration practices to local environments and variable climates. The goal is to increase the chance of achieving successful seedling establishment in a variable and changing climate, by using the knowledge we have about how seedlings interact with their growing environment. The aim was addressed through the following research questions:

I. Can survival of planted seedlings be improved by choosing planting position depending on local environmental conditions? (Paper I, III)

II. Will addition of a slow-release organic nitrogen fertilizer in the form of arginine phosphate improve establishment and early growth of planted seedlings? (Papers I, II, III)

III. How can seedling establishment be improved in proximity to mature trees? (Paper IV)

The thesis will, hopefully, offer guidance for forest managers about how to improve their ability to achieve regeneration goals in boreal forest silviculture, both in the present and under future climate scenarios. In the following chapters, more detailed descriptions of the environmental conditions in Sweden, plant physiological needs and forest regeneration practices will be introduced, followed by a summary of our materials and methods as well as main results. The last chapter comprise a discussion of the results and avenues for future research, followed by concluding remarks.

2. Forest regeneration in Sweden

> "It is important to determine which resources are likely to limit growth prior to choosing the site preparation treatment. The limiting resources are ecosystem specific. The effect of different treatments can also vary with the ecosystem being treated." SPITTLEHOUSE & STATHERS, 1990

As emphasized by SPITTLEHOUSE & STATHERS, it is important to consider the ecosystem specific conditions that affect growth. Overarchingly, the ecophysiological conditions across Sweden is strongly characterized by the northern climate, with short vegetation periods and relatively cold temperatures even during the growing season. In this chapter, I first describe the climate and forests in Sweden. I then describe the main factors that limits tree seedlings establishment, survival, and growth in these forests following clear-cut harvesting. Thereafter, I describe Swedish forest regeneration practices and some methods developed to mitigate the limiting factors to enhance seedling establishment and growth.

2.1 Climate in Sweden

The boreal climate and daylight conditions are strongly seasonal, with cold winters and a relatively short growing season. In addition, light conditions vary greatly with latitude within the boreal biome: maximum daylight hours in the growing season vary from 16 hours in the south to 24 hours in the north (Thiffault 2019). Sweden spans latitudes 55-69° N, with a general increase in altitude towards the northwest, presenting a large variation in length of growing seasons (Fig. 2a). Annual precipitation is commonly 600-800 mm

(Fig. 2b), and annual mean temperature is highest in the south, decreasing with latitude and altitude (Fig. 2c). The climate has changed the last 30 years compared to the previous 30 years, with a general increase in growing season, mean annual mean temperature and precipitation in large parts of the country (Fig. 3a-c).

Despite an over-all trend towards increasing precipitation in Sweden since the beginning of the 20th century, especially in the winter and in northern areas, the southeast part of the country has become drier (Chen *et al.* 2021), and an increase in drought periods during the growing season is predicted for large parts of the country, especially in spring (Spinoni *et al.* 2018).

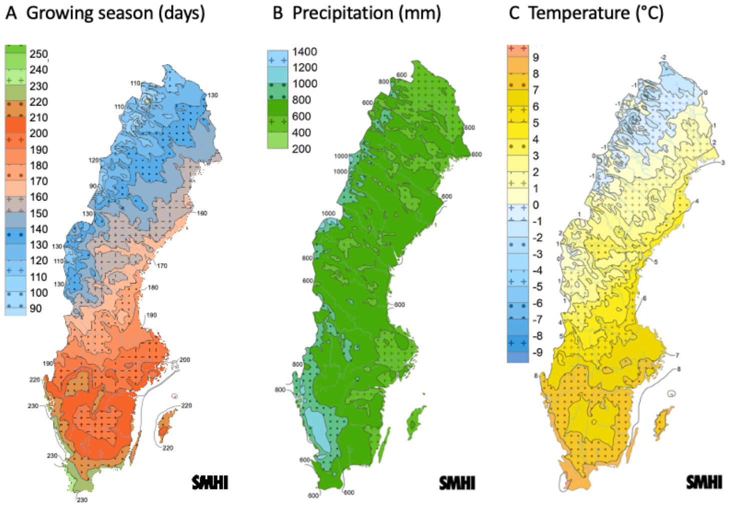

Figure 1. Annual mean values of A) length of growing season (days), B) precipitation (mm), and C) temperature (°C), for the reference period 1990-2020 (SMHI 2023).

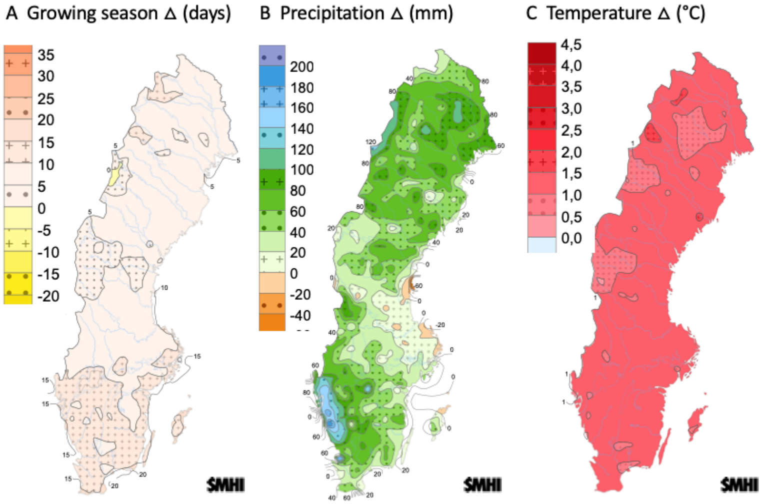

Figure 2. Difference in mean annual A) length of growing season (days), B) precipitation (mm) and C) temperature (°C) between the previous reference period 1961-1990 to the reference period 1991-2020 (SMHI 2023).

2.2 Forests in Sweden

The most common tree species of Swedish forests are the native conifers Norway spruce (*Picea abies* (L) H.Karst) and Scots pine (*Pinus sylvestris* L.). These are also the most utilized tree species in Swedish forestry. Each of these conifers accounts for approximately 40 % of the forests considered productive in Sweden, i.e., a forest growing more than 1 m^3 ha^{-1} yr^{-1} according to the definition of the Swedish Forest Agency (Skogsstyrelsen 1995). Norway spruce is more dominant in the southern parts of the country and Scots pine in northern parts (SLU 2021). The most common deciduous tree species are downy birch (*Betula pubescens* Ehrh) and silver birch (*Betula pendula* Roth). All these species are adapted to be able to grow in the area despite the comparatively short growing season (Prentice et al., 1992). However, as with all other plants, these tree species also need sufficient light, water, and nutrients to survive and grow. The availability of these resources is influenced by the surrounding environment: weather, occurrence of other vegetation, as well as soil moisture holding capacity and nutrient availability (Margolis & Brand 1990). How effectively these resources can be utilized also depends on other factors such as temperature and soil texture (Örlander *et al.* 1990; Stathers & Spittlehouse 1990). All these factors vary with geographical location and landscape position.

The tolerances to different site conditions vary between tree species. For example, species referred to as shade-intolerant grow better in high-light conditions but suffer from higher mortality in low-light conditions than shade-tolerant species (Kobe *et al.* 1995). The expression “shade tolerant” does not exclusively refer to light conditions, since a shaded position, in many cases, simultaneously experiences competition for belowground resources, such as under a canopy of mature trees. Rather, a shade-tolerant species is a species that can cope better with competition than a shade-intolerant species (Binkley 2021). Norway spruce is shade-tolerant and grows well on medium to fertile soils. Scots pine is shade-intolerant but more drought tolerant and can, therefore, be planted at sites where spruce would grow poorly, such as dry sandy to coarse soils with low fertility. Even though both species can regenerate naturally under a canopy, Scots pine needs very open canopies or open areas to establish, grow well and survive, while Norway spruce can both grow and survive in small openings, 0.05 ha or less (Erefur 2010). In the following sections, plant physiological needs and resource limiting factors are described and set in the context of boreal forests in general and Norway spruce and Scots pine in particular.

Figure 3. A typical Scots pine forest in northern Sweden with a ground cover of ericaceous dwarf shrubs. A naturally regenerated spruce has emerged, while natural regeneration of Scots pine is absent. Photo: B. Häggström.

2.3 Environmental factors limiting forest regeneration

Both environmental abiotic and biotic factors can limit the successful establishment and growth of a tree seedling (Margolis & Brand 1990). These must be accounted for to achieve successful regeneration. There are environmental variations both on large and small scales, i.e., between regeneration sites at the landscape level, as well as within any given regeneration site. In addition, the different factors interfere with each other and vary over time (Messier *et al.* 2013). Hence, the practice of forest regeneration is carried out in a complex context, involving uncertainty and risk. Furthermore, site conditions are affected by local climate. With a warming climate, it is predicted that situations with low soil moisture during the growing season will become more common in many areas in Sweden (Eklund *et al.* 2015).

2.3.1 Water and soil texture

A tree seedling's water balance is determined by available water in the soil and the humidity of the air. The root system of a newly planted seedling is relatively small and, therefore, has very limited access to any soil resources, making it highly susceptible to water stress before new roots have developed (Burdett *et al.* 1983; Burdett 1990). Under water stress, the growth of roots slows down, further limiting the water and nutrient uptake capacity of the seedling (Nordborg & Welander 2001). If the root system cannot provide sufficient water, plants can close their stomata to prevent lethal water loss (Burdett 1990; Örlander *et al.* 1990; Grossnickle 2005). However, closing stomata prevents carbon dioxide from entering the leaf and thus prevents photosynthesis, which is the prerequisite for growth of both the roots and aboveground biomass (Burdett 1990; Örlander *et al.* 1990). Hence, early root growth is essential to ensure sufficient water uptake (Burdett 1990; Grossnickle 2005).

Seedlings' vulnerability to conditions with insufficient water is influenced by the soil properties. In the soil, water moves from areas with high water potential to areas with low water potential by capillary flow (Örlander *et al.* 1990). This enables water to become available to the seedlings from lower parts of the soil profile during periods when the weather conditions are dry and the upper soil layers become depleted by evapotranspiration. Soil texture affects this capillary flow rate as it is slower in coarse soil with large pore spaces, through which water also easily drains away if the soil is dry; soil with relatively finer soil particles has smaller pore spaces that lead and keep water better (Grossnickle 2005). However, water also binds more to the surface of very fine soil particles, which means that soils containing large quantities of silt and clay can still have relatively low amounts of water available for plants to take up (Örlander *et al.* 1990). Hence, medium textured mineral soils have more plant available water than coarse and fine mineral soils. Undisturbed soil is often naturally relatively densely packed and additional compaction of soils by, for instance, forestry machinery can have negative effects on soil properties that are important for successful forest regeneration (Örlander *et al.* 1990). Densely packed soil particles with low porosity present both a low capillary flow rate, and a mechanical obstacle for root penetration, thus affecting root growth negatively (Örlander *et al.* 1990; Kremers & Boosten 2018). In wet conditions, a dense soil can also suffer from oxygen deficit; a minimum air volume of 10 % is generally required to supply enough oxygen for root growth (Örlander *et al.* 1990). Local topography is a strong driver of soil moisture availability (Högberg 2001; Ågren *et al.* 2014), hence low and flat areas are at greater risk to present wet conditions than uphill areas.

Therefore, during planting, it is crucial to be aware of the local topography as well as soil texture and to plant the seedling in a spot where both water and oxygen availability are secured (Burdett 1990; Örlander *et al.* 1990; Grossnickle 2005).

2.3.2 Light and temperature

Light is required to maintain seedlings' photosynthesis, and in northern latitudes the amount of light received by seedlings over the growing season is affected by the position in the landscape more than it is in more southern latitudes. At high latitudes, solar radiation falls at an angle and this affects the amount of radiation received in a small forest gap which is shaded to various degrees by the surrounding trees (de Chantal *et al.* 2003; Erefur 2010). The amount of light received affects the proportions of a tree, partly shaded trees can grow taller but thinner while a tree in intense light grows wider (Pearson 1936). More even light distribution during the day is more beneficial for growth than diurnal variation, which occurs in a gap; this is more important for shade-intolerant species than for shade-tolerant species (Wayne & Bazzaz 1993). Aboveground growth of both Scots pine and Norway spruce increases with increasing solar radiation, but Scots pine more so than Norway spruce due to its higher capacity to utilize sunlight (de Chantal *et al.* 2003). Scots pine can respond to increased light by allocating resources for increased needle length to a higher degree than Norway spruce and thus the species is able to increase its leaf area which, in turn, increases the photosynthetic capacity (de Chantal *et al.* 2003).

A natural consequence of the positive correlation between seedling growth and solar radiation is that seedlings grow more in cleared areas than under canopy cover, as well as more on the south side of trees and south-facing slopes than the north sides and slopes (Spittlehouse & Stathers 1990; Erefur *et al.* 2011).

Light not only affects growth via photosynthesis, but also by increasing the air and soil temperature (Pearson 1936). Altitude, slope, aspect and shade conditions affect the amount of solar radiation that provides the energy to warm the air and soil (Stathers & Spittlehouse 1990). The lower limit of temperature tolerated varies greatly between tree species. Broadleaved evergreen trees in the tropics only tolerate a minimum of 0°C, while the boreal forests' needle-leaved evergreen trees can tolerate -60°C (Prentice et al., 1992). Boreal summer-green deciduous trees can tolerate even lower temperatures (Prentice et al., 1992). The minimum requirement for growth for these cold-hardy species is 5°C and the length of growing season is, hence, the number of days with temperatures above this threshold in the boreal biome (Prentice et al., 1992). As Sweden spans a wide range of latitudes as well as elevations, the length of the growing season ranges from approximately 110 days in the north to 240 days in the south (Fig. 1). Hence, the growth of trees in Sweden is strongly correlated to air temperature sum (Perttu & Morén 1994). Although growth increases with temperature, net photosynthesis decreases above air temperatures of 30°C (Spittlehouse & Stathers 1990).

Soil temperature varies greatly both seasonally and diurnally, with weather and amount of solar radiation as well as with soil moisture, depth and texture (Stathers & Spittlehouse 1990). For example, on a hot day, the soil surface on a southern slope can reach 70°C in an open area while remaining below 30° C in a shaded area (Stathers & Spittlehouse 1990). Furthermore, as a dark surface absorbs more solar radiation than a light surface, soil temperature also increases more on a burnt surface or organic soil surface than on a surface covered with light colored sand (Stathers & Spittlehouse 1990). Temperatures above 50°C are lethal for root cells, while low soil temperatures reduce root growth (Örlander et al., 1990; Grossnickle, 2005). The optimum soil temperature for root growth varies between species (Heninger & White 1974): for Scots pine it is approximately 30°C and for Norway spruce 25°C (Kamra & Simak 1968; Örlander *et al.* 1990). Furthermore, water uptake capacity decreases above and below soil temperatures of 30-35°C for Scots pine and 20-25° for Norway spruce*,* and nutrient uptake decreases, both as a consequence of decreased water uptake capacity and reduced root respiration with decreasing temperature (Örlander et al., 1990). Organic soil quickly warms, but also works as insulation and the mineral soil below remains cold (Örlander *et al.* 1990; Stathers & Spittlehouse 1990). In the Nordic countries, the temperature below the humus layer rarely exceeds 20°C (Örlander et al., 1990).

Even if the soil surface is warm, the temperature can drop quickly with depth (Stathers & Spittlehouse 1990). Soil texture and moisture content affects heat transfer in the soil. Dry soil surfaces change temperature faster and thereby warm faster than wet soil surfaces, but heat transfer is slower in dry soil, which means that below the surface it will still be colder in a dry than a wet soil (Örlander *et al.* 1990). Heat transfer also increases with air content and decreases with humus content (Örlander et al. 1990; Stathers & Spittlehouse, 1990). Heat holding capacity also differs between soils: organic soils can store less heat than mineral soils, meaning that even though a dry organic soil surface can warm quickly during the day, it also releases more heat to the atmosphere and thus becomes colder than a mineral surface at night (Stathers & Spittlehouse, 1990).

When canopy cover is removed by tree harvesting, more light reaches the ground and the temperature at the ground increases (Grossnickle, 2000). Transpiration decreases due to the removal of trees, leading to increased stream flow and potentially higher soil moisture (Grossnickle 2000). The temperature can vary greatly between day and night in a cleared area since the long-wave radiation from the ground to the cooler atmosphere is not interrupted by any canopy cover; the ground temperature varies less under the shelter of a canopy, where less heat comes in during the day and less goes out at night (Örlander & Karlsson, 2000; Hannerz & Gemmel, 1994). Retention of so-called shelterwood, where some mature trees are left during the regeneration phase, can, therefore, offer an environment that is less affected by both frost and heat (Hagner 1962; Hannerz 1994). However, for the new generation to survive and grow continuously, the shelter trees must eventually be removed.

2.3.3 Nitrogen

Nutrients are mainly made available to plants from the decomposition of plant litter on the forest floor by soil microorganisms i.e., bacteria and fungi (Högberg *et al.* 2017). As in many other forest types globally (LeBauer & Treseder 2008), nitrogen is generally the limiting nutrient in boreal forests and most plant-available nitrogen is found in the humus layer (Hesselman 1926; Tamm 1991; Grossnickle 2000; Bhatti *et al.* 2006; Hyvönen *et al.* 2008; Högberg *et al.* 2017). Some nitrogen is added to the system by atmospheric nitrogen deposition and dinitrogen-fixing bacteria active in soil, mosses and in some tree species, and some is removed by denitrification and leaching, but most nitrogen in boreal forests is re-used within the local plant-soil ecosystem (Sponseller *et al.* 2016; Högberg *et al.* 2017).

Nutrients are heterogeneously distributed in forest soils (George *et al.* 1997). Some tree species, like Norway spruce and Scots pine, respond by increased root growth in nutrient richer soil patches (George *et al.* 1997). Plant available nitrogen in boreal forest soil is mainly in organic form (amino acids), but inorganic sources (ammonia and nitrate) are also utilized (Nordin *et al.* 2001; Inselsbacher *et al.* 2011; Inselsbacher & Näsholm 2012; Högberg *et al.* 2017). The soil microorganisms retain most of the available nitrogen in these nitrogen-limited soils and the turn-over rate is high (Schimel & Bennett 2004; Kielland *et al.* 2007; Högberg *et al.* 2017). Soil microorganisms not only degrade litter, but also utilize easy degradable carbon substrates that are exuded by tree roots, and the high carbon availability enables high nitrogen consumption as well (Clarholm 1985; Nazir *et al.* 2009; Högberg *et al.* 2017). Among the microorganisms, mycorrhizal hyphae have a competitive advantage over bacteria in nutrient poor soils due to their ability to transfer carbon to nutrient-rich areas in the soil and nutrients back to carbon-rich soil areas (Gower et al. 2001; Lindahl et al. 2002; Boberg et al. 2010).

The dominant plants of boreal forest, such as Norway spruce and Scots pine, as well as ericaceous dwarf shrubs such as bilberry (*Vaccinium myrtillus* L), lingonberry (*Vaccinium vitis-idaea* L*)*, heather (*Calluna* *vulgaris* L.) Hull) and crowberry (*Empetrum nigrum* L*)* common to Swedish forests, live in symbiosis with mycorrhizal fungi, which colonize the root tips and provide nutrients to the plant in exchange for carbon (Franklin *et al.* 2014; Högberg *et al.* 2017). The mycorrhizae also increase the area accessed for nutrient and water uptake for these plants (Bréda *et al.* 2006; Brunner *et al.* 2015). However, mycorrhizal fungi quickly immobilize any free nitrogen source in poor soils and only transfer what they do not need themselves to grow (Öhlund & Nasholm 2001; Alberton et al. 2007; Näsholm et al. 2013; Franklin et al. 2014; Högberg et al. 2017). In intermediate soils with more abundant nitrogen, the host trees receive relatively more nitrogen per invested C while in richer soils the microbial community is instead carbon-limited and the nitrogen cycle is more open, both with more incoming N with downwards flow and with more leaching of NO_3^- and denitrification (Högberg et al. 2006; Högberg et al. 2017).

The nitrogen supply rate is also affected by temperature, as mineralization increases with increasing temperature (Rustad *et al.* 2001; Strömgren & Linder 2002). Nitrogen is released when microorganisms and plant roots die, but also if their supply of carbon decreases (Högberg et al., 2017). Naturally, when trees are harvested, the supply of carbon decreases, followed by release of nitrogen which can be utilized by the next generation of trees.

2.3.4 Vegetative competition

One of the main obstacles to successful forest regeneration is vegetation competition (Wagner *et al.* 2005). This includes competition for light as well as belowground resources, and competition from mature trees as well as ground vegetation. Methods to decrease vegetation competition greatly enhance the outcome of both forest regeneration and long term productivity worldwide (Wagner *et al.* 2005). Herbicides are used in many countries (Wagner *et al.* 2005; Willoughby *et al.* 2009), but in Scandinavia this is prohibited. Instead, mechanical soil preparation (MSP) is the common tool to reduce vegetative competition during the regeneration phase.

Different tree species have different levels of tolerance to competition. Numerous studies have concluded that Scots pine seedlings are suppressed within 5-10 m of mature trees, even in full sunlight along clear-cut edges and near retained mature trees (Aaltonen 1919; Björkman 1945; Hagner 1962; Valkonen *et al.* 2002; Elfving & Jakobsson 2006; Kuuluvainen & Yllasjarvi

2011). The relative impact of competition for light and belowground resources (i.e., water and nutrients) depends on which of the resources is most limiting: on a dry and poor soil, the competition for water and nutrients limits the potential positive effects of increased light availability (Coomes & Grubb 2000).

In Swedish forests the most common field layer species are the ericaceous shrubs bilberry (*Vaccinium myrtillus* L.), lingonberry (*Vaccinium vitis-idaea* L.*)*, crowberry (*Empetrum nigrum* L.*)* and different grasses like the common wavy hair grass (*Avenella flexuosa* L.) (SLU 2023). The most common bottom-layer species are the red-stemmed feather moss (*Pleurozium schreberi* (Brid.) Mitt**.**), the splendid feather moss (*Hylocomium splendens* (Hedw.) Schimp.) and various peat mosses (*Sphagnum* L. spp.) (SLU 2023).

Regeneration of Norway spruce in bilberry dominated forest in northern boreal spruce forest is mainly restricted to spots where the ground vegetation is disturbed (Arnborg 1990; Kuuluvainen 1994), and failure of Scots pine regeneration is often associated with intermediately fertile sites where bilberry or grasses dominate the ground vegetation. Bilberry can take up organic nitrogen (e.g., glycine) more effectively than Scots pine (Näsholm *et al.* 1998), and feathermosses, heather, and wavy hairgrass are also known to inhibit germination and growth of seedlings by competition for nutrients (Zackrisson *et al.* 1997; Norberg 2000). Some understory species can also affect tree seedlings' establishment negatively by allelopathy, i.e., release of chemical compounds that may inhibit germination and growth. Ericaceous shrubs, such as bilberry, lingonberry and crowberry all produce phenolic compounds that can bind nitrogen, thus inhibiting the growth of conifer seedlings by further reducing the availability of nitrogen in an already nitrogen limited forest (Örlander *et al.* 1990; Pellisier 1993; Mallik & Pellissier 2000; Mallik 2003; Thiffault *et al.* 2015). Many studies have shown that especially bilberry and crowberry can inhibit seedling establishment and growth by both direct resource competition and allelopathic effects (Nilsson & Zackrisson 1992; Pellisier 1993; Gallet 1994; Nilsson 1994; Jäderlund *et al.* 1996; Jäderlund *et al.* 1997; Zackrisson *et al.* 1997; Jäderlund 2001). The effect from an allelochemical depend on concentration, and production of allelochemicals increase at stress such as low resource availability, extreme temperatures, disease etc. (Reigosa *et al.* 1999). The production of phenolic compounds is also affected by change in environmental conditions, for example it is higher in bilberry on clear-cuts than under closed canopies (Nybakken *et al.* 2013). Interaction between different plant species by allelopathy and direct competition for resources is complex and vastly more explored in agriculture than in forestry, but as more advanced analytic techniques develop, the chances of entangling growth inhibiting effects increase (Weidenhamer *et al.* 2023).

Competitive interactions between forest understory species and tree seedlings are very different in a closed forest compared to an area of forest newly harvested by clear-felling, as some ground vegetation species that occur sparsely in the forest become more abundant after harvest can pose problems for forest regeneration. When the tree canopy is removed by harvesting, grass species are generally strongly favored as are nitrogen-loving shrub species like raspberry (*Rubus idaeus* L.). Furthermore, colonization of bracken (*Pteridium aquilinum* (L) Kuhn.) on harvested areas can present strong competition for resources as well as seasonal chemically inhibitory effects for tree germination and growth (Dolling *et al.* 1994). While direct competition between tree seedlings and Ericaceous shrubs may predominantly occur as competition for belowground resources, grasses and raspberry may also compete with tree seedlings for light as they can overgrow tree seedlings in open areas if the nutrient availability is sufficient for rapid grass expansion. However, belowground competition from ground vegetation for both water and nutrients can be more important than light competition for planted seedlings (Nilsson *et al.* 1996).

Trees within a stand also compete against each other. This competition is important for structuring the stand and, by managing it, different outcomes can be reached. When suppressed trees are relieved from competition, such as when retention trees and trees remaining after a partial harvest or thinning are removed, they first allocate growth to roots before aboveground growth increases (Kneeshaw *et al.* 2002; Pretzsch *et al.* 2014; Lehtonen *et al.* 2023). It has been suggested that this is a strategy to adjust the shoot:root ratio so that the root uptake of water and nutrients can match the increase in photosynthesis rate and transpiration that follows from increased solar radiation (Kneeshaw *et al.* 2002). The time lag before the tree responds to relief from competition of larger trees with height growth varies between species. For example, lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) exhibited a time lag of 2-3 years before height growth increased relative to the growth before partial harvest of the overstorey (Kneeshaw *et al.* 2002), while Norway spruce seedlings in gap cuttings exhibited a time lag of five years before responding with increased height growth (Hökkä & Mäkelä 2015). This time lag in *Picea* spp. have been hypothesized to be because the needles that had adjusted their photosynthetic capacity to the low light conditions and needed to be replaced before the higher light conditions could be utilized. However, recent research has shown that photosynthesis rate in Norway spruce increased immediately in response to increased light conditions after partial harvest (Lehtonen *et al.* 2023). Naturally, the response rate in growth also varies between different site conditions and gap sizes (Hökkä & Mäkelä 2015), as well as overstorey density before and after the harvesting of trees (Nilson & Lundqvist 2001; Mäkinen & Isomäki 2004).

2.3.5 Pine weevil

Pine weevil (*Hylobius abietis* L.) is a major threat to newly planted seedlings in Sweden and elsewhere (Leather *et al.* 1999; Day *et al.* 2004; Nilsson *et al.* 2010). MSP can reduce the attack rate of pine weevil, but in weevil-dense areas additional measures to protect the seedlings are generally necessary (Petersson & Örlander 2003). Insecticides that were previously used for this purpose are no longer legal in Swedish forestry (Nilsson *et al.* 2010), instead various mechanical approaches are used, such as sand or wax applied to the lower part of the seedling (SLU 2016).

Mature pine weevils are attracted by the scent of phenols from recently harvested trees. They lay their eggs belowground either within the bark of root stumps or in the adjacent soil (Nordlander *et al.* 1997), where they later develop into larvae feeding within the bark of root stumps (Leather *et al.* 1999). Mature pine weevils feed on the bark of seedlings and twigs of mature trees (Day *et al.* 2004). One individual can damage and kill several seedlings (Eidmann & Lindelow 1997; Wainhouse *et al.* 2004). The number of damaged seedlings is related to weevil population size, and the life cycle of weevils generally results in overlapping generations and increased numbers of weevils 2-3 years after harvest (Örlander *et al.* 1997; Von Sydow 1997). The generation time can vary from 1-4 years depending on temperature sum and development time is faster on sunlit than on shaded sides (Bakke & Lekander 1965; Bejer-Petersen 1975; Inward *et al.* 2012). Even within one site, the time of development from egg to a mature pine weevil can vary by more than 2 years (Moore *et al.* 2004). The temperature dependence consequently means that the population peak is earlier in southern and coastal parts of the country than inland and northern parts. The life cycle is also affected by the harvested species, as pine weevil eggs and pupae develop faster and grow larger on pine than on spruce (Bakke & Lekander 1965; Thorpe & Day 2002; Inward *et al.* 2012). The risk of lethal damage by girdling is higher for small seedlings and the threat of lethal pine weevil damage decreases after the seedling reaches a stem basal diameter of approximately 10-12 mm (Thorsen *et al.* 2001; Wallertz *et al.* 2005).

2.4 Forest regeneration practices in Sweden

In the Nordic countries, forest owners are obliged to ensure sufficient regeneration after final harvest (Sikström *et al.* 2020). In Sweden, approximately 1 % of the productive forest area of 23.5 million hectares is harvested by final felling annually. The harvested area fluctuates between years and has increased in recent years: between 2008 and 2022 an average of approximately 203 000 hectares per year was harvested, but in the last 5 years, the average was 251 000 hectares per year (SLU 2023). The majority of the harvested areas, on average 176 000 hectares between 2008 and 2022, is regenerated by replanting with containerized seedlings grown in nurseries, and in total, on average, 380 million seedlings are produced per year (Skogsstyrelsen 2023). Of these, most are pine and spruce. Planting is commonly undertaken in the same year or one year after harvest in the south part of the country, while in the northern parts it is more common to wait 2-3 years after harvest before planting (Öhlund *et al.* 2023). The number of planted seedlings is generally around 2000 – 2500 per hectare. Where planted material perishes, natural regeneration often results in a different species composition than was originally planted (Ara *et al.* 2021). In addition, to comply with the requirements of the Forest Act, forest owners undertake supplementary planting if the number of seedlings are not sufficient within three years of final felling, when the minimum number of stems per hectare is 1000 for site index <18 and 1500 stems for site index >18 (Skogsstyrelsen 2022). Annually in Sweden 20-50 million supplementary seedlings are planted (Skogsstyrelsen 2023).

As pointed out in previous chapters, a newly planted seedling is vulnerable to vegetation competition, predation, and resource deficiencies.

The faster a seedling establishes and starts to grow, the higher the chance that it will become a mature tree (Grossnickle 2005). Mechanical soil preparation (MSP) is a tool to aid the early phase of the seedling's life when it is most vulnerable. Another potential tool to further increase the benefit of MSP is addition of slow-release fertilizer at planting (Burdett et al. 1984; Brand 1991; Jacobs et al. 2005; Thiffault & Jobidon 2006). This is not a common practice in Sweden, but the use of an organic slow-release fertilizer based on arginine-phosphate has increased in recent years in commercial forestry. The results appear variable, and one of the aims of the research described herein was to evaluate potential benefits of this measure.

It is important to understand that site conditions vary both between and within sites and also to understand how these variations may affect the outcome of regeneration measures when choosing seedling material, MSP method, and planting position. In the following sections I describe some important details regarding the seedling material used in Swedish forestry, effects of mechanical soil preparation, and the background to arginine phosphate fertilization.

2.4.1 Seedling material

The seedling material used in Swedish forestry is mainly containerized pine and spruce seedlings grown in nurseries (Wennström 2016). Compared to bare-rooted seedlings, containerized seedlings can be produced at lower cost, are less sensitive to handling and easier to plant, which also reduces the cost of planting (Nilsson *et al.* 2010). Bare-rooted conifer seedlings are generally not used today other than in highly fertile sites in southern Sweden; due to their larger size they withstand pine-weevil attacks better and can compete with the faster growing ground vegetation at such sites.

The success of forest regeneration by planting is often superior to natural regeneration and direct seeding (Simonsen 2013; Grossnickle & Ivetić 2017). One reason why planted seedlings perform better than natural regeneration is due to the high proportion of seed material coming from seed orchards, where parent trees are chosen for their desired traits, such as high growth and straight stems. The main source of seeds for the nursery grown seedlings is from openly pollinated seed orchards (Wennström 2016). Even though variable amounts of external pollination from trees surrounding seed orchards reduces the optimal gain from the seed orchard trees, seedling material originating from such orchards is superior in growth to natural generation across sites; however, when seedlings are planted in the field, the choice of planting position in order to benefit most from this genetic gain is important (Heuchel 2023).

Currently, 85 % of the seed material used for pine and spruce seedling production in Sweden comes from seed orchards (Black-Samuelsson *et al.* 2020). The first large-scale seed orchards in Sweden were established in the late 1940s (Lindgren *et al.* 2007; Prescher 2007; Werner 2010). Development and breeding have been ongoing continuously, of pine and spruce on national scale including a varied but currently increasing interest for birch, along with smaller scale of other tree species (Werner 2010). The parent trees in the seed orchards represent different breeding zones, currently there are in total 24 zones for Scots pine, 22 for Norway spruce and 7 for birch, based on photoperiod and temperature, to give seed material appropriate for different climate zones in the country (Fahlvik *et al.* ; Almqvist *et al.* 2010; Heuchel 2023). National breeding programs are currently managed by Skogforsk, including pine, spruce, and birch as well as other tree species.

Different nurseries often have different container systems, and the seedlings can be grown in containers with different cell sizes. Common cell sizes are 30, 50 and 90 cm^3, but there are even smaller and larger sizes available. The roots of a container grown seedling are confined to the volume of the cell it is grown in and have a very limited area of contact with surrounding soil. It is, therefore, important that root growth starts as early as possible when it is planted in the field so that the seedling can reach soil resources for the shoot and root to grow further (Burdett *et al.* 1983).

The advantage of choosing larger seedlings is that they are less sensitive to damage and competition than small seedlings, while smaller seedlings are cheaper to produce and often have an initially lower shoot:root ratio (Jobidon *et al.* 2003; Johansson *et al.* 2015). A seedling that has a good balance between shoot and root volume is fitter when exposed to field conditions, since a seedling must have a root system that can provide water to match the rate of transpiration (Burdett 1990; Grossnickle 2012). Hence, a seedling with a lower shoot:root ratio has a greater ability to tolerate drought stress than a seedling with a higher shoot:root ratio (Burdett 1990; Grossnickle 2012). However, a too low a shoot:root ratio would pose problems with providing enough carbon to sustain root growth. Susceptibility to drought depends on seedling condition as well as site conditions. During a drought period, a seedling with a high shoot:root ratio planted in a fully sunlit area on coarse soil with an elevation far above ground water level is at higher risk of water deficiency than a seedling with balanced shoot:root ratio. Wet conditions can also be lethal, if a seedling is planted in a fine-textured soil on a flat area and precipitation is high, the roots suffer from oxygen deficiency (Örlander *et al.* 1990).

2.4.2 Mechanical soil preparation

Research on how to improve regeneration, in particular of planted Scots pine and Norway spruce, has been and still is of great importance to Swedish forestry (Nilsson *et al.* 2010). It was realized early on that mechanical site preparation (MSP) improves regeneration success (Hagner 1962), and this has been confirmed in more recent research both in Scandinavia and elsewhere (Örlander *et al.* 1990; Spittlehouse & Stathers 1990; Sutton 1993; Thiffault & Jobidon 2006; Nilsson *et al.* 2010; Löf *et al.* 2012; Henneb *et al.* 2019; Hjelm *et al.* 2019; Nilsson *et al.* 2019; Sikström *et al.* 2020; Wotherspoon *et al.* 2020; Reicis *et al.* 2022). In addition, the positive effects of MSP have also been found to persist over time in the form of increased growth (Örlander *et al.* 1996; Hjelm *et al.* 2019). However, as MSP affects the ground conditions and can have negative consequences for other ecosystem services, for example by temporarily reducing ground vegetation that is important for various herbivores, such as reindeer (*Rangifer tarandus* L.). The more intense MSP, the more effect on other ecosystem functions.

The removal of field- and ground vegetation and the humus layer by mechanical soil preparation exposes the underlying mineral soil. This measure provides a temporary decrease in vegetation competition as well as an increase in mineral soil temperature due to removal of the insulating organic material, it also loosens the mineral soil (Örlander *et al.* 1990; Sutton 1993; Löf *et al.* 2012). Increased soil permeability enhances potential root growth by reduction of physical resistance, increased aeration, as well as increased temperature, which in turn also increases nitrogen mineralization (Örlander *et al.* 1990; Stathers & Spittlehouse 1990; Sutton 1993; Grossnickle 2000; Löf *et al.* 2012). Furthermore, pine weevils (*Hylobius abietis* L.) tend to move faster and in straighter lines across exposed flat mineral soil areas and, therefore, spend less time on mineral soil than on humus or other organic material (Kindvall *et al.* 2000). Hence, damage by pine weevil decreases when a seedling is planted in a spot surrounded by mineral soil (Örlander & Nilsson 1999; Thorsen *et al.* 2001; Björklund *et al.* 2003; Petersson & Örlander 2003; Petersson *et al.* 2005; Wallertz *et al.* 2005; Nilsson *et al.* 2010; Luoranen *et al.* 2017; Wallertz *et al.* 2018).

MSP is currently used in approximately 85 % of the annually regenerated areas in Sweden (Skogsstyrelsen 2023). Disc-trenching is the most common method (60 %), followed by mounding (30 %), while patch scarification, inverting and other methods are less common (Skogsstyrelsen 2018). Disc-trenching and mounding result in turned soil with a double layer of organic material covered by mineral soil and adjacent areas of exposed mineral soil. Disc-trenching creates continuous berms with adjacent trenches, whilst mounding creates mounds with adjacent pits/patches. Disc-trenching generally results in a higher proportion of disturbed ground area than mounding, while patch scarification disturbs a smaller area than the other methods (Öhlund *et al.* 2023). However, there is large variations between sites, depending on site conditions.

In this thesis, the effect of planting position is addressed in Paper I, where either disc-trenching or mounding was used at each site, and in Paper III where mounding was used. Disc-trenching and mounding offer similar choices of planting positions, each of which has different advantages, and the effect of MSP can vary depending on choice of planting position. The main positions, as described below, are capped mound, mineral soil, and hinge.

In this thesis, capped mound refers to both the berms resulting from disc-trenching and mounds from mounding, as they share similar features of being raised mounds, ideally capped by mineral soil. The purpose of the mineral soil cap is to weigh down the organic material to avoid air pockets that present a risk of desiccation and to reduce the likelihood of attracting pine weevils to the seedling.

The benefits of planting on capped mounds are the direct access to nutrients from the decomposing organic material within the mound as well as an elevated position with increased soil temperature also increasing in the decomposition rate of the organic material (Örlander *et al.* 1990; Sutton 1993; Örlander *et al.* 1996; Petersson *et al.* 2005; Löf *et al.* 2012). The elevated spot also provides a position where aeration is improved compared to ground level, which is beneficial on moist sites to decrease the risk of oxygen deficiency and frost heaving (Örlander *et al.* 1990; Stathers & Spittlehouse 1990). The elevated position is also less frost-prone than lower positions and can, therefore, decrease the risk of frost damage (Langvall *et al.* 2001). However, the organic material interrupts capillary flow from below and increases the risk of desiccation during periods of drought (Örlander *et al.* 1990). Establishment can be improved by deep planting of the seedling, with part of the shoot belowground (Buitrago et al. 2015; Luoranen & Viiri 2016; Pikkarainen et al. 2021). However, coarse obstacles such as rocks and gravel in the soil as well as branches within a capped mound can effectively hinder deep planting. Furthermore, regarding seedlings with pine weevil protection, if the seedling is planted so that the physical pine weevil protection ends up belowground, the weevils can easily reach the unprotected upper parts of the seedling.

The exposed mineral soil areas in trenches and pits/patches represent planting positions where the seedling root will have continuous access to capillary water flow from below and hence depend less on precipitation. However, the deepest positions of trenches/pits present a risk of oxygen deficiency and frost heaving, especially on flat areas and on fine soil, where the water stays following precipitation (Örlander *et al.* 1990). Furthermore, nutrient availability and temperature is generally lower in mineral soil compared to the organic topsoil, which may result in reduced growth compared to capped mounds (Örlander *et al.* 1990; Burton *et al.* 2000).

The hinge, i.e., where the turned soil package meets the exposed mineral soil area, is an intermediate choice of planting position (Burton *et al.* 2000). Here, the seedling has the benefits of access to capillary flow as well as having close access to the nutrients from the decomposing organic material within the adjacent mound.

In addition to the planting positions described, seedlings are sometimes planted in non-prepared positions and wheel tracks. Planting positions resulting from other MSP methods present other variations in microenvironments. Two less common mechanical soil preparation methods with less heterogenous choices of planting positions are utilized in Paper II, spot milling and inversion. At spot milling, a milling head mills a depression, creating a mound of mixed material at the edge of the hole. By inversion, the soil package is placed back upside down in the cavity its was retrieved from. Inversion has been proven successful for seedling establishment in several studies (Örlander *et al.* 1998; Granhus *et al.* 2003; Hallsby & Orlander 2004;

Johansson *et al.* 2012; Wallertz *et al.* 2018). Furthermore, inversion has lower disturbance effect than most other soil preparation methods since no constructed elevations are created with this method (Chaves Cardoso et al., 2020). Inversion is at present not practiced frequently today, but development of technical equipment has raised increased interest in the method (Sundblad 2009; Johansson *et al.* 2012).

The site conditions affect the outcome of MSP both between and within sites, resulting in large variability in the quality of planting positions, especially the capped mounds. Obstacles such as rocks, stumps, residual branches from harvest and dense ground vegetation can effectively prevent the ability of any MSP measure to create homogenous quality of capped mounds (Johansson *et al.* 2012; Löf *et al.* 2012). For example, the optimal cover of clean mineral soil is hard to achieve when the mineral soil contains many larger rocks. In addition, different mechanical soil preparation techniques can give different results with respect to the quality of planting positions, depending on site conditions such as stoniness (Wallertz *et al.* 2018). Furthermore, when there is overall higher survival and good site conditions, the difference between various treatments is less likely to be significant. Hence, the effect of MSP can differ between species related to susceptibility to various damage agents, such as pine weevil (Wallertz & Malmqvist 2013). A species that is a more attractive food source for pine weevil may suffer more damage and then the effect of increased survival by MSP can be significant, while a species that is not as severely attacked may have similar survival rates in non-prepared and MSP spots (Wallertz & Malmqvist 2013). The effect of MSP in reducing pine weevil damage also depends on how many years after harvest the mechanical soil preparation is undertaken (Örlander *et al.* 1997; Von Sydow 1997).

In northern Sweden it is more common to plant on capped mounds, while it is more common to utilize the mineral soil positions in the furrows or patches in the southern part of the country (Öhlund *et al.* 2023). This is related to the general recommendation that the optimal planting position is the capped mound, except during dry weather conditions in southern Sweden (Skogsstyrelsen 2020). Water stress is the most common cause of mortality of planted seedlings (Margolis & Brand 1990; Grossnickle 2012). With a warming climate, the risk of dry conditions will increase in northern Sweden as elsewhere, with consequences such as increased risk of mortality of young tree seedlings (Urli *et al.* 2023). It is clearly evident that recent drought years have had a negative effect on seedling survival; for example, the dry year of 2018 resulted in a doubling of the need for supplementary planting in 2019 compared to the previous year (Skogsstyrelsen 2023). Hence, the planting on capped mound as standard procedure may become more unsecure both regarding drought sensitivity and pine weevil damage. Furthermore, among the utilized capped mounds it is more common that seedlings are planted on mounds with insufficient mineral soil cover due to the high variability of the capped mounds (Sörensen *et al.* 2023). This further increases the risk posed by climate change, as pine weevil pressure increase with temperature.

2.4.3 Fertilization with arginine

To aid the establishment of planted seedlings, slow-release fertilizer can be added at the time of planting (Burdett *et al.* 1984; Brand 1991; Jacobs *et al.* 2005; Thiffault & Jobidon 2006). However, many studies have shown that increased nitrogen availability result in increased shoot:root ratio (Levin *et al.* 1989; Ingestad & Agren 1991; Sattelmacher *et al.* 1993; Hermans *et al.* 2006). The higher allocation of biomass to the shoot due to inorganic fertilization may result in insufficient root mass to provide the seedling with enough water, making them sensitive to drought (Jacobs *et al.* 2004). In case of dry conditions, the salt concentration from the inorganic fertilizer may become too high and further impair the root system (Jacobs & Timmer 2005). Hence, the outcome of inorganic fertilization of seedlings may result in decreased survival of the seedlings and have only short-time effect or no effect on growth at all (Burdett *et al.* 1983; Simpson & Vyse 1995; Thiffault & Jobidon 2006). However, in which form nitrogen is available affects the seedlings' allocation of resources. While inorganic nitrogen is transported to the shoot, organic nitrogen can be retained in the root and be utilized for root growth directly, and a seedling fertilized with organic nitrogen can therefore partition more biomass to roots compared to a seedling fertilized with inorganic nitrogen (Cambui *et al.* 2011).

Commercial fertilizers are commonly based on inorganic nitrogen, i.e., ammonium and nitrate. However, the main sources of nitrogen in the boreal forest soils are from organic compounds, i.e., amino acids (Inselsbacher & Näsholm 2012). Tree roots can take up amino acids directly, at an even higher rate than inorganic nitrogen sources (Näsholm *et al.* 1998; Öhlund & Nasholm 2001; Gruffman *et al.* 2013; Oyewole *et al.* 2016). Of the amino acids, arginine has the highest nitrogen content. Arginine is synthesized in many plants as internal storage units of nitrogen when nitrogen uptake exceeds the need for growth (Edfast *et al.* 1996; Nordin *et al.* 2001). This storage is later utilized for early season growth (Cantón *et al.* 2005).

An organic slow-release nitrogen fertilizer composed of arginine-phosphate (AP), arGrow® (Arevo AB, Umeå, Sweden), has been developed and, in recent years, has been used commercially in forestry, though only on a small scale so far. Arginine is a strong cation and so has a high binding capacity to negatively charged soil particles (Inselsbacher *et al.* 2011). Hence, it is not easily leached from where it is deposited (Hedwall *et al.* 2018). Nursery trials have shown that arginine fertilization results in higher dry weight, lower shoot:root ratio and more root tips colonized by mycorrhiza on conifer seedlings compared to inorganic nitrogen fertilization (Öhlund & Näsholm 2002; Gruffman *et al.* 2012). As the effect is intended to primarily promote early root growth to aid establishment of the seedling, a strong and immediate effect on shoot growth should not be expected. Improved establishment would, however, logically lead to improved long-term growth of seedlings. Using this type of fertilizer could potentially be an option when, for example, planting in mineral soil, to compensate for the low nutrient availability at sites where conditions are not appropriate for planting in capped mounds.

3. Material and methods

Papers I-IV are based on data collected from field experiments, including a total of 16 sites in Sweden. Locations of the sites are shown in Fig.1. This chapter gives a brief overview of the material and methods used; further information is provided in each of the papers included in the thesis.

3.1 Study areas

The study areas included in the research described herein are all located in Sweden, a country in northern Europe where boreal forest is the dominant forest type (Fig. 4). Paper I was based on a field trial covering multiple sites in the boreal part of Sweden; the effects of planting position and arginine-phosphate addition and the relationships to varying site conditions were investigated. Paper II was based on three case studies in which the effects of arginine-phosphate addition on growth and survival of Scots pine, Norway spruce and silver birch were tested. Paper III was based on a field trial in which the effects of seedling size, planting position and arginine-phosphate addition on pine and spruce were tested. Paper IV was based on a field experiment in which the effect of competition from mature pine on sown and planted pine was investigated.

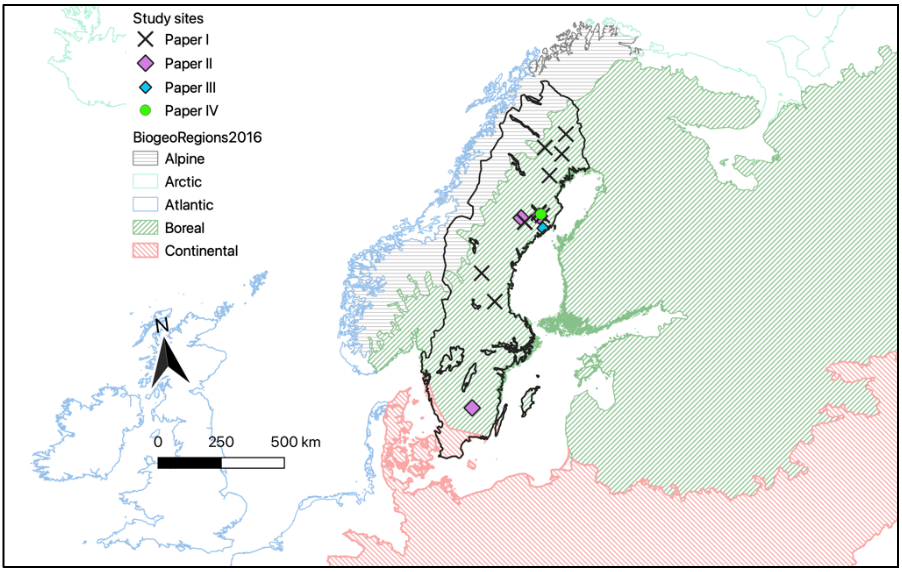

Figure 4. All study areas were located within the boreal biogeographical region of Sweden. Note that several study sites from all four papers are clustered in the northeast part of the country. For exact coordinates, see the field experiments section. Definition of biogeographical regions according to the European Environment Agency (EEA *2016*).

3.2 Field experiments

Paper I was based on a field experiment including 11 sites dispersed across mid- and northern Sweden (Table 1). The experimental plots were positioned in the interior of commercial clear-cuts, with the permission of each forest owner. Scots pine seedlings were planted in three different planting positions: on capped mounds, in exposed mineral soil adjacent to the capped mounds and a control in positions where soil layers and ground vegetation were left intact (Fig. 5). For each site and planting position, seedlings with arginine-phosphate (AP) addition and a control without fertilizer were included.

Table 1. Sites included in Paper I (A-K) are listed from south to north, including site characteristics: latitude; longitude; altitude (meters above sea level); volume (refers to the size of the growing containers, which is the volume the seedlings' roots were restricted to at the time of planting); MSP = mechanical soil preparation (DT = disc trenching, M = mounding); total precipitation the first 30 days after planting; length of growing season in days; SI = site index (maximum average height of trees at age 100, where T= pine); soil texture (dominant fraction); veg. = dominant vegetation (wavy hairgrass, bilberry, strawberry, lingonberry, crowberry, heather, reindeer lichen), and landscape position. All sites were of dry moisture class type except C which was mesic. Yellow highlight = AP treatment significant for growth of seedlings planted in non-prepared positions. **Note: The first eight columns are included in table 1 in Paper I, while the last three are added here to further illustrate the variables included in the variation between sites.**

Site	**Lat. (°N)**	**Long. (°E)**	**Vol. (cm^3)**	**MSP**	**Prec. first 30 days (mm)**	**Grow. season (days)**	**SI**	**Soil text.**	**Dominant ground vegetation**	**Land-scape**
A**	61.06	16.16	50	DT	35	165	T24	coarse	wavy. bilb. straw.	hill
B	62.07	15.09	30/50	DT	36	155	T20	silt	ling, heath, lich	flat
C*	63.95	18.45	50	M	24	145	T22	coarse	bilb, wavy, grass	hill
D	63.95	18.44	50	DT	24	145	T20	coarse	ling, crowb.	flat
E***	64.18	19.91	50	DT	44	145	T22	sand	bilb, ling, heath	hill
F	64.26	19.61	50	DT	45	145	T21	silt	ling, heath,lich	flat
G	64.31	19.64	50	DT	44	145	T22	coarse	bilb, wavy	hill
H	65.62	20.63	30	M	43	140	T19	sand	bilb, wavy, ling, heath	hill
I	66.38	21.82	30	DT	43	135	T19	silt	bilb, wavy, ling, heath	flat
J	66.64	20.30	50	M	48	130	T16	sand	bilb, ling, heath, crow	flat
K	67.09	22.30	30	DT	13	130	T18	silt	bilb, wavy, ling, crow	hill

*non-prepared positions not included

**measurements of seedlings from non-prepared positions not included

***no measurements included

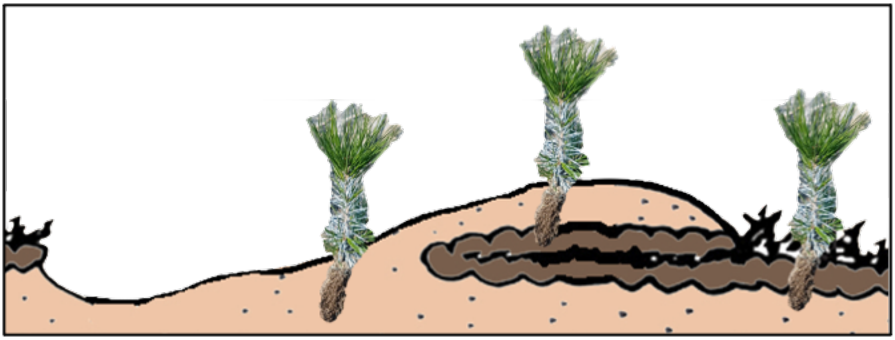

Figure 5. Illustration of pine seedlings in planting positions resulting from mechanical soil preparation, from left to right: mineral soil, capped mound, and non-prepared soil, i.e., control.

Paper II was based on a field experiment including three sites, one in northwest (64.10°N, 18.15°E), one in northeast (64.16 °N,19.66°E) and one in southern Sweden (57.19 °N, 14.82°E). As in Paper I, the experimental plots were positioned in the interior of commercial clear-cuts, with the permission of each forest owner. Different soil preparation methods were used on each site: northwest by inversion, where removed topsoil layers are turned upside down and put back (Fig. 6 D), northeast by spot milling where unsorted material is milled up in a mound (Fig. 6 E), the south site inversion was intended but the shallow soil and stoniness did result more in disturbed soil topsoil than true inversion. Scots pine, Norway spruce and silver birch were planted in plot pairs, one plot treated with arginine-phosphate at the time of planting and the other plot untreated. In total, there were seven plot pairs on each site (Fig. 6). Each of these plot pairs had a different species composition – mono, two-species, and three-species – as the original intention of this field trial was to evaluate species mix effect in the long term as well as the effect of arginine-phosphate addition. All together each species occurred in four plot pairs that were treated as replicates in the study described in paper II, e.g., pine, pine + spruce, pine + birch, pine + spruce + birch etc. The plot pairs were positioned randomly on the southern site (Fig. 6 A) and in blocks on the two northern sites (Fig 6 B, C): one block with all AP-treated plots and one block with all the untreated plots.

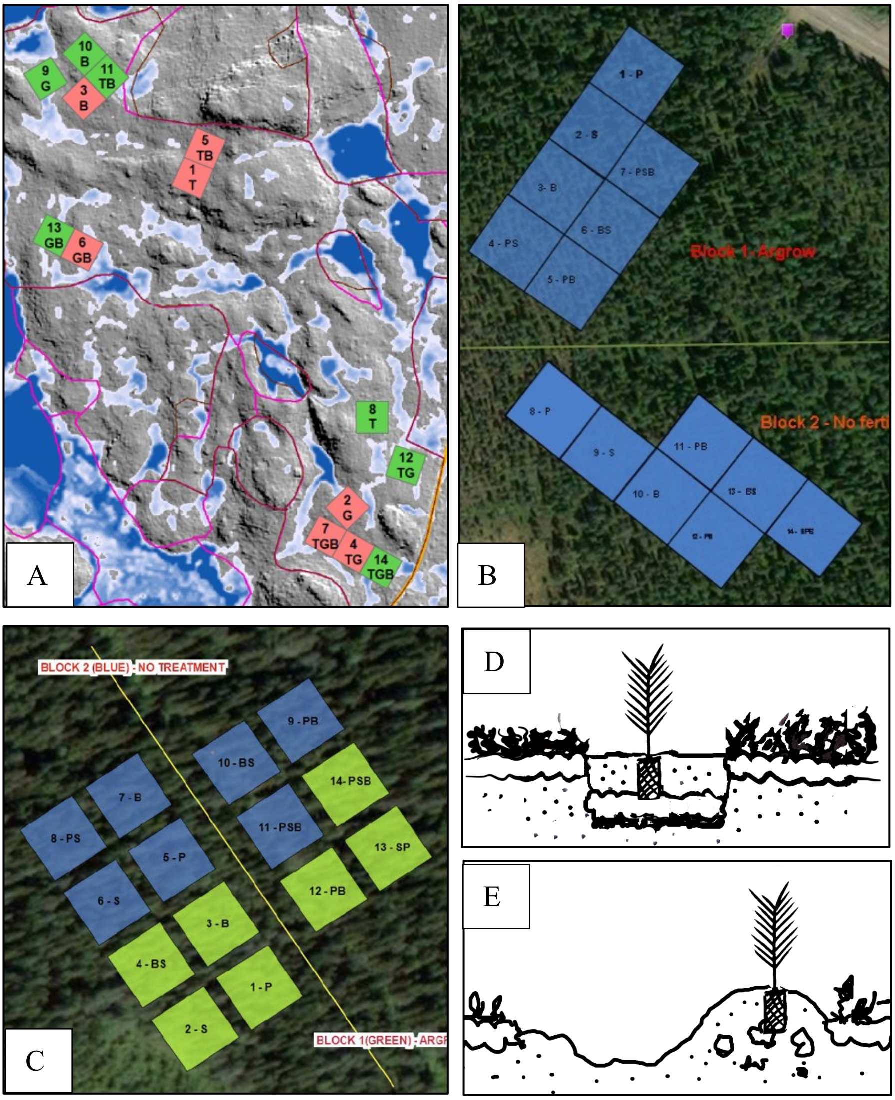

Figure 6. Maps of the plot distribution at the three sites. A) The south site where plots 1-7 were treated with arginine phosphate and plots 8-14 were untreated, B) the northeast site where plots 1-7 were treated with arginine phosphate and plots 8-14were untreated, and C) the northeast site where plots 1-4 and 12-14were treated with arginine phosphate and plots 5-11were untreated. Illustration of mechanical soil preparation methods: D) inversion and E) spot milling. Letters in the plots indicate species where T (tall = Swedish word for pine) and P is pine, B is birch, and G (gran = Swedish word for spruce) and S is spruce.

Paper III was based on a field experiment on one site in northern Sweden (63.72 °N, 19.92 °E). As in Papers I and II, the experimental plots were positioned in the interior of a commercial clear-cut, with permission of the forest owner. Scots pine and Norway spruce were planted in adjacent areas, each 50 x 100 m. For each species, seedlings of three sizes were used, here the size is defined in cubic centimeters (cc) based on the cell volume of the containers they were grown in: 30 cc, 50 cc and 90 cc (see example of the three sizes of Norway spruce in Fig. 7A). The site was mechanically prepared by mounding. The experimental area was positioned on a gentle slope, the higher area was used for pine and the lower for spruce.

Each species area was divided into 14 elongated plots, aligned along the slope. Each plot comprised three rows with mounds, one row for each seedling size. For each mound, a group of three seedlings was planted, one on the capped mound, one in the hinge and one in the mineral soil position (Fig 7 B). Only mounds where there was a representative capped mound present were used, i.e., mounds with insufficient contact with underlying ground or that had no mineral soil cover at all were not utilized for any position.

Every second group of seedlings was treated with one dose of arginine phosphate at the time of planting. Each experimental combination was repeated in 14 blocks on a clear-cut area. A quality assessment of the planting positions was undertaken following planting to enable evaluation of the effect of planting position quality. Planting positions were classified on a 0-9 scale, where 0 was un-prepared soil, 1-4 different mineral soil positions, 5-6 different hinge positions and 8-9 capped mound positions (Table 2). The assessment of positions revealed which seedlings that were planted in positions surrounded by mineral soil (see Fig. 7 B), and which were planted in proximity to organic material (see Fig. 7 C and Table 2).

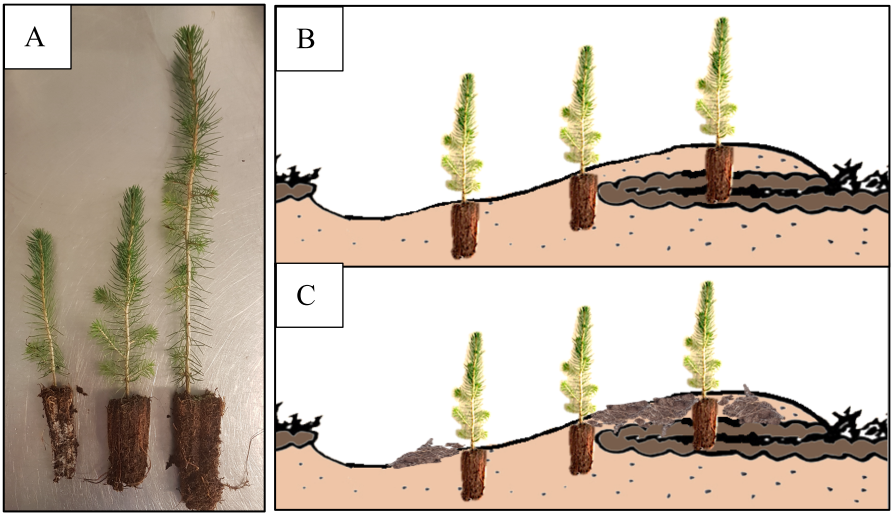

Figure 7. Seedling sizes and planting positions, examples show Norway spruce. A) Three seedling sizes. B) Seedlings planted in mineral soil, hinge, and capped mound positions, all properly covered by mineral soil, i.e., high quality positions according to the definitions in Paper III. C) Seedlings planted in mineral soil, hinge, and capped mound positions, all with organic material adjacent to the seedlings, i.e., low quality positions according to the definition in Paper III.

Table 2: Classification scheme for detailed assessment of planting position following planting. *Since each mound is heterogenous, a seedling in classification 5 could be adjacent to a mound of classification 7, 8 or 9 since the part of the mound adjacent to the hinge does not necessarily match the classification assessment where the mound seedling was planted. Planting positions that can be considered low quality with respect to risk of pine weevil damage are indicated in italics.

Main position	**Description**	**Classification**
Mineral soil	*with peat or decomposing humus in the patch*	*1*
Mineral soil	in the bottom or close to bottom of patch	2
Mineral soil	*less than 10 cm from humus edge in the patch*	*3*
Mineral soil	with relatively high position in the patch	4
Hinge	*max 10 cm from a low quality* mound*	*5*
Hinge	max 10 cm from a capped mound	6
Mound	*without mineral soil cover around the seedling*	*7*
Mound	*capped with a mineral soil mixed with humus*	*8*
Mound	capped with coherent cover of mineral soil	9

Paper IV was based on a field experiment on one site in northern Sweden (64.23 °N, 19.79 °E), within the Svartbergets field research area. The experimental area was fenced to avoid interference from browsing and included a small clear-cut and adjacent mature pine forest. Scots pine seedlings were planted, and Scots pine seeds sown in three environments with different levels of competition from the mature trees: 15 m inside the forest, representing competition for both light and belowground resources; on the clear-cut area 2 m from the forest edge, representing belowground competition; and on the clear-cut area 15 m from the forest edge, free from competition with mature trees (Fig. 8). In each environment, three treatments were tested for both sown and planted seedlings: isolation of seedlings' roots from mature tree roots by a 75 cm deep steel frame, annual N-fertilization, and a control. Each treatment plot was 1.5×1,5 m, in which 8 seedlings were planted on 1.5 × 0.75 m, 120 seeds sown on 0.75 × 0.75 cm and the remaining area of 0.75 × 0.75 was left as a control for natural regeneration (Fig 8). Ground vegetation and organic topsoil layer were removed prior to sowing, while these layers were left intact in the planted and naturally regenerated areas. The treatments were repeated in five randomized blocks.

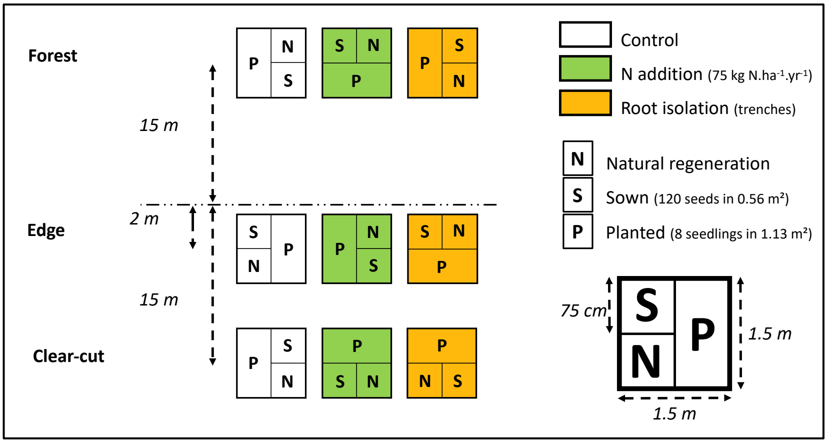

Figure 8. Schematic illustration of the experimental design at the study site with three growing environments: "Forest", 15 meters into the mature pine forest from the forest edge; "Edge", 2 meters out from the forest edge; and "Clear-cut", 15 meters from the forest edge out on the harvested area. For each growing environment there are five replicates. For each replicate there are three randomly distributed treatment plots: control (white), nitrogen (N) addition (green) and root isolation (yellow). Each treatment plot is split in one half where nursery grown seedlings were planted (P), one quarter with sown seeds (S) and one quarter for naturally regenerated seedlings (N). Note: in the schematic illustration figure in Paper IV, the naturally sown areas are denoted "C (spontaneous control), while in this figure the area for natural regeneration is denoted "N" for clarity.

3.3 Data collection

The data used for analyses were from field inventories of survival and growth compiled following two growing seasons after planting for Papers I and II, following three growing seasons after planting for Paper III and following six growing seasons after planting and seven growing seasons after sowing for Paper IV (Table 3). Inventories from previous seasons were used to control for any missing seedlings (Paper I and II), to account for previous damage (Paper III) and to compare survival development (Paper IV). Additional measurements of root and shoot dry weights for a subset of harvested seedlings were included in Paper III. Growth was assessed on the basis of height, length of leader shoot (Scots pine only) and stem basal diameter of a random selection of undamaged seedlings (Paper I), all undamaged seedlings (Paper II) or all surviving seedlings (Papers III and IV). Stem basal diameter was not assessed for sown Scots pine seedlings in Paper IV due to the high density of seedlings in some plots. When seedlings were damaged, the cause of the damage was recorded where applicable, such as characteristic bite-marks on top shoots by ungulates or the gnaw-marks on the bark of the stem from pine weevil.

Table 3. Overview of data included in the analyses for each paper respectively. For each paper is indicated the method of regeneration (planted or sown), season of inventory for which data were analyzed (inventories that were made previous seasons were used for comparisons), which species that were included, and which field measurements that were included in the analyses. Regarding growth: *only undamaged seedlings were measured, **a random selection of undamaged seedlings was measured.

Paper	Method	Season	Species	Field measurements for analysis			
				Survival	Height	Diameter	Leading shoot
I	Planted	2nd	Pine**	X			X
II	Planted	2nd	Pine*	X	X	X	
			Spruce*	X	X	X	
			Birch*	X	X	X	
III	Planted	3rd	Pine	X		X	
			Spruce	X	X		
IV	Sown	7th	Pine	X	X		
	Planted	6th	Pine	X	X	X	

3.4 Statistical analysis

All analyses were conducted in R-studio (R Core Team 2021). Factorial analysis of variance (ANOVA) was used in all papers. The ANOVAs were based on linear models for growth and survival in Paper I, and for survival in Paper IV, while linear mixed models with plot as a random factor were used for all other analyses in Papers II-IV. The response variables for growth were leader shoot (Paper I), height (Paper II, for Norway spruce only in Paper III and for sown and planted seedlings in Paper IV), stem basal diameter (Paper II, for Scots pine in Paper III and for planted seedlings only in Paper IV) and total dry weight (Paper III). Main agents of damage were analyzed as share of living seedlings damaged by browsing or pine weevil in Paper II and share of total number of seedlings (dead + alive) killed or damaged by pine weevil in Paper III. In the analyses, the effects of the following factors on the response variables were tested: site (Paper I), planting position (Papers I and III), arginine-phosphate addition (Papers I, II and III), tree species (Paper II), original seedling size (Paper III), inorganic annual N-fertilization (Paper IV), root isolation (Paper IV) and competition from mature trees (Paper IV).

4. Main results

In this chapter, I present brief summaries of the main results from each paper included in the thesis. For further details, see each published Paper (I, II, IV). The manuscript for Paper III is available in the printed version of the thesis.

4.1 Paper I

In Paper I, I studied the effects of different planting positions and arginine phosphate addition on survival and growth of planted Scots pine seedlings following two growing seasons in the field. The study included 11 sites distributed over mid- and northern Sweden (Table 1) and all sites were located on clear-cut areas. I found that site conditions affected the outcome of seedling survival and growth in different planting positions after two seasons in the field. I connected the site effect to environmental conditions and concluded that the amount of precipitation during the first month after planting best explained differences in survival between mineral soil and capped mound positions (Fig. 9 A, B). Limited precipitation during the first month after planting had a significant negative effect on survival when the seedlings were planted on capped mounds, while seedlings planted adjacent to the capped mounds in the exposed mineral soil displayed high survival despite the low precipitation. Seedlings planted in non-prepared soil showed overall lower survival and growth than seedlings in positions with mechanical soil preparation. Variation in survival between sites in non-prepared soil was best explained by a negative correlation with length of growing season (Fig. 9 C).

Growth of seedlings in positions with mechanical soil preparation was strongly connected to length of growing season (Fig. 10 A, B), an analog of the strong temperature sum dependence for growth in Sweden mentioned in chapter 2.3.2. The effect on growth of arginine-phosphate addition increased with growing season in the positions with mechanical soil preparation and was most pronounced in mineral soil positions. For the seedlings planted in non-prepared positions, growth correlated better with site index (i.e., site fertility), but with a similar tendency of increasing effect of AP with higher SI (Fig. 10 C).

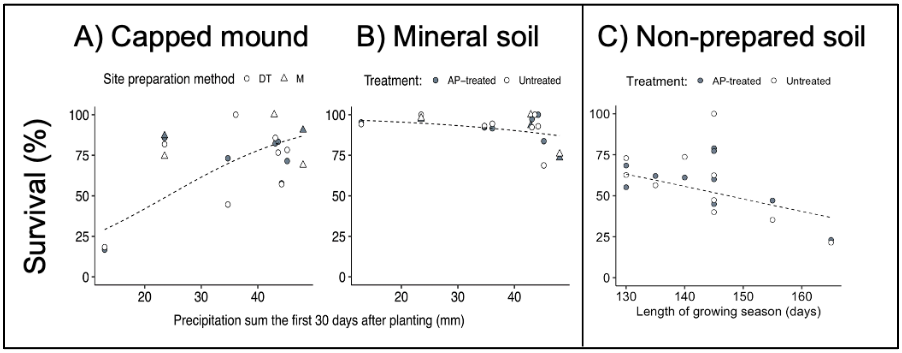

Figure 9. Survival in relation to precipitation during the first 30 days after planting in A) capped mound and B) mineral soil. C) Probability of survival in relation to length of growing season in non-prepared soil. Each site is represented by one survival value for AP-treated seedlings and one for untreated seedlings. The dashed lines represent the predicted curves from logistic regression models for each of the two planting positions.

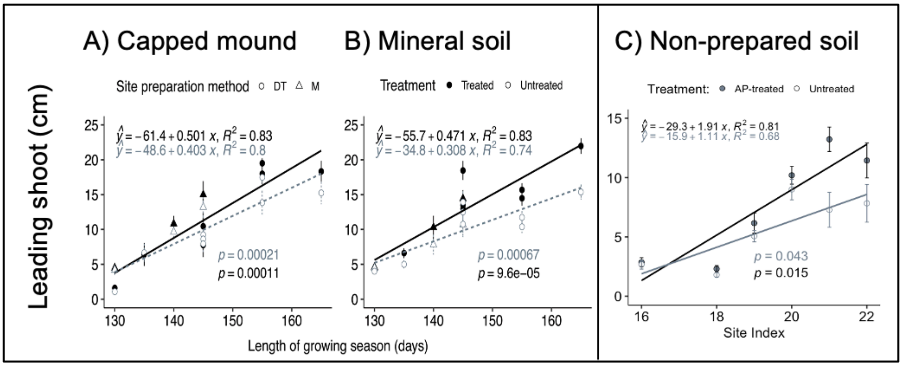

Figure 10. Linear relationships between leader shoot length and A) length of growing season for AP-treated and untreated seedlings in capped mounds and B) mineral soil, and C) with site index in non-prepared soil. Points indicate mean values for sites with the same length of growing season and bars indicate standard error.

4.2 Paper II

In Paper II, I studied the effect of arginine-phosphate on Scots pine, Norway spruce and silver birch on three sites, one in northeastern, one in northwestern and one in southern Sweden. I concluded that the positive effect of arginine phosphate differed between the sites and species. The study was originally designed to compare species composition with and without arginine-phosphate addition, for different tree species compositions (single or mixed stands with two or three species) with the three sites as replicates over a longer period, extending beyond the timeframe for this thesis. However, I took the opportunity to utilize the experiment to get an indication of the effect of arginine phosphate on spruce and birch, which had not been studied previously. I chose to handle the sites as case studies, since I had already concluded in Paper I that the effect on Scots pine was site dependent. I, therefore, focused on how the effect might differ between species on each site. That the effects were site dependent for the other species as well came through in the results passively, by the different outcomes on the different sites. I did not attempt to analyze which environmental aspects were responsible, as I did in Paper I, since any result would be very weak with only three sites to compare.

AP-treated conifer seedlings grew better than the untreated ones on both northern sites, as well as birch on the NW site, where survival of all tree species was improved by the AP addition (Fig. 11). However, the difference in growth between species is also related to other variables, such as how well each species is adapted to the local conditions. Scots pine grew less well than the other species on the southern site compared to the northern sites. Most of the birch was browsed at the southern site, AP treated more so than untreated, resulting in a negative effect of AP addition (Fig. 12). There was a strong positive effect of arginine phosphate on survival of Scots pine on the southern site, although there was no effect on growth. Here, the pine weevil pressure was high, and a large proportion of the surviving conifer seedlings showed scars characteristic of pine weevil damage.

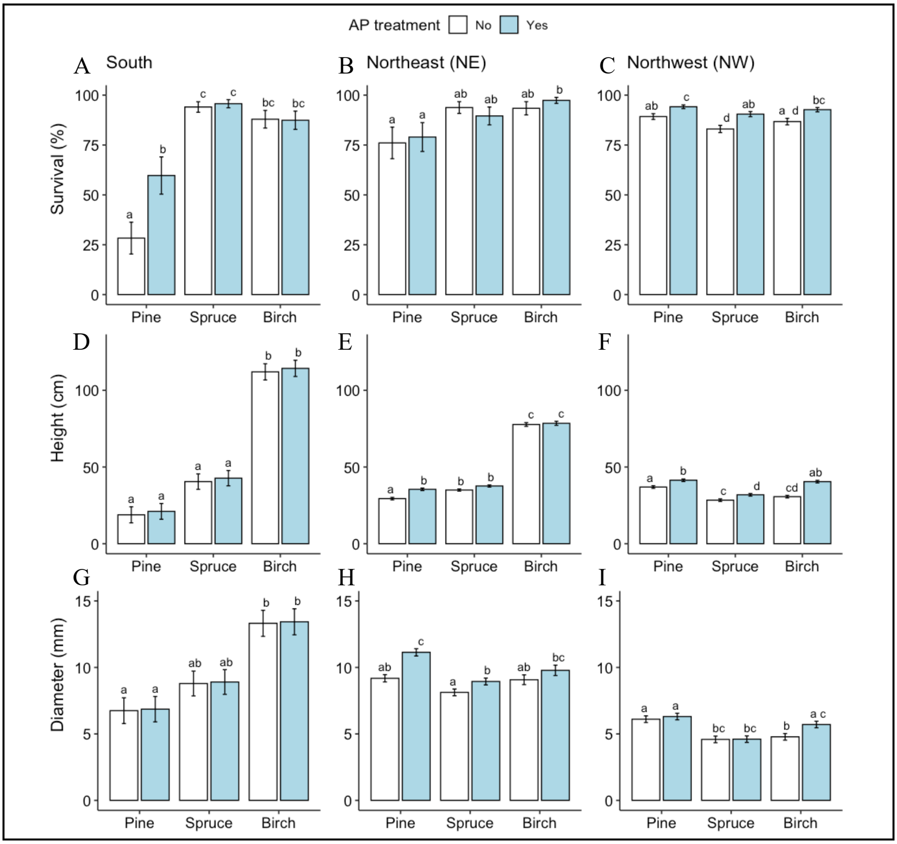

Figure 11. Results from ANOVA for A, B, C) survival, D, E, F) height, and G, H, I) stem basal diameter means for Scot Pine, Norway spruce and silver birch at each site respectively following the second field season. Columns indicate percentage survival and error bars indicate standard error (data transformed back from log scale in survival models). Different letters indicate significant differences. For height and stem basal diameter, only measurements of seedlings classified as living are included.

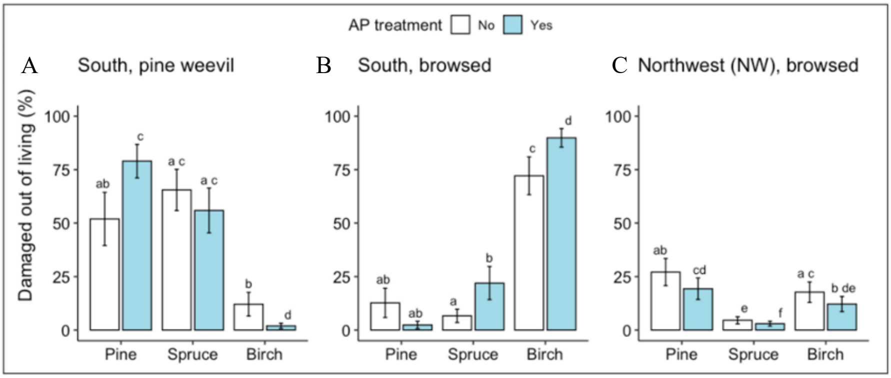

Figure 12. Results from ANOVA for damage to living seedlings of Scots pine, Norway spruce and silver birch by A) pine weevil and B) browsing at the southern site, and C) browsing at the NW site following the second field season. Columns indicate percentage of living seedlings damaged and error bars indicate standard error (data transformed back from log scale used in models.) Different letters indicate significant differences.

4.3 Paper III

In Paper III, I studied the effects of and potential interactions between planting position, seedling size and arginine phosphate (AP) addition for Scots Pine and Norway spruce.

I found that survival was lower in planting positions with organic material adjacent to the seedlings of both species, i.e., planting position classes 1,3,5 & 7 for pine and also class 8 for spruce (Fig. 13). I grouped these positions together as low quality (LQ) positions as a separate group from the main planting positions for all analyses. The remaining classes was re-defined as high quality (HQ) mineral soil (class 2 and 4 for both pine and spruce), high quality (HQ) hinge (class 6 for both pine and spruce) and capped mound (class 8 and 9 for pine), or high quality (HQ) capped mound (class 9 only for spruce). Survival was also lower in the hinge position than in mineral soil and capped mound for pine. The mortality in these positions was related to pine weevil damage (Fig. 14). The number of seedlings damaged by pine weevil increased with increasing original size of seedlings (Fig. 15), albeit with no significant difference in lethal outcome from this damage. There was no effect of AP addition on survival or amount of pine weevil damage.

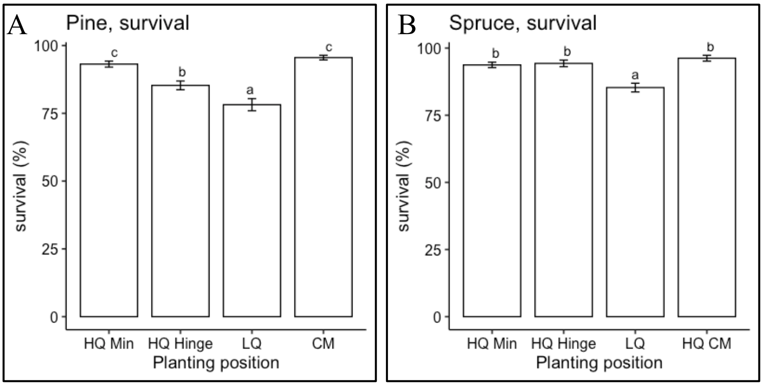

Figure 13. Results from ANOVA for probability of survival for A) pine seedlings and B) spruce seedlings for each planting position group, respectively, following the third field season. Columns indicate survival probability as a percentage and error bars indicate standard error (data back transformed from log scale in survival models). Different letters indicate significant differences. HQ Min = high quality mineral soil position, including assessment classes 2 and 4; HQ Hinge = high quality hinge positions, assessment class 6 for both pine and spruce; LQ = low quality positions, including classes 1, 3, 5 and 7 for pine and in addition class 8 for spruce; and CM = capped mound, including assessment classes 8-9 for pine, HQ CM = high quality capped mound, class 9 for spruce.

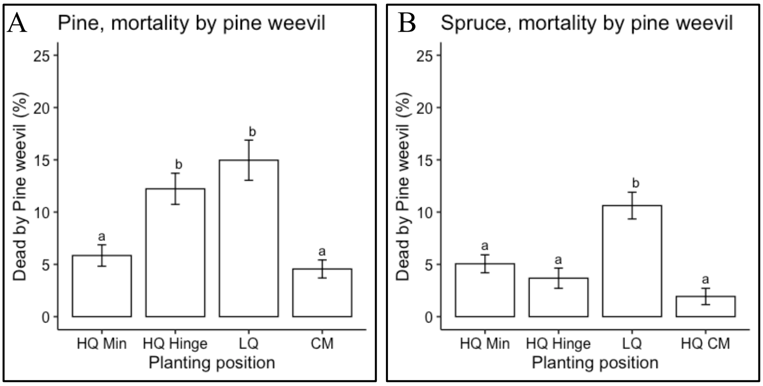

Figure 14. Results from ANOVA for probability of mortal pine weevil damage for A) pine seedlings and B) spruce seedlings for each planting position group, respectively, following the third field season. Columns indicate probability of mortality caused by pine weevil damage as a percentage out of total number of seedlings and error bars indicate standard error (data back transformed from log scale in survival models). Different letters indicate significant differences. HQ Min = high quality mineral soil position, including assessment classes 2 and 4; HQ Hinge = high quality hinge positions, assessment class 6 for both pine and spruce; LQ = low quality positions, including classes 1, 3, 5 and 7 for pine and in addition class 8 for spruce; and CM = capped mound, including assessment classes 8-9 for pine, HQ CM = high quality capped mound, class 9 for spruce.

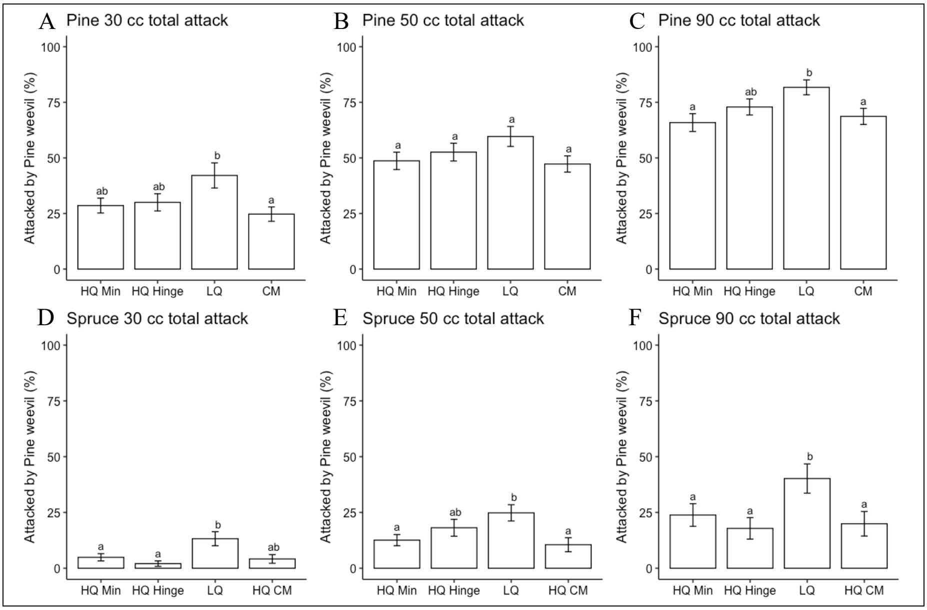

Figure 15. Results from ANOVA for probability of seedlings being attacked by pine weevil for pine size A) 30 cc B) 50 cc C) 90 cc and spruce size D) 30 cc E) 50 cc F) 90 cc, for each planting position group, respectively, following the third field season. Columns indicate probability of pine weevil attack as a percentage out of total number of seedlings and error bars indicate standard error (data transformed back from log scale in survival models). Different letters indicate significant differences. HQ Min = high quality mineral soil position, including assessment classes 2 and 4; HQ Hinge = high quality hinge positions, assessment class 6 for both pine and spruce; LQ = low quality positions, including classes 1, 3, 5 and 7 for pine and in addition class 8 for spruce; and CM = capped mound, including assessment classes 8-9 for pine, HQ CM = high quality capped mound, class 9 for spruce.

Growth of pine was, in general, lowest in mineral soil positions with respect to both stem basal diameter and total dry weight (Fig. 16). Growth was similar in hinge and capped mound positions for 50cc and 90 cc seedlings with respect to stem basal diameter and all seedling sizes with respect to total dry weight. Growth in low quality positions was not significantly lower than in hinge positions for any pine seedling size, but lower than in capped mounds for 50 and 90 cc seedlings. Stem basal diameter growth was enhanced by AP for 30cc and 50cc pine seedlings planted in mineral soil, making them similar to those in the hinge position, and also for 30 cc pine seedlings planted in the hinge position, making them similar to those on the capped mounds. In terms of total dry weight, the only effect of AP addition on pine was for 50 cc seedlings, with an extreme increase for seedlings in the hinge position. It was the shoot dry weight that made this difference significant (Fig. 17A, B). This was related to the higher number of multiple leader shoots on the AP-treated seedlings in the hinge position among the harvested 50 cc pine seedlings. The pattern of AP treated seedlings having more multiple shoots was not significant due to the large variations in the data, nevertheless there was a clear trend for AP-treated seedlings to have higher numbers of multiple shoots both in the HQ hinge and capped mound positions (Fig. 17 C). However, there may have been un-representative amount of multiple top shoots on the harvested seedlings in his position by chance, since the sample size was limited (40 seedlings of size 50 cc in HQ hinge positions, of which 19 received AP addition). Shoot:root ratio of the pine seedlings was significantly higher in HQ hinge positions than in HQ capped mound positions for all seedling sizes, for 30 cc seedlings also being higher than in mineral soil positions and for 50 cc pine seedlings higher than in LQ positions. AP treatment had no significant effect on pine seedling shoot:root ratio. The occurrence of multiple leading shoots in pine increased with seedling size and there was a trend of correlation to occurrence of adventitious bud the previous year (Fig. 18).

Growth of spruce was, lowest in mineral soil positions with respect to both height and total dry weight, except for 50 cc seedlings where height growth in low quality positions and capped mounds was equally low and for 30 cc seedlings where total dry weight was equally low in all planting positions (Fig. 19). AP addition increased growth of spruce seedlings with respect to both height and total dry weight, except for the total dry weight of 90 cc seedlings. 90 cc spruce seedlings had a significantly lower shoot:root ratio in mineral soil positions than in the other positions. AP addition had no significant effect on shoot:root ratio (Fig. 19 G, H, I).

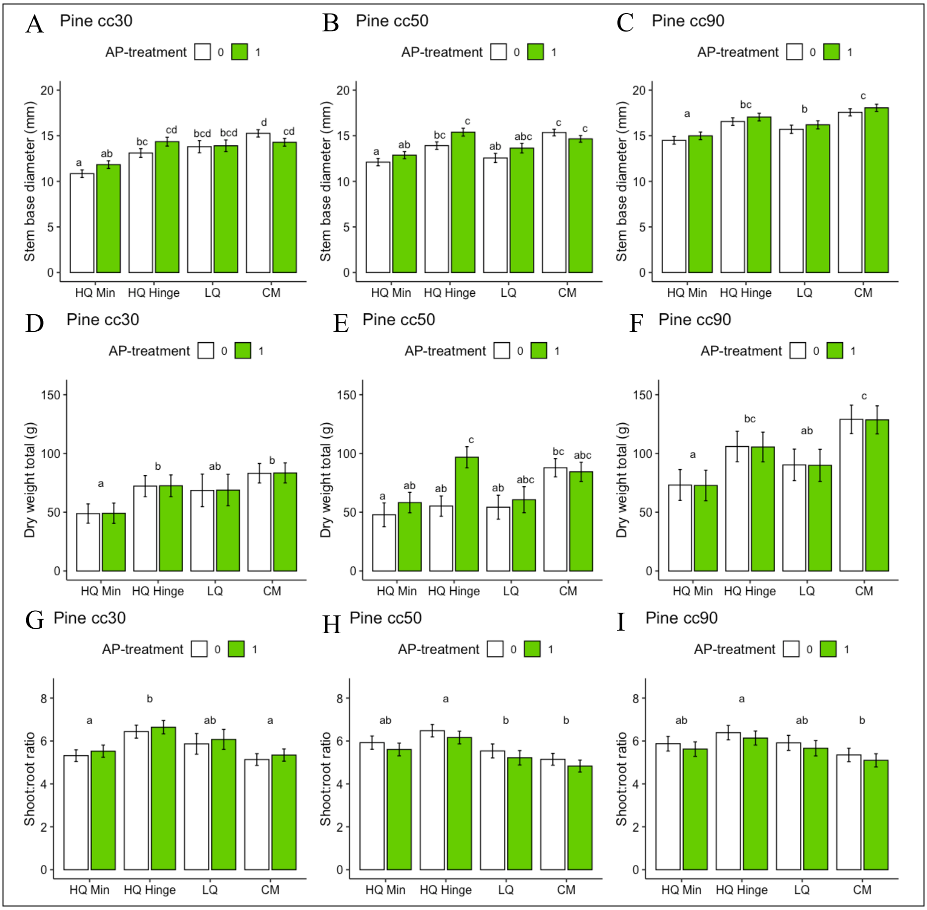

Figure 16. Results from ANOVA for pine seedling stem basal diameter for size A) 30 cc B) 50 cc and C) 90 cc, for harvested pine seedling total dry weight, i.e. root + shoot for size D) 30 cc E) 50 cc and F) 90 cc and harvested pine seedling shoot:root dry weight ratio, for size G) 30 cc H) 50 cc and I) 90 for each planting position group and treatment, respectively, following the third field season. Columns indicate stem basal diameter in mm and error bars indicate standard error. Different letters indicate significant differences. When there was an interaction between the factors, letters are displayed above each column, when there was no interaction, the letters are displayed above each planting position group. HQ Min = high quality mineral soil position, including assessment classes 2 and 4; HQ Hinge = high quality hinge positions, assessment class 6; LQ = low quality positions, including classes 1, 3, 5 and 7; and CM = capped mound, including assessment classes 8 and 9.

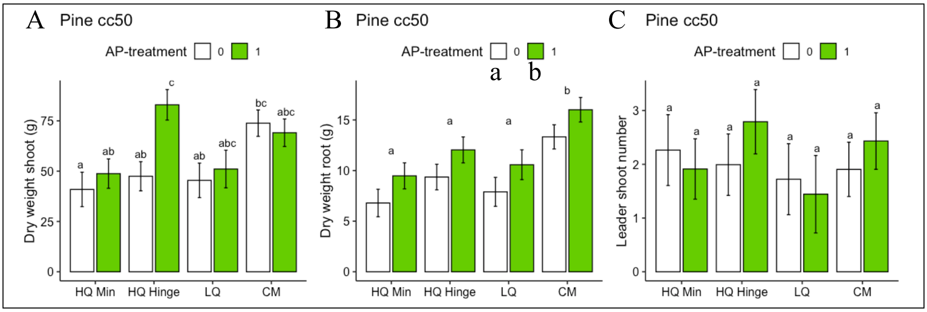

Figure 17. Results from ANOVA for harvested 50 cc pine seedlings A) dry weight shoot B) dry weight root C) number of leader shoots for each planting position group, respectively, following the third field season. Columns indicate dry weight in g (A, B) and number of leading shoots (C) and error bars indicate standard error. The different letters displayed above each planting position group indicate significant differences between these groups averaged over the values of treatment, while letters under the treatment legend indicate significant effect of treatment averaged over the levels of planting position group. HQ Min = high quality mineral soil position, including assessment classes 2 and 4; HQ Hinge = high quality hinge positions, assessment class 6; LQ = low quality positions, including classes 1, 3, 5, and 7; and CM = capped mound, including assessment classes 8 and 9.

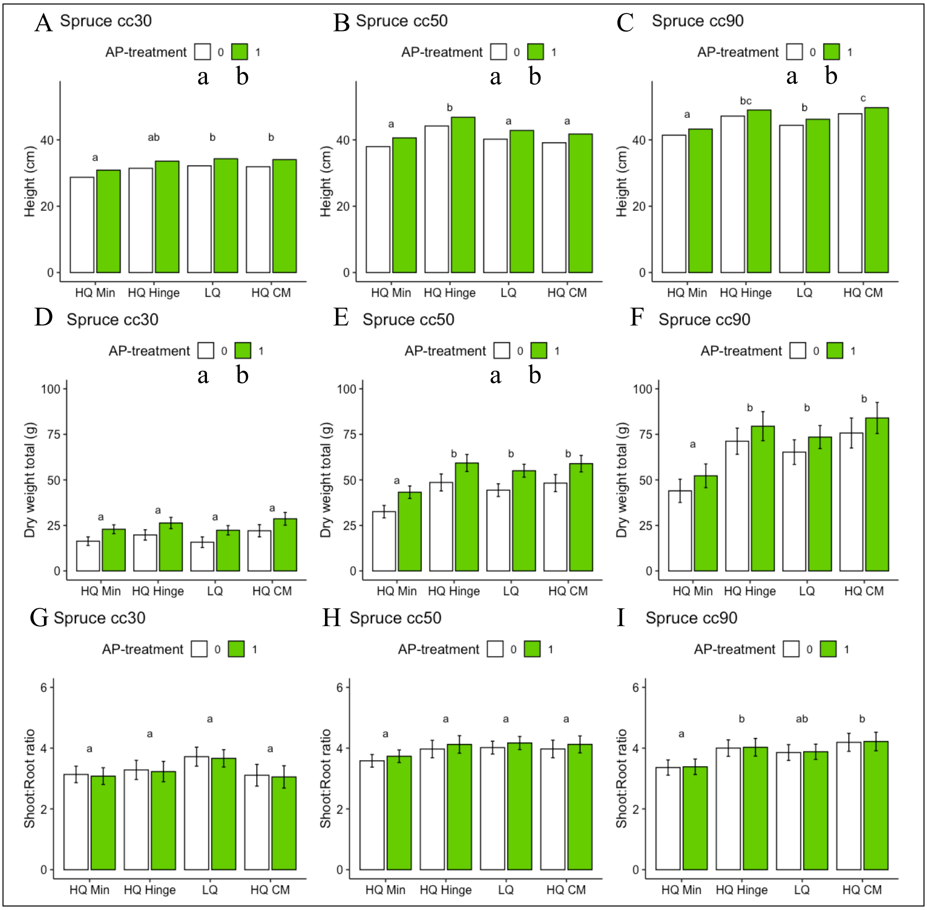

Figure 18. Results from ANOVA for probability of spruce seedling height for size A) 30 cc B) 50 cc and C) 90 cc, for harvested spruce seedling total dry weight, i.e. root + shoot, for size D) 30 cc E) 50 cc and F) 90 cc and harvested spruce seedling shoot:root dry weight ratio, for size G) 30 cc H) 50 cc and I) 90 for each planting position group, respectively, following the third field season. Columns indicate seedling height in cm and error bars indicate standard error. The different letters displayed above each planting position group indicate significant differences between these groups averaged over the values of treatment, while letters under the treatment legend indicate significant effect of treatment averaged over the levels of planting position group. HQ Min = high quality mineral soil position, including assessment classes 2 and 4; HQ Hinge = high quality hinge positions, assessment class 6; LQ = low quality positions, including classes 1, 3, 5, 7 and 8; and HQ CM = high quality capped mound, including assessment class 9.

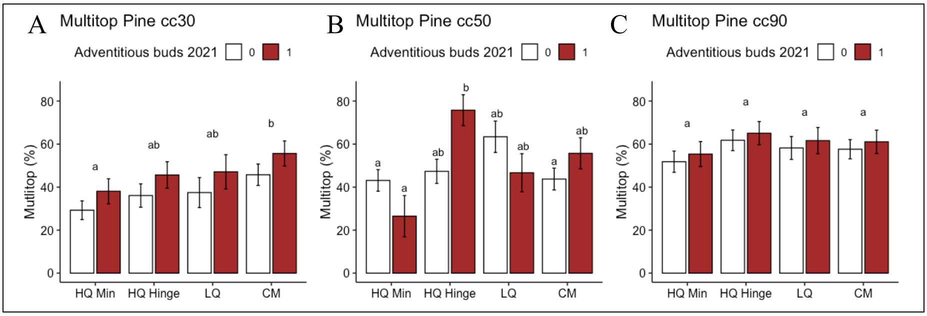

Figure 19. Results from ANOVA for occurrence of multiple leading shoots for pine seedlings for size A) 30 cc B) 50 cc and C) 90 cc for each planting position group and treatment, respectively, following the third field season. Columns indicate multiple leading shoot occurrence probability as a percentage and error bars indicate standard error. Different letters indicate significant differences. When there was an interaction between the factors, letters are displayed above each column, when there was no interaction, the letters are displayed above each planting position group. HQ Min = high quality mineral soil position, including assessment classes 2 and 4; HQ Hinge = high quality hinge positions, assessment class 6; LQ = low quality positions, including classes 1, 3, 5 and 7; and CM = capped mound, including assessment classes 8 and 9.

4.4 Paper IV

In Paper IV, I studied the effects of competition from mature Scots pine on nursery grown planted and direct sown Scots pine seedlings. In planted plots, ground vegetation and humus cover were retained, while these layers were removed prior to sowing in the sown plots. The planted seedlings suffered from very high mortality due to pine weevil, a common scenario when seedlings are planted without site preparation, and the planted seedlings had to be replaced with new ones in the second year of the experiment. The study included regeneration in three alternative environments: under the canopy of mature trees, representing shade and belowground competition in combination; outside the canopy along the forest edge, representing belowground competition in full light; and out on an open clear-cut, representing release from belowground competition in full light. In each environment there were three treatments: trenching in the form of 75 cm deep steel frames, N fertilization and control. Each environment- and treatment combination was represented by five replicates. Height, diameter, and survival of planted seedlings were recorded after six years after planting, and height and survival of sown seedlings were recorded seven years after sowing.

In the control plots, there was a general trend of survival and growth of seedlings being highest on the clear-cut (Fig. 20-21). This trend was strongest for survival of sown seedlings and stem basal diameter of planted seedlings, while it did not come out as significant for survival of planted seedlings or height growth of the sown seedlings. Trenching increased the survival of sown seedlings in forest (Fig. 20), and for planted seedlings trenching increased height growth to be similar to the control on the clear-cut, but only similar to the forest edge for stem basal diameter (Fig. 21). Annual addition of N fertilizer did not have any effect in the in the forest. A higher measured N supply in the forest than out in the open indicated that it was not all retained by the mature trees either. Both trenching and annual N fertilization compensated for growth loss along the forest edge (Fig. 21).

In the plots intended as a control for spontaneous natural regeneration, where the organic layer including ground vegetation was left intact, almost no natural regeneration occurred even though an increase in numbers of seedlings in the sown plots where the organic layer was removed indicated that there had been years where seed-fall had occurred.

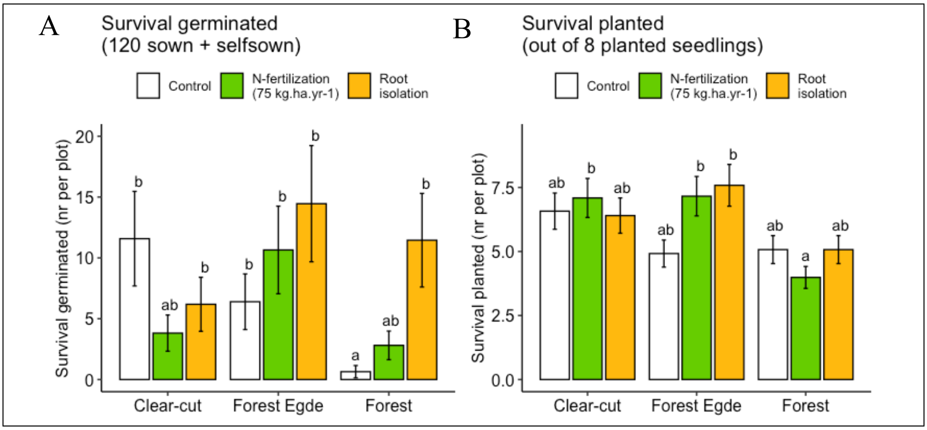

Figure 20. Estimated marginal means from linear models for survival of A) germinated seedlings out of 120 sown per plot plus additional self-sown seedlings after 7 years and B) planted seedlings after 6 years in field. Letters indicate significant differences including interaction. Values are transformed back from natural logarithmic scale. Error bars indicate standard error.

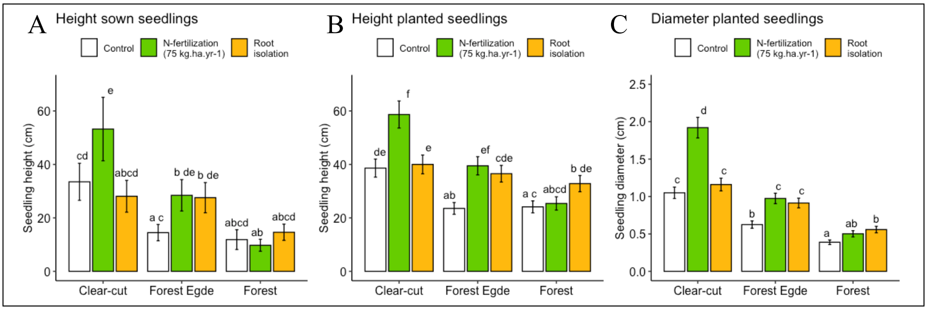

Figure 21. Estimated marginal means from linear mixed models for height of A) sown seedlings after seven years. B) planted seedlings and C) stem basal diameter of planted seedlings after six years in the field. Letters indicate significant differences including interaction. Values are transformed back from natural logarithms. Error bars indicate standard errors.

5. Discussion

Climate change is interfering with the established framework for our current silvicultural practices. Each site presents a unique combination of factors that can affect the outcome of forest regeneration practices, including local weather which is highly variable between years. How climate change will affect each specific site is therefore difficult to predict. However, it has been predicted for large parts of the country that there will be an increase in drought periods during the growing season, especially in spring and early summer (Spinoni *et al.* 2018). Even though there is an overall trend towards increasing precipitation in Sweden since the beginning of the 20th century, this increase is mainly during the winter and in northern areas, whereas the southeast part of the country has become drier (Chen *et al.* 2021). Furthermore, the increase in temperature and length of growing season induces increased occurrence of pests and increased competition of ground vegetation, which can become problematic as the use of pesticides and herbicides is prohibited in Swedish forestry.

Successful forest regeneration practice needs to ensure that the seedlings are well adapted to the site conditions, including potential variations in weather. This thesis took its point of departure in climate change and set out to study how to adjust the current practice of forest regeneration to make it more robust to local weather variations, which might increase further due to climate change. Weather variations is, however, only one of many factors influencing the success of planted seedlings to establish and grow at a given site. Each site presents a unique assemblage of factors influencing the outcome of seedlings to thrive. Furthermore, site conditions such as stoniness and amount of logging residues affects the outcome of mechanical soil preparation (see chapter 2, section 2.4.2). The factors discussed in the studies of this thesis include macro- and microsite abiotic conditions (e.g., geographical positioning, soil moisture, soil texture, etc), as well as biotic interactions like competition from surrounding vegetation and pressures by pests and pathogens (also see chapter 2, section 3). There are also other factors that are important for the outcome of regeneration outside the scope of this thesis, including e.g., the initial status of the seedlings, due to correct handling before planting, as well as the effect of seed origin, i.e., genetics. In the studies included in this thesis, all seedlings were appropriately handled before planting and the origin of seedlings and seeds were appropriate for the study areas. Hence, the effect of handling and seed or seedling origin were not a part of any of the studies.

My studies were mainly focused on planting practices within mechanically prepared soil in clear-cut areas (Papers I-III). However, in the context of the increasing interest in forest management by clear-cut free methods (CCF) by society and policymakers, I included the study presented in Paper IV which examines seedlings' establishment in a setting where forest and forest edge environments were compared to a clear-cut environment. Overall, I have presented results from a total of 16 sites (eleven in Paper I, three in Paper II, one in Paper III and one in Paper IV). In the following sections the results of the papers are discussed in the context of the three research questions framing the aim of the thesis, presented in the introduction chapter.

5.1 Can survival of planted seedlings be improved by choosing planting position depending on local environmental conditions? (Paper I and III)

In Paper I, I evaluated how environmental conditions affected the outcome for Scots pine seedlings in different planting positions with and without addition of arginine-phosphate (AP) and in Paper III, I investigated the effect of planting position in relation to seedling size and AP addition for Scots pine and Norway spruce.

In Paper I, the choice of planting position included the option to plant without mechanical soil preparation (MSP), as well as two options within the prepared spots: mineral soil and capped mounds. Seedlings in non-prepared soil in general displayed lower survival and growth than in MSP planting positions. This finding is in line with many previous studies, where success of forest regeneration was improved by MSP (Hagner 1962; Örlander *et al.* 1990; Spittlehouse & Stathers 1990; Sutton 1993; Thiffault & Jobidon 2006; Kankaanhuhta *et al.* 2009; Nilsson *et al.* 2010; Löf *et al.* 2012; Henneb *et al.* 2019; Hjelm *et al.* 2019; Nilsson *et al.* 2019; Sikström *et al.* 2020; Wotherspoon *et al.* 2020; Reicis *et al.* 2022). There was a negative correlation between length of growing season and survival in non-prepared soil (Paper I). This may be explained by increasing vegetation competition as well as increasing occurrence of pine weevil with a longer growing season, since vegetative competition and pine weevil are two of the major obstacles for successful forest regeneration (see chapter 2, section 2.3.4 and 2.3.5). Hence, choosing to plant in non-prepared soil appear like a generally poor option regarding seedling survival, increasingly so with increasing length of growing season.

Regarding survival in MSP positions, the results in Paper I show an example of the drought sensitivity of capped mounds compared to mineral soil positions. I found that survival in capped mounds was much lower than in mineral soil positions when there was low precipitation during the first month after planting, emphasizing the first of the listed plant physiological needs and limiting factors: a seedling needs sufficient water to survive and grow. This was most clearly expressed at one site (site K, see Table 3), which received exceptionally low amount of precipitation the first month after planting, with low survival in the capped mounds, while the seedlings planted in mineral soil displayed high survival.

Paper III describes an example of the expected increased growth in capped mound compared to mineral soil, with both pine and spruce seedlings generally growing better in capped mounds than in mineral soil positions. Here, sufficient precipitation was received during the first month after planting, in contrast to the dry conditions after planting in Paper I. Pine and spruce seedlings planted close to the capped mound, i.e., in the hinge position, grew equally well as the seedlings in capped mounds and mineral soil, except for the smallest pines (30 cc). Regarding the low-quality positions, seedling growth was only lower than in capped mounds for 50 and 90 cc pine seedlings. This probably reflected the increased attack rate of pine weevil for the larger seedlings in low quality positions, even though I did not find any significant effect of pine weevil damage on growth. However, this lack of effect on growth was probably because many of the seedlings with a high total score, i.e., with severe damage, had died.

In Paper III, survival was in general high and there was no significant difference between planting positions in capped mound and mineral soil as long as both positions were of high quality. For Norway spruce this was also true for the hinge positions. However, there was lower survival of Scots pine in the hinge positions than in capped mounds, and a significant trend of lower survival in positions of low quality, i.e., with organic material near the planted seedlings. The proximity to organic material increases the risk of attack by pine weevils, which was also the main reason for seedling mortality in this study. At the study site of Paper III, there had been sufficient amount of precipitation following planting, thus, the drought-sensitivity of capped mounds did not pose any problem. However, it should be noted that there was a higher share of capped mounds that was classified as low-quality positions compared to the share of low-quality positions in hinge and mineral soil positions, indicating that the risk of lower survival due to pine weevil can be enhanced if the main choice of planting position is the capped mound. In commercial planting, the careful assessment of each mound made in this experimental study would be too time-consuming, as the planters generally are paid per planted seedling. A general issue concerning the quality of a capped mound position is the abundance of harvest residues at the regeneration area. On the site in Paper I, where seedlings did grow better in the capped mounds at only one out of ten sites, there was very little harvest residues at this particular site compared to the other sites. There were also many other site attributes (see Table 3) as well as different MSP methods that may have affected the quality and effect of the capped mounds. In this context it should be mentioned that the seedlings in mineral soil positions in Paper I were planted on relatively high spots in the mineral soil areas, often relatively close to the capped mounds, but were not classified with the same precision as in Paper III. If the trend for seedlings growing equally well in hinge positions as in capped mounds from Paper III is representative of a wider range of sites, that might also explain why there was so little difference in growth between the MSP planting positions in Paper I.

In situations with dry weather following planting, as the case in Paper I, and potentially also at sites with high pine-weevil pressure and variable quality of the capped mounds, as the situation in Paper III, it might improve regeneration success if the capped mounds were not the recommended planted position. Many seedlings are planted in the spring, or early summer in the northern inland parts of Sweden where the ground is frozen for a longer period. As the forecast for increased drought events is most pronounced in spring (Spinoni *et al.* 2018), it is becoming increasingly important to consider the choice of planting position for each site, rather than having a general prescription. Importantly, such considerations should include an assessment of the specific site conditions, such as soil moisture class, soil texture and topography. For example, on a moist site or a flat valley site with fine soil, an elevated position, as presented by a capped mound, might be crucial for the seedlings' survival even though the weather forecast at the time of planting is warm and dry, because a lower position might be flooded during periods of high precipitation. In a depression in a landscape where cold air can increase the risk of frost during cold nights, the elevated position can also decrease the risk of frost damage (Örlander *et al.* 1990). Furthermore, fine mesic and moist soils presents a high risk of frost heaving, i.e., ice lenses in the soil that grow from below and push upwards, which can cause young seedlings' root substrate being pushed up from the ground (Goulet 1995). The risk for frost heaving has been found to decrease in capped mounds, likely due to the lower soil moisture in these elevated spots, and also in undisturbed humus where surrounding vegetation decrease temperature fluctuations (Goulet 1995; Sahlén & Goulet 2002). In contrast, a seedling planted in an elevated position on a site with very permeable soil on a south-facing slope will probably suffer from drought in the case of dry weather following planting.

However, it may be hard to plan regeneration measure choices according to weather forecasts. Moisture maps based on digital terrain indices is a tool that might be useful for predicting probability of the site being dry or prone to waterlogging over a longer period of time (Ågren *et al.* 2014; Larson *et al.* 2022). Further research would be necessary to assess at which level of probability of drought or waterlogging any planting position choice should be preferred for a certain site and soil moisture maps can be useful tools to guide the choice of planting position (Nordin *et al.* 2023). It would also be useful to take the soil texture into account, if e.g., a digital map for planting position choice would be developed, since a fine soil could potentially present problems with frost heaving and also water logging in depressions following precipitation events also on hills and slopes, while this risk for this would be lower on a more permeable soil.

Although I found some underlying patterns that in part explained site differences, there are too many factors that co-vary between sites to discern a pattern for each of them in a dataset with so few sites as in Paper I. However, detailed data on seedling establishment and growth environment conditions are recorded in a new large countrywide forest regeneration inventory project, in which sample plots are distributed both on company- and privately owned forest land (Öhlund *et al.* 2023). That dataset, including a vast number of sample sites, will be a valuable source for investigating correlations between growth/survival and various specific site conditions that eventually can be used to develop decision tools for advising on where to plant on capped mounds and where to avoid it.

5.2 Will addition of a slow-release organic nitrogen fertilizer in the form of arginine phosphate (AP) improve establishment and early growth of planted seedlings? (Papers I, II, III)

In Papers I-III, I investigated the effect of adding arginine phosphate on survival and growth of the planted seedlings. One of the aims was to find out whether AP addition could compensate for the lower availability of nutrients in mineral soil positions, compared to capped mound positions. Additionally, arginine additions to seedlings have been found to particularly support their root development, hence enhancing the seedlings' capacity for both nutrient and water uptake (Gruffman et al. 2012, Lim et al. 2022).

Seedlings often grow better on capped mounds than in mineral soil, due to the release of nitrogen from the organic material decomposing within the mound, if sufficient water is available (Örlander *et al.* 1990). However, in Paper I there was no significant difference in growth of seedlings on capped mounds and in mineral soil in nine out of ten sites. The positive effect of AP addition on pine seedling growth was higher in mineral soil positions than in capped mounds and increased with increasing growing season length. The lower effect of AP addition in capped mounds than in mineral soil is interesting and could have several explanations. The AP-granulates may have dispersed within the relatively porous organic material within the capped mounds and in this way becoming less available to uptake by the seedlings. It could also be an effect of the presence of organic material to which the arginine can bind and become unavailable to plant uptake, or that micro-organisms that are more abundant in the organic material than in the mineral soil, may have immobilized the arginine (see chapter 2, section 2.3.3 and 2.4.3). In a previous study on arginine fertilization of seedlings, a higher nitrogen dose of arginine than of inorganic nitrogen was needed to achieve the same growth response, which was suggested to be due to greater microbial competition and/or adsorption of the arginine (Wilson *et al.* 2013).

In Paper I it was demonstrated that the relatively low seedling survival in non-prepared soil (vs. that in prepared soil) was not counteracted by AP-addition which had no significant effect on seedling survival in this planting position. However, in the non-prepared soil AP-addition had a positive effect on seedling growth. This was only apparent on sites with a site index above 20 (i.e., relatively fertile sites), and these were also the sites with longest growing season included in the analysis (see yellow-marked sites in Table 1). In the light of the findings in Paper II, where AP addition seemed to enhance the pine seedlings' capacity to withstand pine-weevil damage on the south site, the positive growth effect of AP-addition on these two sites in Paper I might be related to that the seedlings could withstand pine weevil pressure and thus grow better than the untreated seedlings. This could be a topic for further studies. It is also interesting that the sites with poorest performing seedlings in non-prepared positions had crowberry present (Table 1), which is known to have a negative impact on seedling growth resulting from chemical inhibition (Nilsson & Zackrisson 1992). However, the short growing season is naturally a cause of lower growth, as seen in the analysis of growth of seedlings in the MSP positions.

The increasing positive effect of AP addition on seedling growth with increasing length of growing season and site index noticed in Paper I may indicate that the more the environmental conditions allow seedlings to grow, the greater the potential beneficial effect of nutrient addition. Other pre-conditions may however have had a greater influence on growth than the benefit of higher nutrient availability: on many of the northernmost sites the seedlings were smaller when planted and on the two sites with shortest growing season there was no effect of AP addition at all (site J and K, see Table 1). At site K, the precipitation was exceptionally low and here the low water availability may have prevented the seedlings to benefit from nutrients. Site J instead received the highest amount of precipitation of the sites included in the study, perhaps even too high to be optimal in the mineral soil as survival was one of the lowest in this position. This site had a relatively low position in the landscape, with a nearby bog at a similar elevation, indicating that the water table might have been quite close to the surface even though it appeared dry at the time of inventory. Hence, the effect of quite high precipitation the first month after planting as well as potentially high precipitation later in the season or at snowmelt in the following spring may have negatively interfered with the effect of AP addition by adversely affecting soil oxygen conditions. Before deciding on planting in mineral soil and using AP addition to compensate for the lower nutrient levels compared to capped mounds, it may be relevant to consider the depth to the water table as well as current weather conditions and soil texture. I did not further explore the interaction between precipitation and depth to the water table. However, soil moisture condition effects on AP addition may be an interesting topic for further studies.

In Paper II, on the north-western site, the effect of AP addition was positive for both growth and survival for seedlings of pine, spruce, and birch. Here the site was prepared by inverting the soil, thus avoiding high positions with the risk of drought, but providing the benefit of nutrients from decomposing organic material, since inverting basically means taking a package of topsoil and underlying mineral soil, flipping it upside down and putting it back. Hence, the variation in quality found in capped mounds are likely less in inverted spots. However, there may have been interference with the design of the study since all plots with the AP-treatment were placed adjacent to each other in one block and the control plots were placed adjacent to each other in another block. Although the blocks were both on the same clear-cut, within-site variation may have affected the results. I brought this up in the discussion in the paper, i.e., that the positive effects could be due to other environmental differences between the blocks. For example, the AP addition block was closer to the road, hence the effect of lower browsing and higher growth seen among the seedlings with AP addition may in part have been due to browsing animals' behaviour being affected by disturbance from vehicles passing by. There was also less damage by browsing among the seedlings where AP was added on this site. Consequently, the effect of lower browsing of the seedlings that were given AP at this site may have allowed more of the larger seedlings to remain intact in this area of the clear-cut and in this way given a biased positive effect of AP addition on growth. Nevertheless, if the positive effect on growth and survival, or at least part of it, was truly from AP addition, it is interesting that seedlings seem to respond well to the AP-treatment on inverted soil. As none of the studies in this thesis included different MSP methods on the same site, we cannot draw any conclusions about whether AP has different effects according to MSP method, but this could be a topic for further studies.

On the north-eastern site there was a positive effect of AP addition on growth for conifers but not for birch. Here, the site was prepared by spot milling, a method rarely used in Sweden, resulting in depressions from which soil was milled into an adjacent pile of mixed material. As at the north-western site, the different treatments were divided into blocks, making within site variation likely to interfere with the results.

At the southern site, where the plots were randomly distributed, there was a positive effect of AP addition on survival for pine, but no other effects. In the discussion of Paper II, I hypothesized that the AP-treated seedlings may have benefited in relation to chemical defences, making them withstand pine weevil damage to a higher degree than the control seedlings. As mentioned in the discussion of Paper II, T. Näsholm found higher levels of phenylalanine, a precursor to chemical defence compounds, among arginine-fertilized seedlings in a previously unpublished small pilot study. This is certainly a topic for future study, as all measures to decrease damage caused by pine weevil are important. If further research, on larger scale than this case study, would show that AP addition could improve a seedling's ability to cope with pine weevil, this could be an important finding since pine weevil is one of the greatest threats to newly plated conifer seedlings.

In Paper III, where AP addition was tested in relation to different planting positions and planted seedling sizes, we found positive effects on growth of spruce seedlings of all sizes, regardless of planting position. The effect of AP addition on pine seedlings was less clear: none for the largest seedling size and differing according to planting position for the medium and small seedlings. An interesting result was that there was a trend towards increased growth with AP addition in mineral soil and hinge positions, while there was the opposite (but not significant) trend for decreased growth of AP-treated seedlings in the capped mound positions for pine. As with the lower effect of AP addition on seedling growth in capped mound compared to mineral soil positions in Paper I, and according with hypothesis by Wilson et al 2013 on the need for higher dose of arginine-phosphate compared to mineral fertilizer as previously mentioned, this may be related to microbial competition and/or adsorption to organic material in the capped mounds. However, this opposing trend of the effect of AP treatment in the different positions was not occurring for the spruce. This might in part be due to soil moist conditions. The area that was planted with pine seedlings in this experiment had slightly higher abundance of coarser soil and was located upslope, presenting an over-all drier environment than the spruce seedling area, which may have created enough difference between capped mounds and the other positions to interfere with the effect of AP addition. However, as there clearly was enough precipitation for the seedlings of both species to establish well in the capped mounds on this site, there is likely some other reason for the clearer positive effect of AP addition on spruce in all planting positions. From the harvested seedlings, spruce had a lower shoot:root ratio than pine following three growing seasons in field, indicating that spruce grew relatively more belowground compared to pine. Norway spruce is also more nitrogen demanding than Scots pine (Tamm 1991; Nikolov & Helmisaari 1992), and has been found to respond to nutrient enrichment with higher increases in both root- and shoot growth than pine (George *et al.* 1997). This may make spruce more effective than pine in uptake of the added arginine, and potentially also a stronger competitor against microbial nitrogen immobilization in the capped mound. The fate of arginine in capped mounds and the relative competition strength between tree species for the added resource might be topics for further studies. In this study, we found no effect of AP addition on pine weevil damage. This neither corroborate nor contradict the hypotheses discussed regarding the positive effect of AP addition on survival in Paper II, as there are many other site-specific factors that could be involved in the outcome, such as a potential higher occurrence of pine weevil as well as much higher occurrence of ground vegetation on the south site in paper II compared to the study site in paper III.

The question whether AP addition can be a useful tool to aid early establishment and growth, or to compensate for growth loss of seedlings planted in mineral soil versus seedlings planted in capped mounds has a complicated answer, as the results of AP addition were variable. The take-home message is that the effect of AP addition depends on which other factors that simultaneously affect the seedling. I found that at most of the studied sites, growth was in fact not any better in capped mounds, hence there was no growth-loss to compensate for (Paper I). The effect of AP addition was higher in mineral soil positions than in capped mound for pine, which may be related to dispersal of the AP granulate in the organic material, competition for nutrients by microorganisms, adsorption and/or soil moisture conditions (Paper I and III). Based on these results, I suggest that use of AP addition in capped mounds should not be recommended until more is known about which underlying reason that hampers the effect on pine growth in this position.

Among the factors I observed, it appeared that conditions that improve growth in general also improved the effect of AP addition, as the effect increased with length of growing season and site fertility (Paper I). However, the most southern site in Paper II deviated from this general pattern as here increased survival of pine was the only significant effect from the AP addition. It appeared that the AP addition may have improved the pine seedling's ability to withstand pine weevil damage. However, I suggest more research on this topic before using AP as a tool to mitigate high pine weevil pressure. The lack of any effect of AP addition on the larger (cc90) pine seedlings in Paper III also indicates that it may be a question of dosage, i.e., larger seedlings may need a larger dose. Lastly, the effect of AP addition may be affected by different species nitrogen uptake efficiency and how they allocate their growth resources, as indicated by the consequently positive effect on spruce seedlings which also had lower shoot:root ratio than pine following three seasons in field (Paper III). In conclusion, I found that AP-addition may enhance both survival and growth of the here studied seedlings, but more studies are needed to disentangle the AP-addition effects from the effects of the other environmental factors as well as the weather conditions at the time of planting, to optimize the use of AP-addition as a tool to adapt forest regeneration practice to the future climate.

5.3 How can seedling establishment be improved in proximity to mature trees? (Paper IV)

Recently the EU published its guidelines for Closer-to-Nature forestry, encouraging avoidance of clear-cutting and site preparation (EC 2021). The results from Paper IV points out some challenges with such a forest regeneration approach, at least in some parts of forests in Sweden. For a pine dominated forests on nutrient poor soils in northern Sweden it was demonstrated in Paper IV that forest regeneration is promoted by the environmental conditions created by clear-cut harvesting, as the number of surviving seedlings seven years after sowing was approximately ten times higher on the clear-cut area than on the area beneath the forest canopy, with intermediate values for the forest edge, i.e. the area between the clear-cut and the closed canopy forest. Paper IV further demonstrates that alleviating the seedlings' belowground competition with the mature trees in this forest edge area, via annual nitrogen-fertilization and/or root isolation by soil trenching, increased the seedlings' growth to levels like those of the seedlings on the clear-cut area (with no nitrogen fertilization or soil trenching). In this forest edge environment, the seedlings were exposed to full light, allowing higher photosynthesis than under the canopy, thus higher transpiration leading to higher nutrient uptake.

I interpret these results as that in very nutrient poor forests, seedlings' establishment in proximity to mature trees could be improved with nitrogen fertilization and trenching, at least along forest edges. The smaller a harvested area is, the larger is the proportion of it that is edge environment, and it could potentially be necessary to aid the regenerating trees in areas where growth is hampered by belowground competition. Annual fertilization would perhaps be too costly; however, it might be a case for future studies to test the effect of arginine-phosphate along a transect from a forest out to a clear-cut to see whether this effect would be sufficient to compensate for the growth loss due to belowground competition along the forest edge. Further, root isolation by steel frames, like done in Paper IV would be unfeasible in practice. However, deep trenching, via e.g., some kind of mechanical soil preparation, to cut off mature tree's roots where seedlings are planted could be an option. This would require further research, to avoid hampering growth of the mature trees along the forest edge.

Inside the forest beneath the canopy of the mature trees, root isolation also enhanced the survival of sown seedlings and growth of the planted seedlings. This indicated that belowground competition between the seedlings and the mature trees had negative effects on both survival and growth of the seedlings. Water availability was not measured here and could, thus, not be directly compared between treatments. However, fertilization of the seedlings, without soil trenching, did not improve either seedling survival or growth. I hypothesized that this added nitrogen may have remained in the soil to a greater extent in the forest due to nutrient uptake ability limitation because of competition for water among the trees and seedlings in the forest. I conclude that fertilization alone does not seem like an option to aid forest regeneration under a canopy of mature trees, at least not on dry sites like in this study. Even if root isolation improved establishment and growth in the forest to some degree, applying the needed soil disturbance would probably cause so much damage to the mature trees so that the overall stand health and productivity may be severely hampered.

Although both planting and seeding was included in Paper IV, no direct comparison between these methods was made since the main topic of the study was to compare effects of the soil trenching and nitrogen fertilization treatments in different forest regeneration environments (clear-cut, edge, forest). The intention was to include also natural regeneration in the study, and in each experimental block a plot was designated for this purpose. In these plots, the ground vegetation was left intact. However, a lack of naturally regenerated seedlings in these designated plots made any comparison unfeasible. A negative result is however still a result, and it may be used to illustrate one of the reasons why the practice of soil preparation and planting is often superior to natural regeneration: the practice alleviates the hostile environmental factors (see chapter 2.3) that challenges successful seed germination and the juvenile seedling stage.

For instance, natural regeneration relies on seed production from nearby trees (Hagner 1962). More seed falls close to a seed-tree than further away, however, when the seeds have germinated, proximity to the mature tree negatively affects growth of the new generation (Hagner, 1962). A very small proportion of the dispersed seeds succeed in establishing (Nilsson *et al.* 2002). This is a pattern I recognize from Paper IV, where more additional regeneration occurred in sown plots in the forest environment than on the clear-cut following one of the studied years, but where seedling survival at the end of the study still was lower in the forest environment. The reasons for low germination rates can be multiple, including direct competition from the ground vegetation as well as seed predation (Nystrand & Granstrom 2000; Nilson & Hjältén 2003; Erefur *et al.* 2008) and allelopathy (Mallik & Pellissier 2000; Mallik 2003; Zeng *et al.* 2008; Friedman 2017), or simply be because of the seed landing on a surface where water is not available. Germination success is also dependent on adequate warmth during the growing season (Hagner, 1962), and is highest at optimal soil water availability and on recently exposed mineral soil beds where the seed can settle between soil particles before precipitation has smoothed the surface (Grossnickle & Ivetić 2017). For the seeds that germinate, predation on juvenile seedlings by slugs is a threat that is higher in moist areas and also increases with increasing canopy-cover since slugs need humid and shady conditions to prevent desiccation (Nystrand & Granström, 2000). Whether the lack of natural regeneration in the control plots in my study was due to direct competition, allelopathy or because seed predators thrive better in vegetation remains unknown, since the fate of seeds that might have been present was not monitored. However, this highlights that not only competition from mature trees but also the ground vegetation cover is an obstacle for natural regeneration, showing the importance of site preparation to enhance germination and survival of sown and naturally regenerated trees.

In the sown plots, the organic layers were removed prior to sowing and, after seven years, there was still very little ground vegetation that could interfere with germinated seedlings. However, due to the small size of the trial plots, where 8 seedlings were planted on an area of 75 × 150 cm and 120 seeds sown on 75 × 75 cm, the internal competition between seedlings gave rise to large variability in both survival and growth. Consequently, seven years after beginning the trial, there was in general a few seedlings growing taller than the others in each plot. Furthermore, there was large variability in survival of sown seedlings, with 0-39 living seedlings in each plot, while 3-8 of of the planted seedlings were alive after six years in each plot. Directly sown seedlings, in general, achieve lower survival (Grossnickle & Ivetić 2017). However, in this study, there was a set of seedlings that were planted the same year as the sown ones, of which almost all perished as a result of pine weevil damage. The remaining planted seedlings were removed, and the planted part of the trial was re-started the following year. Furthermore, the organic layer was not removed for the planted seedlings, which affected the occurrence of pine weevil as well as vegetation competition. Hence, the outcome of the different regeneration methods was not directly comparable.

6. Concluding remarks

It needs to be highlighted that the results presented in this thesis are to large extent specific to site conditions and regeneration practices in Sweden. The forest regeneration practices discussed here are, however, practiced in many other parts of the world, and some of the ecological issues related to forest regeneration are universal: all tree seedlings need enough water, nutrients, and light to establish, grow and survive. The results cover a limited number of sites, and further studies would be needed on the topics studied in this thesis to provide general regeneration recommendations. Nevertheless, my findings provide indication of which topic that need further study, such as which specific conditions that may acquire an alternative recommendation of planting position and which conditions that allows a positive effect of AP addition.

Different local site conditions present different challenges which need to be considered when performing forest regeneration. In agreement with many previous studies (Örlander *et al.* 1990; Spittlehouse & Stathers 1990) and similar recent research in southern Sweden (Nordin 2023), I have, as part of this thesis, concluded that adapting the choice of planting position to site and microsite conditions is crucial for successful regeneration also in the northern parts of the country. The changing climate alters site conditions, and it is becoming increasingly important to consider the site conditions before choosing regeneration approach. There is no such thing as an optimal planting position, since the local site conditions directs which planting position that is most appropriate in any given area. Local weather is highly variable and needs to be considered during the time of planting, while simultaneously considering the soil texture and local topography. The local site conditions also highly affect the outcome of mechanical soil preparation, and there are no guaranties that it is possible to create an appropriate capped mound on any given site. I point out that the accumulated knowledge may soon be enough to enable some kind of decision support tool for practitioners, either as a qualitative assessment tool or as a map layer, of what is the best suited planting position under the given environmental conditions.

Arginine phosphate addition can support seedlings' survival, but perhaps particularly enhance seedling growth. A positive effect of AP addition on seedlings' growth appears mainly in mineral soil positions since the effect of AP addition in capped mounds seems to be counteracted by the occurrence of organic material. However, other environmental conditions may have a stronger effect on the seedlings' development than the AP addition and there are no guaranties that the effect of AP addition will be equally beneficial across sites. Nevertheless, knowledge is accumulating also concerning this topic, and it may be possible to support practitioners with development of decision support tools on where and when to apply AP to enhance forest regeneration outcomes.

As it comes to regenerating Scots pine forests in vicinity to mature trees, it appears clear that the complex interactions between abiotic and biotic factors is more directly influencing the many steps along the way from seed to an established and vital seedling in vicinity of mature trees than under planting practice in cleared areas. Importantly, belowground competitive interactions between the seedlings and the mature trees may be decisive for the regeneration outcome and methods supporting the seedlings' competitive strength may be key to a successful regeneration result under continuous cover forest regeneration practices.

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Popular science summary

The topic of this thesis is about adapting forest regeneration practices to site conditions in boreal forests of Sweden to sustain a good forest regeneration result in a variable climate. Forest regeneration in Sweden is mainly done by planting nursery grown Scots pine and Norway spruce seedlings on areas where forest is harvested. The main part of this thesis is therefore focused on planting seedlings on harvested areas (Paper I-III). However, there is and increasing interest for other methods of harvesting, which leaves smaller gaps in where regeneration is more affected by competition from adjacent trees. The last part of my thesis is therefore about how we can improve regeneration adjacent to mature trees (Paper IV).

When a seedling is planted, it has a very small root system and therefore needs to grow new roots as fast as possible to be able to reach water and nutrients in the adjacent soil to grow and survive. There are many challenges for the seedling, such as competition from ground vegetation and other trees, insects like pine weevil which eats the bark and may kill the seedling, and browsing by various animals, for example moose and deer. To enhance the establishment of the seedlings, the harvested area is commonly prepared by mechanical soil preparation, often by disc-trenching or mounding, resulting in mounds with adjacent depressions. The mounds comprise the material from the depressions, where the ground vegetation, organic soil and top layer of the mineral soil is turned upside down on top of the adjacent intact soil. This practice has several general benefits for the seedling: the removal of ground vegetation decreases competition; the mineral soil becomes warmer when the ground vegetation and topsoil layer is removed, and the risk of damage by pine weevil decrease when organic material is removed. The increased temperature, of the otherwise relatively cold soil in Nordic conditions, is good for root growth. Planting is often done on the mounds because the organic material within the mounds provides nutrients for the planted seedling and presents a drier environment which can be important at moist sites. However, if there is a period without rain, the mound can become too dry, because the organic material in the mound slows the movement of water that rise from the soil below. If the seedling instead is planted in the depression beside the mound, there is less nutrients available, but there is water available in the soil below so that dry weather is less of a problem. In my studies I found such a pattern, where seedlings planted in furrows and depressions displayed high survival despite very dry weather, while the seedlings in ridges and mounds showed high mortality in such conditions.

With the changing climate, the weather is predicted to become dry in spring and early summer more often in the future. Many seedlings are planted in this period and the planting in the depression could therefore be a safer choice than to plant on the mounds, at least on areas that have soil where water easily drains away. However, the lowest parts of depressions should be avoided, because when it rains, the low areas could be water filled, especially on soils with very small soil particles where the water cannot easily drain and on low lying areas. Fine and moist soils can also present a problem with frost heaving when the temperature fluctuates around 0°C and ice lenses in the soil can push the seedling up from the ground.

The lower availability of nutrients in the depressions could be compensated by adding organic fertilizer when planting the seedling. However, in my studies I found that the effect on early growth and survival of organic fertilizer varied depending on site conditions, planting position, seedling species and size. To find out how the effect develops over time, long-term investigations would be needed.

Regarding seedling establishment adjacent to mature trees, I found that fertilising and isolating the seedlings' roots from competition of mature trees enhanced seedling growth along a forest edge. This can be useful when smaller areas are harvested, since the share of edge environment with competition from the adjacent mature trees becomes larger when the harvested are becomes smaller.

By considering the local environmental conditions, such as soil type, position in the landscape and weather forecast before planting, early seedling survival and growth could be improved and sustained in a variable climate.

Populärvetenskaplig sammanfattning

Denna avhandling handlar om att anpassa skogsföryngringsmetoder till lokala förhållanden i boreal skog i Sverige, för att upprätthålla goda föryngringsresultat i ett all mer varierande klimat. Skogsföryngring i Sverige består främst av plantering av plantskoleodlade tall och- granplantor på avverkade områden. Huvudparten av avhandlingen fokuserar därför på plantering på avverkade områden. Dock finns ett ökat intresse för andra avverkningsmetoder som lämnar förhållandevis små föryngringsytor jämfört med dagens metoder, där föryngringen blir mer påverkad av konkurrens från närliggande större träd. Därför handlar den sista delen i avhandlingen om hur man kan förbättra överlevnad och tillväxt av plantor i närheten av större träd.

En nyligen planterad planta har väldigt liten kontaktyta mot omgivande jord och rötterna behöver därför börja växa snabbt så att plantan får den tillgång på vatten och näring den behöver för att växa och överleva. Det finns många utmaningar för plantan, som konkurrens från andra växter och träd, insekter som snytbagge som gnager på plantans bark och på så vis kan döda plantan, samt beting av växtätande djur, till exempel rådjur och älg. För att förbättra plantans chans att etablera sig, utför man vanligtvis markberedning innan man planterar, oftast med harvning och högläggning i svenskt skogsbruk. Dessa metoder resulterar i högar med intilliggande fördjupning vid högläggning. Högarna, s.k. "omvända torvor" består av materialet från fördjupningarna där markvegetationen, det organiska jordlagret och det översta lagret av mineraljord är vänt upp och ned och placerat ovanpå den orörda jorden intill. Markberedning har flera generella fördelar: konkurrensen från markvegetation minskar; minrealjorden blir varnare när det isolerande täcket av markvegetation och organiskt material är förflyttat, och risken för angrepp av snytbagge minskar när plantan är omgiven av mineraljord. Den ökade temperaturen är positiv bland annat för rottillväxt eftersom förhållandena i Norden är relativt kalla. Plantering görs ofta i högarna eftersom det organiska materialet i dem utgör ett förråd av extra näring. Det upphöjda läget utgör också en torrare position vilket kan vara viktigt på våta marker. Dock kan högen bli för torr om det är torra väderförhållanden eftersom det organiska materialet i högen saktar ner flöde av vatten från den underliggande jorden. Kvalitén på högarna varierar också mycket i och med olika mängd sten i marken, avverkningsresten och olika markvegetation påverkar hur sammansättningen på högen blir. Om man i stället planterar plantan i fördjupningen intill högen, så finns mindre näring tillgängligt men vattentillgången är säkrare så att torrt väder blir mindre problematiskt. I mina studier hittade jag ett sådant mönster, där en lägre andel av plantorna i högarna överlevde vid torrt väder månaden efter plantering, medan plantor planterade i fåran till hög grad överlevde trots det torra vädret.

Med ett klimatförändringarna kommer torrperioder under våren och försommaren troligen att bli allt vanligare. Många planterar just under våren, och plantering i fåran eller fördjupningen kan därför vara ett säkrare alternativ än högen, åtminstone i områden där vatten lätt dräneras bort. Dock bör man undvika den lägsta punkten, eftersom den vid regn kan bli vattenfylld, speciellt på finkorniga jordar där vattnet inte dräneras lätt och på lågt liggande områden i terrängen. I finkorniga fuktiga jordar kan också plantan utsättas för uppfrysning när temperaturen rör sig runt 0°C och islinser bildas i jorden som kan trycka upp plantan så att rotkontakten försämras. Dock fann jag i mina studier att effekten av organisk gödning kan variera mellan lokaler, planteringspunkter, trädslag och plantstorlek. För att veta hur effekten utvecklas över tid skulle undersökningar över en längre tid behövas.

Gällande plantetablering i närheten av fullväxta träd fann jag att gödsling och isolering av plantornas rötter från de större trädens rötter ökade plantornas tillväxt längs skogsbrynet. Detta kan vara användbart när man skördar träd på mindre ytor, eftersom andelen av ytan med konkurrens från intilliggande större träd ökar ju mindre yta som är skördad.

Genom att ta hänsyn till lokala förhållanden, så som jordtyp, landskapsposition och väderförhållanden innan plantering, skulle man kunna öka tidig överlevnad och tillväxt i ett varierande klimat.

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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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Pinus sylvestris; forest regeneration; seedling survival; seedling growth; planting positions; arginine phosphate

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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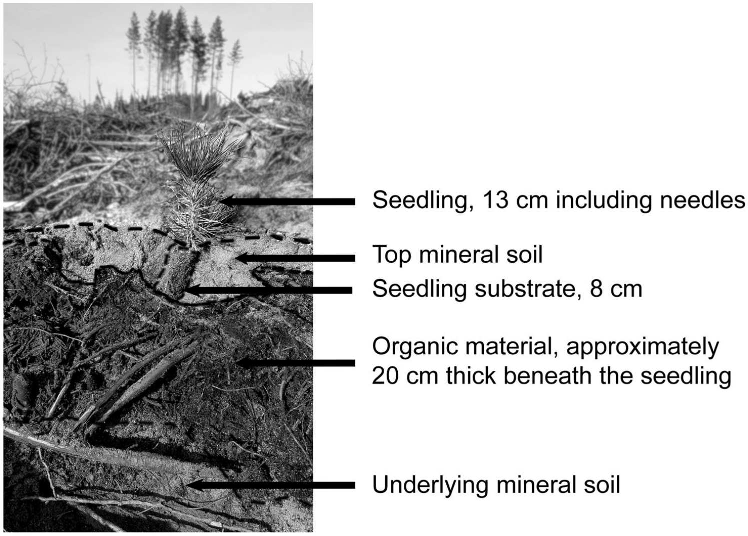

Figure 1. A cross section of a capped mound that would be classified as optimal when looking from above ground. The cross section reveals that the planting position is not optimal for the seedling to reach capillary water. Dashed lines mark the top surface of the capped mound, top and bottom of the organic 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".

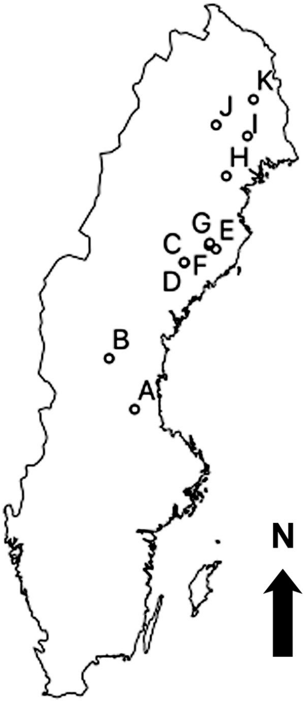

Figure 2. Distribution of sites within the boreal forest area of northern Sweden between latitudes 61.1°N and 67.1 °N.

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**

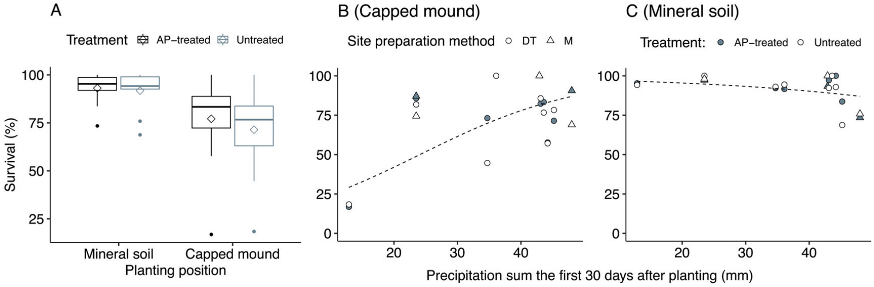

Figure 3. (A) Box and whisker plots of the observed proportional survival range of seedlings planted in mineral soil and on capped mounds with (black) or without (gray) arginine phosphate (AP) treatment across eleven study sites along a north-south gradient in northern Sweden. The diamonds indicate mean 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.

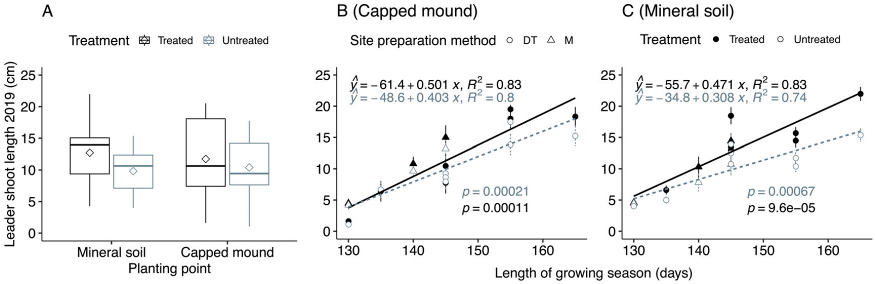

Figure 4. (A) Box and whisker plots of the range of observed mean leader shoot length values of seedlings planted in mineral soil and on capped mounds with (black) or without (gray) arginine phosphate (AP) treatment across eleven study sites along a north-south gradient in northern Sweden. The diamonds 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)).

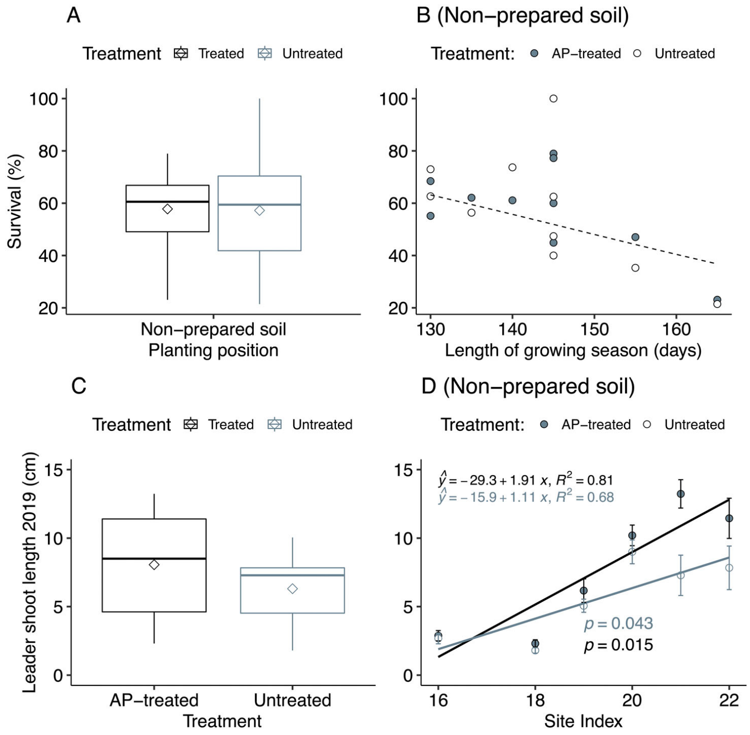

Figure 5. (A) Mean survival of seedlings planted in non-prepared soil with (black) or without (gray) arginine phosphate (AP) treatment across eleven study sites along a north-south gradient in northern Sweden. The diamonds indicate mean survival values for each position and treatment in (A) and mean 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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Effect of arginine-phosphate addition on early survival and growth of Scots pine, Norway spruce and silver birch

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Highlights

- Arginine-phosphate addition (APA) represents a potential tool to aid regeneration of planted trees, especially to increase survival of Scots pine seedlings on sites where susceptible to pests.
- Effects of APA however varies between different sites.

Abstract

Applying arginine-phosphate (AP) to tree seedlings at planting is a novel silvicultural practice in Northern Europe to improve the success of forest regeneration. We present three case-studies of the potential advantages of adding AP at planting on the establishment and damage susceptibility of seedlings in pure and mixed plantings of Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) H. Karst.) and silver birch (*Betula pendula* Roth) over two years in the field. Location of study sites were in southern (S), northeastern (NE) and northwestern (NW) Sweden. The main agents of damage were pine weevil (*Hylobius abietis* L.) on conifers at the south site, browsing of birch at all sites and browsing/other top damage to conifers at the north sites. The effect of adding AP varied between the sites. It was positive for survival of pine at site S, despite considerable damage by pine weevil. However, at the S site more of the surviving spruce and birch were browsed when treated with AP. At the NE site AP-treatment had positive effects on conifer growth. At the NW site adding AP positively affected survival and growth of all three species, and AP-treated seedlings of all species were less browsed than untreated seedlings. AP treatment presents a potential tool to improve the success of forest regeneration, especially when establishing pine stands in south Sweden.

Keywords *Betula pendula*; *Picea abies*; *Pinus sylvestris*; arginine; forest regeneration; seedling survival; seedling growth

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1 Introduction

In the Nordic countries, forest regeneration practice mainly involves planting of nursery grown Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) seedlings as single species stands. However, the two most common broadleaved tree species, downy birch *(Betula pubescens* Ehrh.) and silver birch (*B. pendula* Roth) are increasingly becoming more important commercially. The distribution between the two birch species varies in different regions of Sweden (Dahlgren Lidman 2022) and are generally not separated, but commonly referred to as “birch” in Swedish forest statistics (Skogsdata 2021). Birch is in general naturally regenerated in Sweden (Skogsdata 2021), but when planted it is commonly nursery grown silver birch since this birch species grow faster and have a higher timber quality than downy birch (Heräjärvi 2001; Rytter et al 2014).

The success of forest regeneration in the shortest possible time is important both to reach aimed production goals and to shift the harvested area from a carbon source to a carbon sink. Newly planted seedlings have limited access to water and nutrients before their roots extend into the soil of the planting site and thereby face challenges of drought and slow initial growth. They are also highly susceptible to damage by biological agents in this stage both due to their small size and because their chemical defense is limited until they have reached a balance between resource availability and needs. Damage from pine weevil (*Hylobius abietis* L.) is the most common biological agent of damage for newly planted tree seedlings in the Nordic countries. Pine weevils are attracted to newly harvested conifer forest where they reproduce and feed on the bark of twigs and seedlings of pine and spruce, while they are less attracted to broadleaved species (Day et al. 2004; Löf et al. 2004; Månsson and Schlyter 2004). The loss of bark hampers seedling growth, and if the damage becomes severe, the seedling will die (Örlander 1990; Thorsen et al. 2001). Once the small seedlings have outgrown the risk of severe damage by pine weevil, browsing by cervids is the next threshold to overcome. The most common browsing cervids in Sweden are roe deer (*Caprerolus capreoulus* L.) and moose (*Alces alces* L.) that both frequently damage young trees (Bergqvist 2017). The level of damage cause by each cervid species on each tree species depends on many factors, such as the local cervid population density, the local quantity and quality of the tree species as well as availability of other food sources and shelter (Gill 1992; Niemelä and Danell 1988; Bergqvist et al. 2014; Pfeffer et al. 2022). Moose is often in focus when browsing damage is studied (Wallgren et al. 2013; Bergqvist et al. 2014; Pfeffer et al. 2022) and the national browsing damage inventory ÄBIN stands for “älgbetesinventering” (= moose-browsing inventory). Due to the larger size, a moose can reach higher and consume more than a roe deer. Moose can also easier cope with greater snow depths is therefore the dominant species in the northern Sweden. The winter diet of moose is dominated by pine (Felton et al. 2020), which is the dominant conifer species in north Sweden. However, in south Sweden row deer populations are larger along with increasing populations of red deer (*Cervus elaphus* L.) and locally fallow deer (*Dama dama* L.), the two latter can also utilize various tree species in their diet (Roberge 2012; Bergqvist 2017). Broadleaved species are generally preferred by all browsing cervids, although pine is also frequently browsed during winter by both moose and roe deer (Bergqvist 2017). Silver birch is preferred over downy birch (Danell et al. 1985) and in the north part of Sweden the natural composition is dominated by downy birch (Dahlgren Lidman 2022), which make planted silver birch more attractive as forage than the natural regenerated birch in this area. Spruce is generally less browsed but can also suffer from such damages (Vehviläinen and Koricheva 2006).

One option to enhance early growth and survival of seedlings is to add a slow-release nitrogen source at planting (Brand 1991; Thiffault and Jobidon 2006). Forest growth is often limited by low nitrogen availability in boreal regions (Tamm 1991; Grossnickle 2000; Bhatti et al. 2006) where et al. 2011). Conifers synthesize the amino acid arginine as an internal nitrogen store (Nordin et al. 2001); this and other amino acids can be taken up by trees through their roots (Öhlund and Nasholm 2001; Gruffman et al. 2013). A commercially available nitrogen source – arGrow® Granulat (Arevo AB, Umeå, Sweden) has been developed in which arginine is crystallized with phosphate and formulated as slow-release granules. As arginine is a strong cation, it binds to soil particles (Inselsbacher et al. 2011) and is thus retained in the soil and prevented from leaching away (Hedwall et al. 2018). Pine and spruce seedlings grown on arginine in nurseries have shown greater development of fine roots as well as increased mycorrhizal colonization of these roots compared to seedlings grown on inorganic fertilizers (Gruffman et al. 2012). The early root growth is essential for successful establishment of a newly planted seedling (Burdett 1990; Grossnickle 2005); moreover, mycorrhiza further increase the ability of seedlings to take up water and nutrients (Bréda et al. 2006; Brunner et al. 2015). ArGrow®, i.e., arginine phosphate (AP), has in recent years been commercially used with the intention that the extra cost at planting will be financially returned in the form of increased early survival and improved growth so that more of the planted trees will be a part of the future stand. The planted material in Sweden is generally grown from a seed mix from open pollinated seed orchards, i.e., with at least one parent being one chosen to give improved performance compared to the average naturally generated trees. With the faster initial growth and the genetic benefit gained from higher survival of the planted seedlings as compared to the naturally regenerated trees that become incorporated and kept in the stand where planted seedlings perish, the rotation period is expected to shorten as well. So far, there are only few studies in field conditions to test the effect of AP on forest generation success, where it has been demonstrated that survival and early growth after planting and sowing of Scots pine seedlings in north Sweden can be enhanced by the addition of AP (Castro et al. 2021; Häggström et al. 2021; Domevščik et al. 2023). However, it is not known if the same effect might occur in this species in southern Sweden; nor if the regeneration of Norway spruce and silver birch might be equally enhanced. The aim of this study is to provide further knowledge for forest owners as to how the use of AP could be beneficial not only for Scots pine, but also for Norway spruce and silver birch.

In our present three-site case-study, we investigate the effect of AP treatment on early performance of Scots pine, Norway spruce and silver birch and the potential for an AP treatment to affect their susceptibility to their most common biological agents of damage, i.e., pine weevil on conifers, and ungulates browsing on birch. For this experiment we utilized a setting that was intended for long-term monitoring of different species compositions, where one site in the south and two sites in the north of Sweden were regenerated with Scots pine, Norway spruce and silver birch seedlings, with and without the addition of AP. This first study does not consider the effects of competition for resources in the different species compositions, since the trees are yet too small to reveal these competitive interactions of tree species mixing. However, the data from this study set a baseline for the future study by providing the original variability in performance due to differing site conditions. Nevertheless, we use this opportunity to quantify the levels of damage caused by pine-weevil in different species compositions in comparison with the previously known preference patterns of this common agent of damage. Our hypotheses were that: 1) Adding AP enhances the survival and growth of all three tree species similarly at all three sites; and 2) Adding AP increases the vitality of seedlings enabling them to withstand damage from their local pests, better than seedlings with no AP added.

2 Material and methods

2.1 Experimental sites and setup

The tree species included in the trial are Scots pine, Norway spruce and silver birch. Each of the three sites included in this study comprised 14 plots. Seedlings in seven of the plots were treated with a single dose of arginine-phosphate formulated as arGrow® Granulat (Arevo AB, Umeå, Sweden). Each dose contained 40 mg N and 22 mg P, the active substance being L-arginine phosphate ($C_6H_{17}N_4O_6P$). The species composition differed among each of the seven treated and untreated plots as follows: 1) only pine; 2) only spruce; 3) only birch; 4) pine + spruce; 5) pine + birch; 6) spruce + birch; and 7) pine + spruce + birch. Thus, each species occurred in four untreated and four AP-treated plots and formed our experimental replicates. In the mixed plots, the different species were planted alternately. All plots were 24 m × 24 m surrounded by a buffer zone of the same species as in the plot, making a total area of 35 m × 35 m.

All seedlings were grown in container systems in nurseries and freezer stored. All seedlings were handled according to common practice regarding transport and thawing of freezer stored seedlings, irrigation prior to planting was made when needed. All seedlings were vital at planting. For each site, all seedlings of the same species were of the same type and of the most appropriate commercially available proveniences (Table 1.) Planting was carefully made by experienced planters with Pottiputki planting pipes according to recommended practice, i.e., deep enough for the substrate to be covered by soil when compacted around by pushing firmly but carefully with one foot after planting. For the AP-treatment, a Pottiputki with an attached arGrow® dispenser (commercially designed for this purpose and used in practice) was used. One dose is dropped into the pipe when it is inserted in the ground and prior to putting the plant in the pipe, for the dose to end up directly below the seedlings' roots. The south site was planted 17th of June 2020, the northeast site 22nd of June 2020 and the northwest site 17th of June 2019 (Table 1).

The three sites represent commonly occurring soil conditions in Swedish forest landscapes: at the south site a mesic to dry stone-rich shallow sandy-silty podzol, at the NE site a mesic clay-rich silty podzolized deep glacial till with low stone abundance and at the NW site a dry to mesic silty-sandy podzolized deep glacial till with moderate-high stone abundance (Mantel et al. 2023; SLU 2023). As well as many other environmental differences between the sites (Table 1), there were also minor differences in site preparation methods, but all produced isolated planting spots. At all sites, harvest and site preparation occurred in the same year as trial establishment. At the south (S) site, the aim was to make inverted planting spots, but shallow soil and high stoniness compromised the outcome, leaving patches of disturbed soil rather than true inversion. At the northwest (NW) site the soil conditions allowed for true inverted spots. At the northeast (NE) site an alternative method was used, with a milling aggregate producing a depression with mixed soil material in small mounds on each side of the depression. The reason behind the choice of method on this site was in part related to the site conditions with a fine mesic soil and partly flat areas. In fine mesic soil with high clay content the risk of water logging is relatively high. Water logging is less likely on elevated spots, which are not produced at inversion; this method was not therefore considered appropriate at the NE site.

Each prepared spot was planted with one (S, NW) or two (NE) seedlings. Seedlings were marked up with sticks to aid the identification of those to be included in the trial. For the NE site, only one of the two seedlings planted at each prepared spot was chosen to be included in the trial first at the time of the first inventory. We planted two seedlings at each spot at this site because of the soil conditions. The fine mesic soil presents a high risk of frost heaving, which can cause newly planted seedlings' root substrate being pushed up from the ground. Hence, two seedlings at each spot

Table 1. Description of the conditions at the three study sites located in the south, northeastern and northwestern parts of Sweden respectively, including plot setup, number of seedlings planted and seedling material details for the three sites and for Scots pine, Norway spruce and silver birch respectively. Growing season, mean annual temperature and mean annual precipitation extrapolated for the Swedish Meteorological and Hydrological Institute (SMHI) maps showing normal length of vegetation period 1981–2010 (SMHI 2022a-d). All seedlings were containerized. *Theoretical numbers since the true number for each row sometimes deviated depending on availability of planting positions. **Approximate mean sizes common for the container system, not actual measurements of the seedlings.

Site		South (S) site	Northeast (NE) site	Northwest (NW) site
Coordinates		57.193157,14.821763	64.162174, 19.661918	64.102337, 18.149540
Elevation (m. a.s.l)		225–230	160–165	295–300
Trial establishment date		June 17th 2020	June 22nd 2020	June 17th 2019
Landowner		Sveaskog	Private	Sveaskog
Growing season (days)		190–200	150–160	140–150
Coldest month avg. T (°C)		–1 to –2 (January)	–7 to –8 (January	–9 to –10 (January)
Warmest month avg. T (°C)		+16 to +17 (July)	+15 to +16 (July)	+14 to +15 (July)
Mean annual T (°C)		6–7	2–3	1–2
Mean annual precipitation (mm)		600–800	600–800	400–600
Moist class		mesic to dry	mesic	dry–mesic
Harvested stand		spruce	spruce	pine
Landscape		Hummocky, but with relatively flat plot areas	From flat to moderate W slope	Ridges, from flat to gentle slope
Vegetation type		Grass + *Rubus idaeus* L.	*Vaccinium myrtillus* L.	*Vaccinium myrtillus* L. + *Vaccinium vitis-idaea* L.
Vegetation 2nd season		Very rich	Moderate	Sparse
Tot. size harvested area (ha)		21	5	20
Seedlings per plot*		9 × 9	9 × 9	12 × 12
Seedling spacing (m)		2.6 × 2.6	2.6 × 2.6	2 × 2
Seedling material				
Pine	Age (yr)	1	1	2
	Nursery	Lilla Istad, SSP	Skogforsk, Sävar	Skadom nursery
	Seed origin	Seed orchard	Seed orchard	Seed orchard
	Provenience	30-G7 Lilla Istad	FP-T8 Dal	FP 625 T8 Dal
	Container system	S50	Hiko VAB90	SP90
	Height (cm)**	13	13.2	25
	Stem base (mm)**	2.45	3.1	5
	Pine-weevil protection	yes, conniflex	no	no
Spruce	Age (yr)	1.5	1	2
	Nursery	Trekantens nursery, SSP	Skogforsk, Sävar	Skadom nursery
	Seed origin	Seed orchard	Seed orchard	Forest
	Provenience	FT-907 Ekebo	FP-130 Domsjöänget	Fullsborn 61*25
	Container system	Svepot 115	Hiko VAB90	SP90
	Height (cm)**	30.5	24.4	30
	Stem base (mm)**	4.6	3.1	6
	Pine-weevil protection	yes, conniflex	no	no
Birch	Age (yr)	1	1	1
	Nursery	Mellanå Plant AB	Skogforsk, Sävar	Skadom nursery
	Seed origin	Seed orchard	Seed orchard	Seed orchard
	Provenience	Ekebo 5 B	Lat 62–64° (Finland)	SV 413 Oitti (Finland)
	Container system	PLEK 36	Plantek 49F	SP120
	Height (cm)**	40–80	N.A.	40
	Stem base (mm)**	N.A.	N.A.	6

safe-guarded against a high mortality from frost heaving. Only spots where both seedlings had died became classified as 'dead'. At spots where only one seedling had died, the living one was chosen; where both seedlings survived, the healthiest looking one was chosen. At the S site the plots were randomly distributed and scattered over a large area, some being adjacent and some isolated. These plots were located on relatively flat parts of an otherwise hummocky harvested landscape. At the NE and NW sites, all the treated plots were placed adjacent to each other in one area, and all the untreated plots adjacent to each other next to the treated plots, i.e., within the same harvested area but not randomly positioned (maps of the three sites in Supplementary file S1, available at https://doi.org/10.14214/sf.22013). Thus, within-site differences in the landscape could interfere with the effect of AP. However, since there was variation in slope both within and between plots on both sites and in both treatments, we assumed most within-site variation to be equally represented in both treated and untreated plots. Lastly, another difference between sites was that at the two northern sites a second dose of AP was added at the base of each treated seedling in the following year, by manually dropping one dose of AP with an arGrow® dispenser at the base of each seedling.

Differences between sites in outcome for survival, seedling growth, and degree of damage for the different species is naturally expected due to both the environmental differences as well as differences in methods and trial setup between the sites. This makes it hard to disentangle causality behind differences in performance between sites. However, since analysis of causality behind site differences would be doubtful with only three sites anyway, it does not form a part of this study. Thus, in the present study these preliminary data are analyzed for each site as separate case studies.

2.2 Data collection

Survival and growth of the seedlings were recorded following the second growing season in the field for all sites, the south site early December 2021, the northeast site early September 2021 and the northwest site in the middle of October 2020. Seedling survival was defined as the number of seedlings that were not dead or missing. The missing seedlings were detected by matching the inventory against the number of seedlings in a survival inventory made following the first year in field. At the NW site, one row in block 6, two rows in block 10 and one row in block 12 were missed in the second season's inventory; these rows were therefore removed from analyses to avoid creating a bias towards lower survival. Vital seedlings were defined as those in vitality class 1 (no, or minor damage recorded). The cause of damage was registered when such was identifiable.

Seedling growth in all three species was quantified by seedling height and stem base diameter. Only measurements of seedlings defined as vital were used in the analyses. The analyses of growth data should therefore be seen as potential growth given that no damage affected the seedlings. Number of measured seedlings in each plot differed between 0 (2 plots) and 72 due to: 1) different numbers of seedlings planted because of the species mix used, and site because of different plant density; 2) difference in number of available vital seedlings to measure depending on both site and species; 3) differences in inventory protocols between sites – for the NW site, only every second available vital seedling was measured. For details of alive and vital seedlings per plot, see Suppl. file S2.

Seedling damage at the south site was identified visually according to a vitality class scale from 0–6 (0 = no visible damage, 1 = minor damage, i.e., visible damage that was not severe enough to cause any visual decrease in vitality of the seedling, 2 = medium damage, i.e., some appearance of decrease in vitality of the seedling, 3 = severe damage, i.e., the seedling has clearly visible decrease in vitality, 4 = lethal damage, i.e., the seedling do not appear to be able to survive, 5 = dead and 6 = missing or registered as dead already at the time of the previous inventory). Cause of damage was registered when this was possible to determine visually, including the categories fungi, frost, drought, oxygen deficiency, vegetative competition, browsing (i.e., when branches and/or leaves are clearly removed by a large herbivore, including bitemarks where a branch is removed and stripped branches), pine weevil (i.e., small but deep gnaw-marks on the stem characteristic for pine weevil), other insects or other/unknown. Damage recording at the north sites was less detailed. Seedlings were classified as undamaged when no visible damage occurred, damaged when the seedling displayed visible damage, or as dead. Damage type was registered, such as multiple stems, bent, dry top, broken top etc. Damage cause was registered when this was possible to determine, such as browsing, water logging and drought. For an overview of seedling status including dead, damaged and vital seedlings, see Suppl. file S3.

With only one plot of each species mix for each AP-treatment at each site, potential species mix effects on damage were not suitable for statistical analysis at site level. Regarding browsing, the lack of replicates increases the risk that any given plot might be one through which ungulates move more frequently due to the position in the landscape that might affect the ungulates roaming patterns (e.g., distance to forest, roads, water, good feeding areas etc.), regardless of the species mix. We did not therefore attempt to find out whether species composition had any effect on browsing. However, pine weevil can be assumed to be present in all plots due to their attraction to fresh stumps regardless of other site features. To get an indication of whether species composition had any effect on susceptibility to pine weevil damage, we therefore quantified the levels of damage in the different species mixes in relation to AP-treatment at the S site.

2.3 Statistical analyses

R-studio was used for all analyses (R Core Team 2021). Each site was analyzed separately. Generalized mixed effect models were constructed for survival and damage by specific agents respectively using the glmer function in the [lme4] package (Bates et al. 2015), with binomial distribution as the response variables, where 1 = alive, 0 = dead for the analyses of survival and 1 = damaged by specific agent, 0 = not damaged by specific agent for the analyses of damage. Linear mixed models were constructed for height and stem base diameter using the lmer function in the [lmerTest] package (Kuznetsova et al. 2017). Only measurements of seedlings classified as vital were used in the analyses. AP-treatment and species were set as fixed factors and species composition nested within species was set as a random factor. The random factor was set to account both for and the varying numbers of seedlings between the different species compositions, and other potential within-site variability.

Each model was tested for interactions between treatment and species with ANOVA type III using the [car] package (Fox and Weisberg 2018). In cases where there was no significant interaction, the interaction term was dropped from the model and the reduce model was tested again with ANOVA type II using the [car] package. The [emmeans] package (Lenth 2021) was used to produce estimated marginal means from the models and the [ggplot2] package (Wickham 2016) was used to present results graphically.

3 Results

3.1 The south site

At the S site, survival rates of spruce and birch seedlings following two vegetative growth periods were generally higher than that of pine (Fig. 1a). For the pine seedlings, AP-treatment increased the survival rate: 60% of the AP-treated pine seedlings had survived compared to 28% of the non-treated control seedlings (Fig. 1a, Table 2). According to the measurements of seedling height and

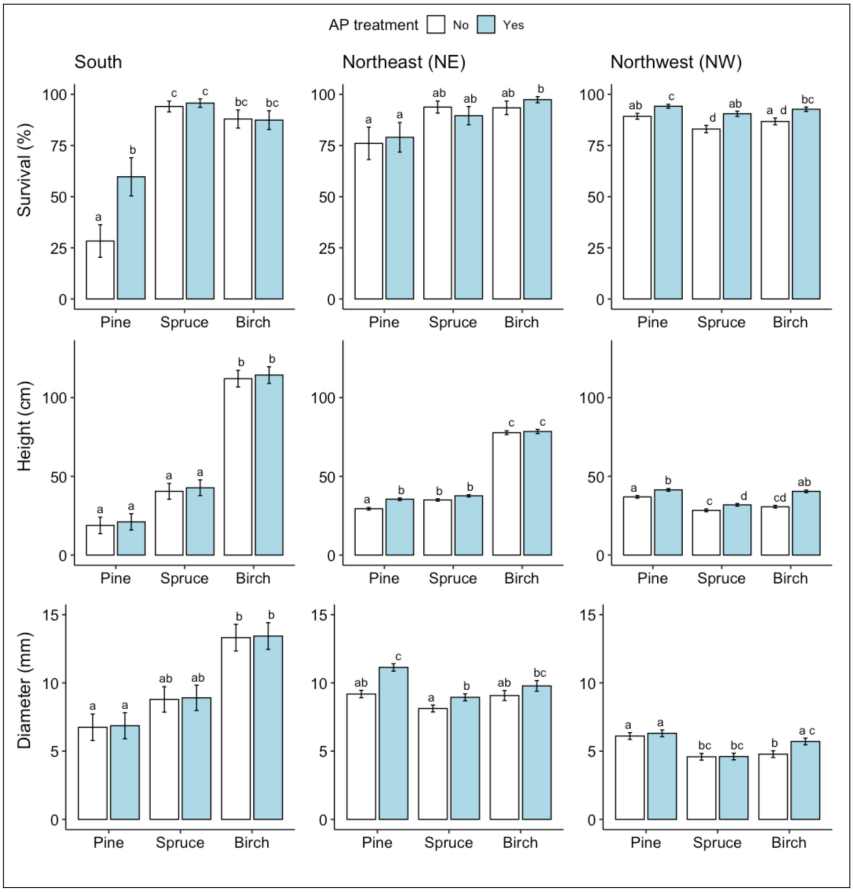

Fig. 1. Results from ANOVA analysis for A) survival, B) height, and C) stem base diameter means of Scots pine, Norway spruce and silver birch at each site respectively following the second field season. Columns indicate percentage survival and error bars indicate standard error (data backtransformed from log scale in survival models). Different letters indicate significant differences. For height and stem base diameter, only measurements of seedlings classified as vital are included.

stem base diameter used as proxies for seedling growth, AP-treatment had no effect on growth. Birch seedlings grew more than pine and spruce seedlings regardless of treatment (Fig. 1b-c, Table 2). The main damage suffered by seedlings that had survived two vegetative growth periods was from pine weevil, followed by ungulate browsing. Pine weevil damage was frequent on the conifer seedlings with more than 50% of both pine and spruce seedlings being damaged by them, while less than 25% of the birch seedlings showed any signs of pine weevil damage (Fig. 2, Table 3). For the pine seedlings, a significantly higher proportion of the AP-treated seedlings (79%) than the control seedlings (52%) were damaged (Fig. 2, Table 2). For the birch seedlings, a significantly lower proportion of the AP-treated seedlings (2%) than the control seedlings (12%) were damaged. On birch seedlings, browsing damage was very common with >70% of the seedlings having been browsed, while the proportion of browsed seedlings among both pine and spruce was always <25%

Table 2. ANOVA (Type II/III Wald chi-square tests) on generalized mixed linear models for probability of survival and linear mixed models for height and stem base diameter for each site following the second growing season in the field. Significant results are highlighted in bold.

	South (S)			Northeast (NE)			Northwest (NW)		
Survival	X^2	df	Pr(>X^2)	X^2	df	Pr(>X^2)	X^2	df	Pr(>X^2)
AP	8.26	1	**0.004**	0.99	1	0.319	19.19	1	**<0.001**
Species	34.57	2	**<0.001**	8.40	2	**0.015**	8.79	2	**0.012**
AP × Species	13.44	2	**0.001**	8.92	2	**0.012**	-	-	-
Height									
AP	2.55	1	0.1103	17.12	1	**<0.001**	137.51	1	**<0.001**
Species	177.43	2	**<0.001**	2089.17	2	**<0.001**	80.16	2	**<0.001**
AP × Species	-	-	-	8.57	2	**0.014**	30.34	2	**<0.001**
Diameter									
AP	0.20	1	0.65	44.94	1	**<0.001**	25.55	1	**<0.001**
Species	24.46	2	**<0.001**	23.81	2	**<0.001**	23.14	2	**<0.001**
AP × Species	-	-	-	13.80	2	**0.001**	27.17	2	**<0.001**

(Fig. 2, Table 3). For both birch and spruce the same pattern occurred as seen for the pine weevil damage on pine seedlings, with a higher portion of the AP-treated than the control seedlings damaged by browsing (90% vs 72% for birch and 22% vs 7% for spruce) (Fig. 2, Table 3).

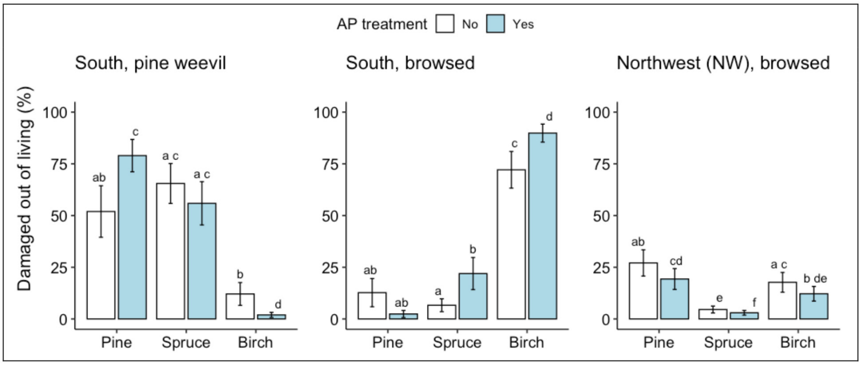

Fig. 2. Results from ANOVA analysis for damage to living seedlings of Scots pine, Norway spruce and silver birch by A) pine weevil and B) browsing at the south site, and C) browsing at the NW site following the second field season. Columns indicate percentage of living seedlings damaged and error bars indicate standard error (data backtransformed from log scale used in models.) Different letters indicate significant differences.

Table 3. ANOVA (Type II/III Wald chi-square tests) on generalized mixed linear models for probability of registered damage following the second growing season in the field; browsing and pine weevil for the south site and browsing for the northwest site. Significant results are highlighted in bold.

	South, pine weevil			South, browsing			Northwest, browsing		
Damage	X^2	df	Pr(>X^2)	X^2	df	Pr(>X^2)	X^2	df	Pr(>X^2)
AP	2.81	1	0.094	0.95	1	0.331	9.70	1	**0.002**
Species	32.29	2	**<0.001**	47.52	2	**<0.001**	17.84	2	**<0.001**
AP × Species	27.74	2	**<0.001**	17.22	2	**<0.001**	-	-	-

For pine, the AP-treatment effect on pine weevil damage levels was consistent for all different species mixes, <60% of the living seedlings were damaged by pine weevil in all untreated plots and >60% in all AP-treated plots. For spruce, we measured more pine weevil damage (>70% of living seedlings) when it was mixed with birch, than when alone or mixed with pine (<60% of living seedlings) independent of AP-treatment, while spruce damage in the three-species mix was intermediate. Pine weevils only damaged birch seedlings planted as single species stands (17% in the untreated plot and 7% in AP-treated plot) or when planted with pine in the untreated plot (43%).

3.2 The northeast site

At the NE site, survival rates following two vegetative periods were generally higher for birch than pine seedlings (>90% vs <80% for the two species, respectively) while survival of spruce seedlings was intermediate (Fig. 1a, Table 2). The difference in survival was, however, only significant between AP-treated birch vs pine, there being no significant positive effect of AP-treatment on survival for either species individually (Fig. 1a, Table 2). Concerning growth, birch grew more than twice as tall as the other species, regardless of treatment (Fig. 1b-c, Table 2). AP-treatment had a significant positive effect on stem base growth of pine and spruce, but not of birch (Fig. 1b-c, Table 2). On average, AP-treated pine was 21% taller and had a stem base diameter that was c. 22% wider than untreated pine, while AP-treated spruce had on average 13% larger stem base diameter than untreated spruce (Fig. 1b-c, Table 2). The main damage at the NE site to seedlings that had survived two vegetative periods was from browsing on birch, and forking, i.e., formation of multiple leader shoots for pine. AP-treatment had no significant effect on either form of damage on birch or pine (~70% of AP-treated and ~65% of untreated birch seedlings were browsed and ~13% of both AP-treated and untreated pine seedlings had multiple leader shoots).

3.3 The northwest site

At the NW site, survival rates of pine seedlings following two vegetative periods were significantly higher (c. 7%) than that of spruce, while survival of birch did not differ from the other species (within the same treatment) (Fig. 1a, Table 2). AP-treatment significantly increased the survival rate of all three species, as higher proportions of AP-treated seedlings had survived than untreated control seedlings (94% vs 89% for pine; 90% vs 83% for spruce; 93% vs 87% for birch) (Fig. 1a, Table 2). The growth of all three species was here more within the same range, as compared to the other sites where birch was growing higher than the other two species (Fig. 1b-c, Table 2). AP-treatment had a significant positive effect on seedling height for all three species (11% for pine, 14% for spruce and 32% for birch), but significantly affected stem base diameter (20%) only for birch (Fig. 1b-c, Table 2). The main damage found on the NW site seedlings was from browsing. The effect of AP-treatment on browsing was significant for all three species: a smaller proportion of the AP-treated seedlings was damaged by browsing than control seedlings (19% vs 27% for pine; 3% vs 5% for spruce; 12% vs 18% for birch) (Fig. 2, Table 3). The lighter browsing damage on spruce compared to pine and birch was significant within each of the two treatments (Fig. 2, Table 3).

4 Discussion

Survival, growth, susceptibility to damage as well as the effect of AP-treatment varied among the three tree species across the three sites, indicating that challenges to the establishment of planted seedlings of all three species depend on site-specific characteristics. The variations in survival and growth between species can be considered a consequence of how well adapted each species is to a particular site and their varying susceptibilities to different agents of damage. Particularly, high mortality in the south suggests the establishment of pine to be a greater challenge in southern than in northern Sweden. One of the reasons for why the establishment of pine is more difficult in this area is that pine weevil pressure is more severe in the south and closer to the coast due to the relatively higher accumulated temperature in these areas compared to northern inland areas of Sweden (Nordlander et al. 2017). In addition, the trees' chemical defenses against pine weevil are weaker in southern than in northern populations in Sweden (Yazdani et al. 1985; Yazdani and Nilsson 1986). Planting in positions where seedlings are surrounded by exposed mineral soil following site preparation, as done on all sites in this study, reduce pine weevil damage since the weevils tend to avoid open areas (Örlander and Nilsson 1999; Thorsen et al. 2001; Petersson and Örlander 2003; Petersson et al. 2005; Wallertz et al. 2005; Nordlander et al. 2011). A complementary protection by some sort of mechanical barrier is commonly used to further reduce the risk of pine weevil damage in pine weevil dense areas, as was done in this study for the conifers at the south site (Table 1). However, no single method can provide full protection in pine weevil dense areas, and it is important to consider any measures that may reduce pine weevil damage further, including enhanced establishment and early growth to overcome the greatest risks of lethal damage.

Our hypothesis of AP-treatment increasing survival and growth of all three species across all three sites was only partly corroborated. While AP-treatment had a positive effect on survival of all three species at the NW site, this was the case only with pine at the S site. At the NE site none of the three tree species showed any significant effect by AP-treatment on survival. It should be noted that the approach of planting two seedlings at each spot at the NE site and choosing the surviving/most vital seedling to be included in the trial created a bias towards higher survival that may have compromised the results for survival at the this site, perhaps making any difference between AP-treated and untreated seedlings less pronounced than they may have been if there was only one seedling planted per spot.

Among the undamaged trees, birch outgrew pine and spruce on both the S and NE sites. This can pose a challenge when the trees grow big enough to interfere with each other's growth space if the purpose is to establish a mixed tree species stand. At the NE-site, the AP-treatment however increased the growth rate of the conifers, but not to the extent that they grew as tall as birch. At the NW site, growth was more equal between species and the AP-treated seedlings of all three species showed both higher survival and growth than the untreated seedlings. This observed pattern of birch being less height dominant with a shorter growing season (the NW site has shorter growing season than the NE site despite similar latitude due to its inland location, see Table 1) could be a natural consequence of birch having a longer duration of height growth as well as responding more strongly to increased temperature than either pine or spruce (Nissinen et al. 2020; Pikkarainen et al. 2022). By contrast, the benefit of AP-treatment for birch was highest at the NW site where there was a positive effect on both survival and growth. Unexpectedly, the height pattern of pine was reversed, it being lower at southern than northern sites. We suspect that the unexpectedly low growth of pine in the S site in comparison to the northern sites might be due to pine weevil damage, which not only affect survival negatively but also hampers growth (Örlander and Nilsson 1999). The positive effects of AP-treatment on pine survival and growth are in line with earlier findings, except for the lack of a positive effect on growth at the S site. Previous research found an increasing positive effect on growth induced by AP-treatment with a longer growing season (Häggström et al. 2021). However, in contrast to the present study, Häggström et al. (2021) did not include the most southern part of Sweden where pests and vegetation competition have a greater effect, possibly overshadowing any positive effect on growth the AP-treatment might have had.

Our hypothesis regarding increased vitality to withstand damage for seedlings treated with AP was also only in part corroborated. Pine survival at the S site was improved by the AP-treatment, despite that the attack rate from pine weevils was significantly higher on the treated than the untreated seedlings. Cause of mortality was generally unknown, but a high proportion of the remaining living seedlings were damaged by pine weevil, so it seems likely that they were responsible for the high mortality rate at the S site. Assuming that pine weevils was equally present in all plots due to their attraction to fresh tree stumps regardless of other site features, the pine weevil damage pressure was likely equal for untreated and AP-treated seedlings. Thus, we interpret the results such as that the pine weevil damage caused a lethal outcome for a larger proportion of the untreated pine seedlings, while leaving a larger number of AP-treated seedlings that remained alive with pine weevil damage. The mechanism behind the enhanced survival of pine seedlings treated with AP may be related to these seedlings being more vital and thereby more resistant to pine weevil damage than untreated seedlings. This finding could potentially have been related to a better growth rate of AP-treated seedlings, since seedlings with a wider stem base are less likely to be girdled by pine weevils (Örlander and Nilsson 1999; Wallertz et al. 2005). However, at the S site neither AP-treated nor untreated seedlings had reached a stem base diameter threshold (10–12 mm) that confers decrease in lethal outcome of pine-weevil damage (Thorsen et al. 2001; Wallertz et al. 2005). Furthermore, the difference in growth between AP-treated and untreated seedlings was not significant, so this mechanical defense is not likely to be the explanation in this case. Another explanation could potentially be that AP-treated seedlings were better able to withstand pine weevil damage due to better water and nutritional status. Though this was not expressed in better aboveground growth, these resources are needed for defense mechanisms as well.

Insects that chew on bark will have to deal with a tree's chemical defenses such as toxic phenols, and terpenoids in resin that act both to kill intruding insects and heal wounds (Trapp and Croteau 2001; Bonello et al. 2006). The terpenoid α-pinene attracts pine weevil to newly cut trees; another, limonene, acts to inhibit the attractiveness of α-pinene (Nordlander 1990; Danielsson et al. 2008). Water stress decreases the ability of trees to produce both resin and limonene, while it increases α-pinene production (Selander and Immonen 1992). This further emphasises the importance of early root growth allowing good water uptake by seedlings. It could be a contributory factor explaining why the AP-treated seedlings exhibited better survival and a greater proportion of vital seedlings, despite their suffering a high level of pine weevil attack. However, the relation between chemical defense and seedling vigor is not always straight-forward. While some studies suggest that limited nitrogen availability negatively affects plant defenses (Bonello et al. 2006), others have found that defense substances decrease in N-fertilized trees (Witzell and Martín 2008). In our case, AP may have improved seedlings root area and ectomycorrhizal colonization to acquire more resources enabling the seedlings to withstand the damage by pine weevil better than the untreated ones.

Yet another potential explanation as to why a larger share of the surviving AP-treated pine seedlings were attacked by weevil, yet experienced lower mortality than untreated seedlings, might be related to plant phenols, which are derived from the amino acid phenylalanine (Bennett and Wallsgrove 1994). The presence of these antifeedant defense substances do not hinder weevils from initially chewing bark, but they will chew less which should lead to decreased risk of lethal damage (Fedderwitz et al. 2016). In a small nursery pilot project, it was found that pine seedlings grown on AP had higher levels of phenylalanine in their bark compared with those grown on ammonium nitrate (Näsholm T. 2022, unpublished data, Suppl. file S4). This finding suggests that AP-treated seedlings should have better potential to produce feeding deterrents. This requires confirmation through further research, but it could be an important tool to improve seedling survival in areas with high pine weevil feeding pressure.

Since there was only one plot of each species mix for each AP-treatment at each site, species mix effects were not suitable for statistical analysis at site level due to the risk of potential interference from other within-site variables. The three sites will be able to be used as replicates in future analyses of species mix effects under inter- and intra-specific competition. However, in the case of damage, this approach would be hard to justify since seedlings' susceptibilities will vary both according to the agent of damage and environmental differences between sites. Nevertheless, we quantified and compared the levels of pine weevil damage in different species compositions to get an indication of whether species composition had any effect on susceptibility to pine weevil damage. The pattern of pine weevil feeding on spruce and birch seemed to be affected by species composition of the stands and related to their feeding preferences. Spruce was more frequently attacked when growing with birch than in pure plantings, a pattern that agrees with pine weevil preferring conifers over broad leaved trees (Day et al. 2004; Löf et al. 2004; Månsson and Schlyter 2004). Spruce was also less frequently attacked when planted with pine, as expected since pine weevils prefer pine when both conifers are present (Day et al. 2004; Wallertz et al. 2005). Birch was only attacked when no, or only very few pine seedlings were available, as in the untreated pine-birch plot where only four living pine seedlings remained, i.e., there was not much else for the pine weevils to feed on other than birch in this plot. Our interpretation of this pattern is that the substantially higher attack rate in the untreated pine-birch plot (43%) compared with the pure birch plots (17% in the untreated and 7% in the treated) might be due to more pine weevil initially being attracted to the plot where pine seedlings were present. As their preferred food source, the pine in the pine-birch plots suffered higher pine weevil pressure per seedling than occurred in the other mixtures. When most of the pine seedlings eventually died in the untreated plot, the remaining pine weevils transferred to the birch seedlings as their food source.

The effect of AP-treatment on browsing was contradictory. At the S site, a large proportion of the birch was browsed upon, and for both birch and spruce more so in AP-treated than in control plots. This would be expected, since fertilization may increase N-content in the seedlings, giving them a higher nutritional value and thus attract browsing herbivores (Månsson et al. 2009; Burney and Jacobs 2011). By contrast, at the NW site the AP-treated trees of all three species were less browsed upon than the untreated seedlings. The opposing results could be due to many reasons. For example, fertilization increases not only nitrogen content but also the levels of chemical defense substances in the trees, which may alter feeding preferences for ungulates (Burney and Jacobs 2011). The different proveniences representing the different sites may have responded in different ways to the fertilization. However, the simplest explanation could be that the positioning of the untreated plots may have happened to be where moose move through more frequently. For example, at the NW site, all AP-treated plots were in the part of the clear-cut which was closer to a road than the untreated plots, and which might therefore affect their browsing behavior if the moose avoid being close to the road. However, any true effect of less browsing by moose on AP-treated seedlings, could be an important tool when regenerating pine. Further research on this topic is required to clarify the issue.

The most common damage registered on pine at the NE site was forking, i.e., multiple leader shoots. Multiple leader shoot can be an effect of previous browsing. However, browsing alone does not account for all occurrences of multiple stems. Another potential pre-cause of multiple leader shoots can be the occurrence of summer shoots (i.e., new shoots already developing during the summer on current year´s buds, instead of the regular two-year process). Summer shoots, termed 'proleptic shoots' that grow from the lateral buds at the base of the current year's terminal bud, can result in a temporary inhibition of apical dominance, which in turn sometimes leads to multiple leader shoots, i.e., forking (Aldén 1971). In southern Sweden the occurrence of summer shoots and multiple stems has increased in recent years, both in planted and naturally regenerated pine seedlings, but the cause is not yet fully understood (Högberg et al. 2021). However, Aldén (1971) found a positive correlation with growth-promoting variables such as increased CO_2, optimal moisture level, as well as nutrient conditions changing from poor to optimal, indicating that increased occurrence of multiple leader shoots might be related to changes in environmental conditions. More recent research also indicates that insufficient chilling time during dormancy of many tree species in temperate and boreal areas can delay budburst, which can lead to growth abnormalities including terminal shoots being shorter than laterals in conifers (Laube et al. 2014; Harrington and Gould 2015; Man et al. 2017). Anyhow, there was no effect of AP-treatment on the number of multiple leader shoots at the NE site, which neither confirms nor contradicts any potential theory regarding the occurrence of this phenomenon.

Our study has demonstrated the effects of AP-treatment to be complex and site specific, i.e., the same results cannot be expected at all sites. Nevertheless, the positive effect on pine seedling survival following AP-treatment appears promising and may improve pine regeneration, especially in the southern part of Sweden. The positive effect on the growth of conifers at the northern sites might present a tool to decrease the time of small seedlings being at risk for damage by insects and herbivores. However, further experimental work is needed to confirm whether the same positive effect of AP-treatment on pine seedling survival in south Sweden and growth in north Sweden might also be observed beyond these specific sites. Further, only one seedling type for each species was used as each site in this study which may have affected the results, since AP-treatment response might potentially differ between seed sources due to genetic variation in nitrogen use efficiency (Li et al. 1991). We therefore recommend future studies to include several different sources of seedling material at each site to evaluate the potential genetic dependent response. Whether the positive effects of AP-treatment are due to the repeated addition of arginine phosphate (as done at the northern sites), or if a single addition (as done at the southern site) would have been sufficient to reach the same result we cannot tell from this study. However, studying the long-term effects on these and other sites, where AP-treatments were only applied at planting, will allow further comparisons to be made. If the effect of a single treatment seems to fade after some time, while repeated treatments continue to give an increased effect, we could assume that repeated additions of AP would be the better option. To be able to compare these effects more exactly, we suggest a trial in which control, single, and repeated additions of AP are tested at the same sites.

5 Conclusion

The effects of AP-treatment on survival, growth and levels of damage varied between the three sites. At the S site, AP-treatment increased survival of pine. A higher share of the surviving seedlings was attacked by pine weevil when AP-treated than untreated, indicating that the increased survival of AP-treated seedlings could be related to increased tolerance against pine weevil damage. More AP-treated than untreated birch and spruce were also browsed at the S site, while there was no AP-treatment effect on growth for any of the three species. On the NE site, there was no effect on survival or level of damage, but a positive effect on stem base growth for pine and spruce. At the NW site, AP-treatment had a positive effect on survival and growth for all three species which were also less browsed when AP-treated than untreated. Birch grew taller than the conifers at the S and NE site, while pine and birch grew more equally at the NW site. The use of AP-treatment appears overall to be more useful regarding effects on growth and survival on the NW site. However, the effects on the level of damage from pine weevil vs survival for pine at the S site indicates that AP-treatment might make pine less vulnerable to lethal pine-weevil damage, which is a topic for further research. In practical forestry, AP-treatment could be a potential tool to increase survival of planted pine in the southern parts of Sweden and to increase early growth after planting of conifers in the northern parts of Sweden to increase the chance of successful establishment of a newly regenerated forest stand.

Supplementary files

S1.pdf,
S2.pdf,
S3.pdf,
S4.pdf,
available at https://doi.org/10.14214/sf.22013.

Declaration of openness of research materials, data, and code

Data files and code for statistics and figures in main manuscript is publicly available at the Swedish National Data Service: Häggström B. (2022). Effect of arginine-phosphate addition on early survival and growth of Scots pine, Norway spruce and silver birch. Swedish National Data Service. Version 1. Swedish University of Agricultural Sciences. https://doi.org/10.5878/p1vn-df79.

Authors' contributions

TL, RL and FS contributed to the conception of the research question and design of the work, BH contributed with acquisition, analysis, and interpretation of data and results as well as scientific writing of the work, AN contributed with scientific writing and AN, RL, TL and FS contributed with revising it critically for sound and intellectual content.

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IV

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ORIGINAL PAPER

Environmental controls on seedling establishment in a boreal forest: implications for Scots pine regeneration in continuous cover forestry

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Abstract

In nutrient poor and dry forest sites common to northern Scandinavia, Scots pine (*Pinus sylvestris* L.) is the most common species both in managed and natural forests. However, Scots pine is sensitive to competition during establishment. Harvesting of all trees within a given area, i.e., clear-cutting, liberates regenerating seedlings from competition with mature trees. However, recently, clear-cut-free or continuous cover forestry has been the subject of substantial debate. When choosing a management method, it is important to recognize how competitive interactions direct the success of Scots pine regeneration. We studied Scots pine regeneration at three environments: beneath the canopy of mature trees, at the canopy edge in full sunlight, and distant from the canopy with no influence of mature trees. We imposed three treatments in each of these environments: root isolation (i.e., trenching), nitrogen (N) fertilization, and control plots. Root isolation enhanced seedling performance under the canopy of mature trees. Nitrogen fertilization enhanced seedling performance to a greater extent in the clear-cut than at the forest edge. However, N fertilization had no effect under the canopy. In the N-fertilized plots, we measured higher N content in the soil under the canopy than in the open environments, indicating that not all excess N was obtained by the mature trees. N-uptake might have been limited by competition for water in the N-fertilized plots. Our results suggest that belowground competition limits the success of regeneration of Scots pine. However, N fertilization presents a tool to compensate for underground competition along canopy edges.

Keywords Continuous cover forestry · Scots pine · Tree regeneration · Belowground competition · Clear-cutting · Forest growth

Introduction

Forest regeneration is at the core of sustainable forest management as the mature trees are harvested and new seedlings establish. A better understanding of the environmental controls on regeneration is needed to predict how it can be successful under the future climate or under new forest policies. In Scandinavian boreal forests, the main tree species used in forestry are the native conifers Scots pine (*Pinus sylvestris* L.) and Norway spruce [*Picea abies* (L.) H. Karst]. Norway spruce is shade tolerant and can reach full growth potential in canopy openings ~ 0.1 ha, while Scots pine is a shade-intolerant competition sensitive pioneer species that has been suggested to require canopy openings larger than 0.4 ha to achieve maximum growth (Malcolm et al. 2001). Shade-intolerant species in general grow better than shade-tolerant species in high-light conditions, while suffering from higher mortality in low-light conditions (Kobe et al. 1995).

Aboveground growth of both Scots pine and Norway spruce has been found to increase with increasing solar radiation, and the highest growth rates have been found north of gap centers (Gray and Spies 1996; Erefur et al. 2011). However, Scots pine has a more flexible morphology that allows it to allocate growth to increased needle length under high-light conditions, which give it a higher capacity to utilize incoming sunlight (de Chantal et al. 2003). Yet, through the history of forestry in Sweden, it has repeatedly been observed that pine regeneration is suppressed within

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5–10 m from single retained mature trees and along clear-cut edges, despite having access to full sunlight (Aaltonen 1919; Björkman 1945; Hagner 1962; Valkonen et al. 2002; Elfving and Jakobsson 2006; Kuuluvainen and Yllasjarvi 2011). Contrary to suggestions that adult trees promote seedling growth via common mycorrhizal networks, i.e., the "mother-tree" or the "wood-wide-web" (Simard et al. 1997), these patterns suggest that belowground competition serves as an important control on seedling growth in this area since the zone of suppressed seedling growth is similar in size to the zone of mature tree root system activity (Göttlicher et al. 2008; Henriksson et al. 2021).

Soil conditions affect the importance of below versus aboveground competition; belowground resources are naturally more limiting on poor and dry soils than on nutrient-rich, moist soils (Coomes and Grubb 2000). Since Scots pine is relatively drought-hardy, and it is the dominant species on dry sites in northern boreal Fennoscandia where few other tree species thrive, dry and poor soil conditions are common site conditions for Scots pine. Here, light would be expected to be of lower relative importance than soil resources, and in this region, nitrogen (N) availability is generally limiting for forest growth (Tamm 1991; Grossnickle 2000; Bhatti et al. 2006). Also, N is available to plants mainly in organic form (amino acids) in boreal forest soil, but inorganic sources (ammonia and nitrate) are also utilized (Inselsbacher and Näsholm 2012; Högberg et al. 2017). Soil microorganisms further limit the N availability for plants by retaining most of the nitrogen available from decomposing organic material and carbon substrates exudated by tree roots (Nazir et al. 2009; Näsholm et al. 2013; Högberg et al. 2017). When trees die or are harvested, the supply of carbon to the microorganisms decrease, limiting their demand for N. Consequently, N is released which can be utilized by the next generation of trees (Högberg et al. 2017). The simultaneous harvesting of all trees within a given area also liberates regenerating seedlings from competition with mature trees, enabling high initial growth rates (Petritan et al. 2011). This facilitation of regeneration by clear-cutting has been one of the main arguments for proponents of the method (Lundmark 2020).

Rotational forest management (RFM), which includes clear-cutting of mature trees, is currently the most common modern forestry practice in Scandinavia and other boreal forest regions (Lundmark et al. 2013). It enables economically sustainable forest management by ensuring a continuous interannual supply of wood through rotation between different even-aged plots (D'Amato et al. 2020). However, clear-cutting has been the subject of intense debates within the past decades for its potential negative impacts on ecological aspects including biodiversity, habitat quality, and soils as well as aesthetics and climate (Simonsson et al. 2015; Lundmark 2020; Larsen et al. 2022). An alternative to RFM is continuous cover forestry (CCF), i.e., uneven-aged management, where forest cover is maintained throughout the sylvicultural cycle by performing selective cuttings at regular intervals within uneven-aged plots (Pommerening and Murphy 2004; Schütz et al. 2012; Ahlstrom and Lundqvist 2015; Mason et al. 2022). However, CCF requires seedlings to establish and grow within gaps of limited size, where seedlings are influenced by interaction with mature trees to a higher degree than in RFM (McCarthy 2001). The proportion of edge environments where seedlings are under competition from the adjacent mature trees increases as the gap size decreases, eventually leading to a decrease in volume growth of the trees (Walters et al. 2006; Ruuska et al. 2008). Understanding the competitive interactions between seedlings and mature trees is important in assessing how seedling recruitment and growth is affected by different forestry management practices.

Though many observational studies have shown that Scots pine regeneration can suffer from competition of mature trees, experimental data isolating the specific mechanisms for these interactions are scarce (Högberg and Högberg 2022). The aim of our study was to clarify the environmental factors that control survival and growth of Scots pine seedlings in relation to mature trees, which is highly relevant in the context of CCF. We compared seedling establishment and growth of sown and planted Scots pine seedlings in three adjacent environments: within a pine forest, near a clear-cut edge, and on a clear-cut. In each of these environments, we also applied three paired treatments: control, N fertilization to increase the availability of N, and root isolation plots to physically reduce belowground competition between seedlings and mature trees. We tested the following hypotheses: (1) in untreated control plots, seedling survival and growth would be highest in the clear-cut due to the combination of high-light availability and absence of belowground competition with mature trees, (2) root isolation would enhance survival and growth of seedlings, with the greatest effect at the forest edge, where the reduced belowground competition would positively interact with the high-light availability, and (3) N fertilization would enhance seedling survival and growth, with this effect expected to be greatest at the in the clear-cut due to the combination of high-light availability and absence of belowground competition with mature trees. Testing these hypotheses in combination will provide valuable insight into the mechanisms that control pine regeneration, which are highly relevant in a context of adapting management approaches toward new regulations, e.g., clear-cut free forestry (EC 2021).

Material and methods

Study site conditions and experimental treatments

The study site is located near Åheden (64°13′ N, 19°48′ E) within the Svartberget research forest in Västerbotten

Table 1 Weather data from the years of the experiment, 2013–2020, including annual and early summer precipitation sum and mean temperature

	Precipitation sum (mm)		Mean temperature (°C)	
Year	Annual	June–July	Annual	June–July
2013	593	185	3,5	14
2014	622	103	4,1	15
2015	650	147	4	12
2016	626	170	3,1	14
2017	746	124	2,8	13
2018	478	85	3,4	16
2019	588	67	2,8	14
2020	771	193	4,7	15
Average	634,25	134,25	3,55	14,125

Years with less precipitation and higher mean temperature than average during the early summer for the period are marked with increasing color intensity the lower the precipitation sum and higher mean temperature

county, northern Sweden. The site is located approximately 60 km from the coast on an alluvial sand-silt plain. Forests in Västerbotten county are dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) either in single species (46.1% and 23.7% of productive forest area, respectively) or mixed stands (12.9%) (Petersson 2021).

The normal mean annual precipitation in the area is between 600 and 800 mm, the mean annual temperature is between + 2 and + 3 °C, and the length of growing season 150–160 days (SMHI 2023). Snow cover typically lasts from early November to early may (Axelsson et al. 2014). Climate data during the experiment are presented in Table 1.

The soil at the study site is a weakly podzolized sediment of sandy silt, classified as a Cambic Podzol (FAO 1988). The organic mor layer has a depth of *ca.* 2 cm (Högberg and Högberg 2002). The understory is dominated by ericaceous shrubs; lingonberry (*Vaccinium vitis-idea* L.) and bilberry (*Vaccinium myrtillus* L.), as well as a dense moss layer [mostly *Dicranum* spp. Hedw. with some *Pleurozium schreberi* (Brid.) Mitt] (Forsmark et al. 2020). In the clear-cut area, lingonberry also dominates the community but with a much lower cover. Reindeer lichen [*Cladonia rangiferina* (L.) F. H. Wigg.] and common heather [*Calluna vulgaris* (L.) Hull] constitute most of the remaining vegetation cover in the clear-cut.

We set up an experiment at the site utilizing three alternative environments in relation to an intact mature forest (Fig. 1). First, we stablished plots directly beneath the intact canopy, where trees could influence both light and soil resource availability (hereafter "Forest"). Second, plots were established at the edge of the clear-cut (i.e., the south facing edge of the adjacent forest) where belowground competition with mature trees was present, but light competition was absent (hereafter "Edge"). The third environment was in the open clear-cut, where neither below nor above ground competition with the adjacent mature forest was present (hereafter "Clear-cut"). The clear-cut utilized for the study was done in early June 2013, forming a gap in the forest of approximately 100 m by 50 m. The clear-cut area had its long side adjacent to a road, which increased the total open area so that shadow from the trees on the south side would not affect the light availability on the clear-cut. No stump removal or other silvicultural soil preparation methods were used prior to setting up the experiment. Within each of these three environments, fifteen experimental plots (1.5 m × 1.5 m, 2.25 m^2) were laid out in late June 2013 parallel to the forest edge. The plots inside the forest and out on the clear-cut were placed 15 m from the edge boundary, respectively, whereas the edge plots were placed 2 m into the clear-cut.

Within each of the three environments, fifteen experimental plots were arranged into five blocks where each of three nutrient competition treatments was represented: a control, root isolation, and N fertilization (Fig. 1). The control treatment plots were left untreated, whereas the root isolation treatment involved inserting a 1.5 m × 1.5 m steel frame 75-cm deep to physically prevent competition with mature tree roots, while maintaining water infiltration capacity. The N addition treatment aimed at evaluating whether fertilization with N would result in a similar seedling response pattern to a physical release from root competition. Nitrogen fertilizer was applied at a rate of 75 kg N ha^{-1} yr^{-1}, which was applied in June annually in liquid form. This was accomplished by diluting 16.8 g of NH_4NO_3 in 10 l of tap water and applying evenly on designated experimental plots (2.25 m^2). The unfertilized experimental plots (control and root isolation) were simultaneously watered with 10 l of H_2O without any fertilizer. These three treatments were randomly placed within each of the fifteen blocks (Fig. 1).

Each experimental plot was separated into two 1.5 m × 0.75 m subplots. One was used to plant eight pine seedlings. The other was further divided into two 0.75 m × 0.75 m subplots. One was sown with 120 Scots pine seeds following manual soil preparation (organic layer removed and small depressions created in the soil), and the other left as is as a "spontaneous control" for measuring natural seedling regeneration. Planting and sowing were performed June 19–20, 2013. The planted pine seedlings were attacked in 2014 by large pine weevils (*Hylobius abietis* L.) leading to the death of 72% of planted seedlings (92% in the clear-cut, 80% at the forest edge, and 46% in the forest). This is consistent with what is frequently observed for seedlings planted after a clear-cut without any soil preparation,

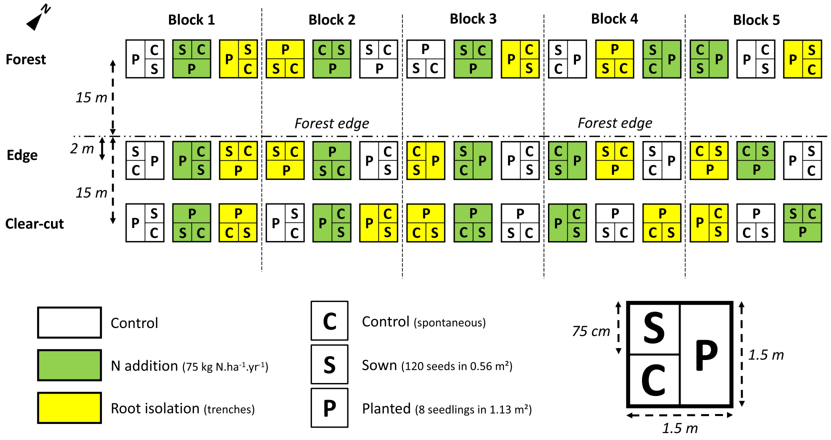

Fig. 1 Schematic representation of the experimental design at the study site. The design incorporates three growing environments: “Forest” is located 15 m into the mature pine forest from the forest edge, “Edge” is located 2 m out from the forest edge, and “Clear-cut” is located 15 m from the forest edge out on the harvested area. For each growing environment, there are five replicates (blocks 1–5). For each replicate, there are three randomly distributed treatment plots: control (white), nitrogen (N) addition (green), and root isolation (yellow). Each treatment plot is split in one half where eight nursery grown seedlings were planted (P), and two quarters with sown seeds (S) and spontaneously regenerated seedlings (C) were measured, respectively

which provides ideal conditions (i.e., stumps, exposed roots, bark, slash, etc.) for the larval and pupal stage of the weevil (Örlander et al. 1997). The remaining seedlings that were planted in 2013 were, therefore, harvested in 2014 and replaced by new seedlings. The data on planted seedlings presented here are, therefore, from the second cohort of seedlings planted in May 2014. The planted seedlings were obtained from Gideå nursery and had an original mean height of 8.5 cm, a mean diameter of 2.3 mm, and a dry weight root:shoot ratio of 0.33.

PRS™ probes

We estimated soil nitrogen in the form of nitrate (NO_3^-) and ammonium (NH_4^+) availability using Plant Root SimulatorTM (PRSTM) probes (Western Ag Enterprises, Inc., Saskatoon, Canada). PRSTM probes consist of ion-exchange resin membranes (IEM) fitted on a plastic frame and are inserted vertically into the soil to sorb ions. Each measurement included two pairs of probes (four probes in total) with either an anion IEM (adsorbs NO_3^-) or cation IEM (adsorbs NH_4^+).

The nitrogen supply rate was measured in the planted subplots only. The probes were inserted into the soil on July 6, 2020, and removed after 6 weeks on August 17, 2020. A first cleaning of the probes was done on site using a light brush removing most of the attached soil. The probes were then taken to the laboratory and thoroughly cleaned using distilled water. The four probes per sample were packaged together in individual resealable plastic bags and sent to Western Ag for processing (elution of the adsorbed ions using HCl) and analysis. Results from both probes of each type were pooled prior to measurements by Western Ag. Inorganic N concentration (NH_4^+–N and NO_3^-–N) was measured colorimetrically using an automated flow injection analysis system (Skalar San + + Analyzer, Skalar Inc., NL), while the remaining elements were measured by inductively coupled plasma optical emission spectrometry (ICP-OES). Data are reported as the total quantity of each element adsorbed in µg per 10 cm^2 of ion-exchange membrane surface area per incubation period.

Seedling inventories

We counted the number of surviving pine seedlings in each treatment plot the first 4 years in the field (2013–2016 for sown and 2014–2017 for planted seedlings) to follow the early development. A follow-up inventory was done in June 2020, when we in addition measured the individual height of each surviving seedling as well as stem base diameter for the planted seedlings. The 2020 inventory data were analyzed in this paper. For the sown seedlings, we did not measure the stem base diameter because high seedling density made this intractable. Naturally regenerated seedlings were absent in most of the spontaneous control plots that were neither sown nor planted, we, therefore, excluded these spontaneous control plots from our analysis.

Statistical analysis

RStudio was used for all analyses (R Core Team 2021). Seedling survival and nitrogen availability were analyzed using linear models, with the lm function in [stats] package (R Core Team 2021). The number of living seedlings per plot was used as response variable for survival analyses of planted and sown seedlings, respectively. Linear mixed models were made for height with plot nested within forest type as random factor to account for within-site variability, using the lmer function in the [lmerTest] package (Kuznetsova et al. 2017). Environment and treatment were used as fixed factors in all models. The natural logarithm of the response variable was used in all models except for planted seedling survival to fulfill the assumptions of homoscedasticity and normal distribution of residuals for the models. For sown seedlings, some subplots had 0 survival; therefore, 1 was added to each plot prior to analysis to be able to use the natural logarithm transformation.

Each model was then tested for the main effects of and interaction between forest type and treatment with ANOVA type III using the [car] package (Fox and Weisberg 2018). The [emmeans] package (Lenth 2021) was used to produce estimated marginal means from the models, and the [ggplot2] package (Wickham 2016) was used to present results graphicly.

Results

Seedling survival

For survival, there was significant interaction between environment and treatment for both sown and planted seedlings (Table 2). In the control plots, survival of sown seedlings was significantly higher in the clear-cut and forest edge than in the forest (Fig. 2A). The only significant effect of any treatment on sown seedling survival was inside the forest (Fig. 2A), where root isolation resulted in approximately 10 times higher sown seedling survival compared to the control plots (Fig. 2A). For the planted seedlings, there was no significant difference in survival between either control plots in the different environments or the three treatments within each environment (Fig. 2B). The only noticeable effect was that survival was significantly lower in the fertilized forest plots than on the fertilized clear-cut as well as fertilized and root isolated forest edge plots (Fig. 2B).

Table 2 Results from ANOVA on linear models for survival of sown and planted seedlings, respectively, with environment and treatment as fixed factors, including interaction. Significant results are defined by bold text in the table

Survival	Sown seedlings				Planted seedlings			
	Sum Sq.	Df	*F* value	Pr (> F)	Sum Sq.	Df	*F* value	Pr (> F)
Environment	1.15	2	9.93	**< 0.001**	4.69	2	4.92	**0.013**
Treatment	0.14	2	1.19	0.316	6.81	2	7.14	**0.002**
Environment × treatment	0.64	4	2.75	**0.043**	9.37	4	4.90	**0.003**
Residuals	2.08	36			17.19	36		

Seedling growth

For growth, there was significant interaction between environment and treatment (Table 3). In the control plots, height growth of sown seedlings was not significantly different between the three environments (Fig. 3A) while planted seedlings had grown significantly higher, and with thicker stems, in the clear-cut than in the forest edge and forest (Fig. 3B and C). The planted seedlings had significantly thicker stems in the forest edge than in the forest (Fig. 3C). Fertilization promoted the growth of seedlings most noticeably in the clear-cut, and this was the case for both the sown and the planted seedlings (Fig. 3). In the clear-cut, both sown and planted seedlings on fertilized plots were > 50% higher, and the planted seedlings had about 90% thicker stems than their respective counterparts on control plots (Fig. 3). In the forest edge, both the fertilization and the root isolation had a significant positive effect on seedling growth, for both sown and planted seedlings, the heights were > 50% higher (Fig. 3A, B), and the planted seedlings had c. 70% thicker stems in these plots than on control plots. In the forest, it was only the root isolation that had a positive effect on seedling growth, but only for the planted seedlings (Fig. 3B and C).

Soil nitrogen concentration

In the fertilized plots, the nitrate supply rate was significantly higher than in control and root isolated plots in all environments, but with no significant difference between the three environments in any treatment. There was no significant difference between spontaneous control and planted subplots within any treatment in any of the three environments (Fig. 4A).

The ammonium supply rate was significantly higher in fertilized plots compared to both control and root isolated

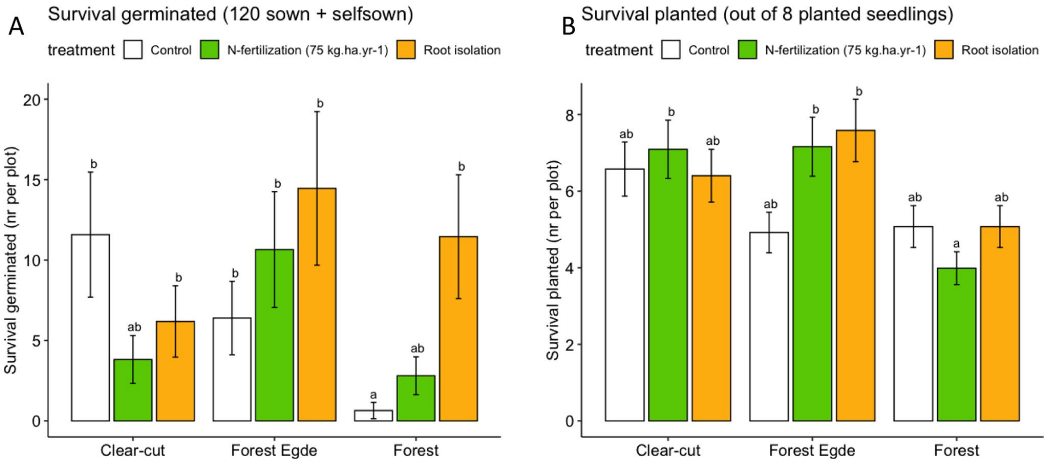

Fig. 2 Estimated marginal means from linear models for survival of **A** germinated seedlings out of 120 sown per plot plus additional selfsown seedlings after 7 years and **B** planted seedlings after 6 years in field. Letters indicate significant differences including interaction. Values are back-transformed from natural logarithmic scale. Error bars indicate standard error

Table 3 Results from ANOVA on linear mixed models for height of planted and sown seedlings, respectively, and stem base diameter of planted seedlings with environment and treatment as fixed factors including interaction and with plot nested within environment as random factor to account for within-environment variability. Significant results are defined by bold text in the table

		Sown seedlings			Planted seedlings					
		Height			Height			Stem base		
	Df	F	Df.res	Pr (> F)	*F*	Df.res	Pr(> F)	*F*	Df.res	Pr (> F)
Environment	2	7.27	12.97	**0.008**	11.23	12.05	**0.002**	69.00	12.04	**< 0.001**
Treatment	2	4.45	400.37	**0.012**	25.03	255.14	**< 0.001**	48.86	255.44	**< 0.001**
Environment × treatment	4	13.86	400.04	**< 0.001**	9.14	255.13	**< 0.001**	9.15	255.43	**< 0.001**

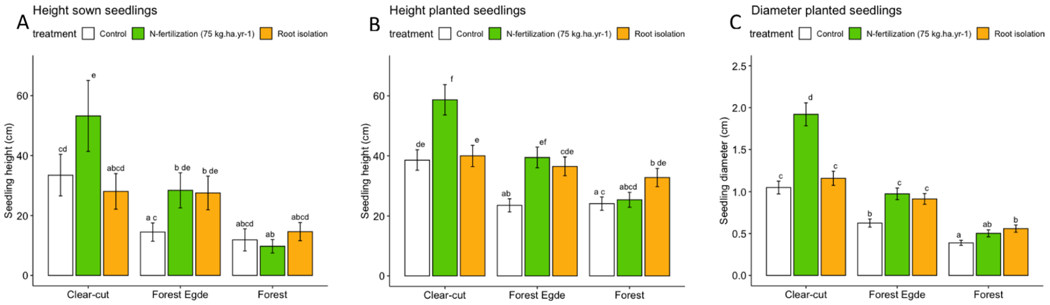

Fig. 3 Estimated marginal means from linear mixed models for height of **A** sown seedlings after 7 years, **B** planted seedlings, and **C** stem base diameter of planted seedlings after 6 years in field. Letters indicate significant differences including interaction. Values are back-transformed from natural logarithmic scale. Error bars indicate standard error

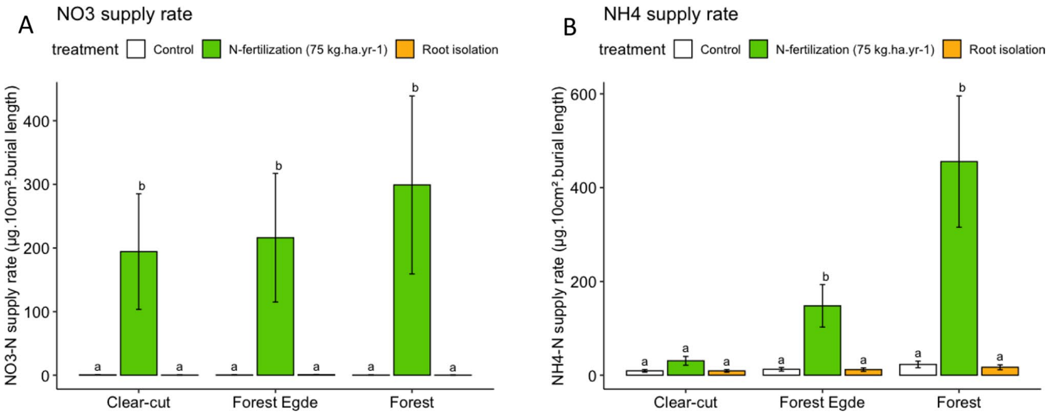

Fig. 4 Nitrogen supply rate measured by PRS™ probes over 6 weeks in the summer of 2020 in the planted subplots in form of **A** nitrate and **B** ammonium. The results are estimated marginal means from linear models. Letters indicate significant differences including interaction. Values are back-transformed from natural logarithmic scale. Error bars indicate standard error

plots in the forest and forest edge, but not in the clear-cut. As with nitrate, there was neither any significant difference in ammonium supply rate between root isolated and control plots in any of the three environments, nor between environments in these treatments (Fig. 4B).

Discussion

In northern forest ecosystems, success of forest regeneration is known to be influenced by both above- and belowground competitions. A key aim of this study was to separate between these two controls, by applying three treatments along a forest to clear-cut gradient.

A general observation regarding both sown and planted seedlings in this experiment was a consistent visible trend of one or two seedlings being larger than the others in each plot, clearly displaying internal competition among the seedlings. Further, a larger share of sown seedlings died during the period of the study as compared to the planted seedlings, leaving a higher variability for sown (0–39 per plot) than for planted (3–8 per plot) seedlings. This was expected since survival of direct sown seedlings in general is lower than for planted seedlings (Grossnickle and Ivetić 2017). The higher variability allows for larger differences in survival between treatments and environments among the sown seedlings than the planted ones. The most severe decreases in sown seedling survival occurred in 2014, in both the clear-cut and in the N-fertilized plots in the forest edge (i.e., the environments where the initial germination numbers were highest). In 2020, mortality was high in all environments and treatments. These peaks in mortality followed years with dryer than average early summer conditions (2014, 2018, and 2019), which likely intensified inter-specific competition for water (Fig. 5). An increase in sown seedling numbers in 2016, that was highest in the forest, suggests that there were also newly germinated self-sown seeds included in the measurements. The internal competition and the addition of self-sown seedlings caused a large variability in growth in most plots that made patterns difficult to detect. Regardless, we found significant treatment responses which were large enough to be detected against this background noise caused by internal seedling competition.

With our first hypothesis, we expected that seedling survival and growth in the control plots would be higher the further away from the mature forest canopy cover due to less belowground competition from mature trees. In support of our hypothesis, the number of surviving sown seedlings in the control plots was about ten times higher in the clear-cut environment than in the forest environment, while it occurred at an intermediate level at the forest edge. Regarding the lower germination and survival success of sown seedlings in the forest, direct competition for resources is the most likely explanation for these patterns. However, it is possible that several other processes contributed to this response, such as seed predation by carabid beetles and seedling predation by slugs, which have been shown to be higher under canopies than in clear-cut areas (Nystrand and Granstrom 2000). Further, the soil temperature increases following canopy removal, since more light energy reaches the ground (Grossnickle 2000). The optimal temperature for germination of Scots pine is 20–30 °C (Kamra and Simak 1968; Örlander et al. 1990), and these temperatures are less likely to occur under the shading canopy than on the clear-cut.

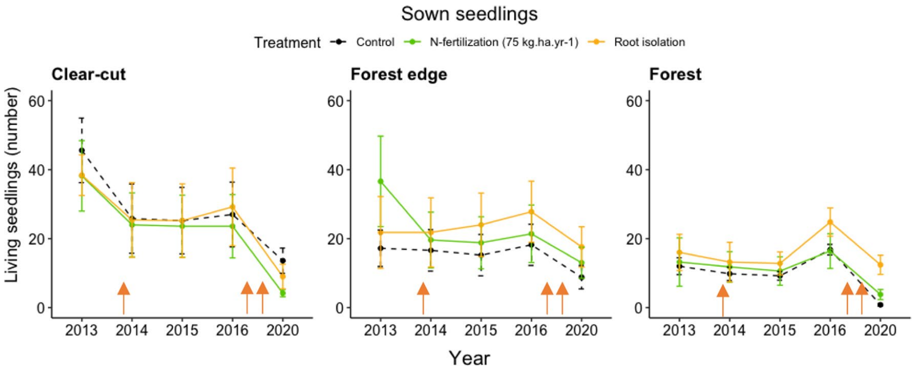

Fig. 5 An overview of the development of sown seedling germination and survival from 2013 to 2020. The summers 2014, 2018, and 2019 were unusually dry, marked by arrows. Large decreases in numbers of sown seedlings coincided with those dry summers, especially between 2016 and 2020. An increase in numbers of sown seedlings in 2016 indicates that addition of self-sown seedlings occurred

It should in this context also be mentioned that the higher occurrence of ericaceous shrubs under the canopy than in the open areas could have inhibitory effect on regeneration of conifers (Mallik 2003). However, since the ground vegetation and organic layer was removed prior to sowing in the sown plots, this would affect the planted seedlings more than the sown. In addition to survival, the growth patterns we observed also supported our hypothesis, as growth of planted seedlings was highest in the clear-cut, intermediate in the forest edge, and lowest in the forest. However, the trend of increased height growth of sown seedlings away from the forest canopy (i.e., in the clear-cut) was not significant due to the large variability in heights.

For our second hypothesis, we expected that root isolation would enhance survival and growth of seedlings by suppressing competition from mature trees for water and nutrients. We also expected this effect to be strongest at the forest edge, where the seedlings still have full access to light, but where they are suppressed by belowground competition. In partial support of our hypothesis, we found that root isolation enhanced survival of sown seedlings in the edge environment, achieving similar survival as observed in clear-cut control plots. However, inconsistent with our hypothesis, we found that this response occurred also in the forest environment, suggesting that the higher light in the edge environment was not an important factor contributing to the root isolation response. This indicates that underground competition rather than light competition is the primary limitation for the establishment of sown seedlings in the forest. This brings up a question regarding the previous hypothesis: If light availability was not a main driver of survival in the forest, why was the survival of sown seedlings higher in the forest edge control plots than in the forest control plots when the main difference between the two environments was light availability? One explanation is that the belowground competition in the forest edge was reduced, since approximately half of the roots of mature trees in the forest edge environment are dead ones from the harvested side of the edge. An additional explanation might be the increase in temperature following canopy removal. The optimal soil temperature for root growth and water uptake capacity is 30–35 °C for Scots pine (Örlander et al. 1990), temperatures less likely to occur under the canopy than in full light. Further, the nutrient uptake capacity of seedlings has been found to decrease at soil temperatures below 15 °C (Örlander et al. 1990). Temperature increase can also enhance nutrient availability, through higher mineralization rates (Rustad et al. 2001; Strömgren and Linder 2002).

Regarding growth, both sown and planted seedling growths were enhanced by root isolation in the edge environment, in line with our hypothesis. Growth of planted seedlings was also enhanced by root isolation in the forest, achieving similar growth as observed in clear-cut control plots, despite the lower light conditions in the forest. This indicates that underground competition rather than light competition limits the growth of seedlings in the forest, similarly as for the survival of sown seedlings as described above. An early root isolation experiment conducted in the same area as the current study showed that pine seedlings growing in a root isolated area under closed canopy of mature pine grew better than the seedlings outside the isolated area, despite the lower light conditions; though the experiment was only made on a single plot and was not replicated (Björkman 1945). However, we found no effect of root isolation on sown seedling growth in the forest, indicating that mortality (described above) may be a more important mechanism by which belowground competition impacts sown seedlings. The absence of enhanced growth of sown seedlings in response to root isolation in the forest may also have been due to higher intra-specific competition among the sown seedlings themselves, as the significantly higher survival resulted in more seedlings to share the resources in the plot. Nevertheless, the positive responses of root isolation in our study are in line with experimental root trenching studies on other tree species resulting in positive responses from seedlings that are relieved from underground competition (Coomes and Grubb 2000; Devine and Harrington 2008; Wagner et al. 2010; Petritan et al. 2011). These findings are also relevant regarding recently popular discussions regarding the “mother-tree” or the “wood-wide-web,” where positive effects of adult trees on seedlings are proposed (Simard et al. 1997; Klein et al. 2016; Cahanovitc et al. 2022). Clearly, our data do not provide any support for these propositions. To the contrary, our results suggest that strong belowground competitive effects from adult trees suppress seedlings, in line with recent arguments questioning the validity of the mechanisms of common ectomycorrhiza networks as a resource transfer tool for adult trees to support seedlings (Karst et al. 2023; Henriksson et al. 2023).

Our third hypothesis was that N fertilization will enhance survival and growth, with the effect expected to be strongest in the clear-cut and weakest in the forest due to greater competition for other soil resources (e.g., water) from mature trees. Inconsistent with our third hypothesis, we found that N fertilization had no effect on sown or planted seedling survival relative to control plots within any of the environments; however, survival of N-fertilized planted seedlings was significantly lower in the forest than in the other environments. A potential explanation for this is that fertilized forest plots showed the highest supply rate of NH_4^+ we observed. The competition for water from mature trees may have increased the salt concentration, which potentially could have had a toxicity effect for small seedlings (Öhlund and Nasholm 2001). Since N fertilization increases nutritional value of plants, predation by herbivores could also have played a role (Ball et al. 2000). A potential increase in seedling predation by slugs in the forest environment (Nystrand and Granstrom 2000) might have been further enhanced by N fertilization since N fertilization has been found to increase the susceptibility of seedling predation by slugs (Albrectsen et al. 2004). Regarding growth, N fertilization significantly enhanced the growth of both sown and planted seedlings in the clear-cut, and to a smaller extent in the forest edge, while in the forest, there was not any significant effect of fertilization on growth at all. This pattern matched the pattern of the nitrate and ammonium supply analyses where less of the N-supply remained in the clear-cut, more in the forest edge and most in the forest, which is likely indicative of the biologically utilized N-supply in each environment. There was no indication from the PRS™ probe measurements that the supply of other major nutrients (P, K, S, Ca, and Mg) was lower in the forest than in the other environments, which otherwise could have helped explain the results if the added nitrogen caused deficiency of other nutrients (see supplementary material Fig. S1). The significantly higher remaining supply of ammonium in fertilized forest plots suggests that competition for other soil resources (e.g., water) between seedlings and mature trees likely also hindered seedling growth, which may have also limited seedling N fertilizer uptake. This would agree with the previous studies finding that water uptake affects uptake of N via mass flow in high N environments (McMurtrie and Nasholm 2018; Henriksson et al. 2021). Likewise, the aboveground growth of fertilized mature trees has been found to co-vary with precipitation (Lim et al. 2015). Soil resource availability may also interact with light availability since light conditions affect the capability of plants to utilize nutrients in the soil (Coomes and Grubb 2000). More light results in a higher potential for photosynthesis and, therefore, higher transpiration, which, in turn, leads to increased N uptake via mass flow (Oyewole et al. 2016; McMurtrie and Nasholm 2018; Henriksson et al. 2021). This would explain why the effect of N fertilization was higher in the clear-cut since the absence of competition for water allows for higher transpiration rates.

The release from competition for nutrients vs water has been studied in a previous experiment near our study site, where mature pine trees were girdled to release belowground competition for nutrients (Högberg et al. 2001; Ahlstrom and Lundqvist 2015). The needles of the mature trees remained the two 2 years after girdling, i.e., the trees still took up water for this period (Bhupinderpal-Singh et al. 2003). In that experiment, the release of competition for nutrients caused by tree girdling resulted in a regeneration pulse already during these first 2 years, when the girdled trees maintained their needles (Axelsson et al. 2014). However, the number of seedlings established doubled the following 2 years after the needles were dropped, i.e., when competition for light and water decreased together with a release of nitrogen from decomposing needles (Axelsson et al. 2014). The seedlings established during the 3rd year after girdling showed the highest yearly increment and total height in a 12-year inventory period after girdling (Axelsson et al. 2014). Our data show similar patterns complementary to these findings by suggesting that simultaneous release from competition of water and nutrients has a better effect than N fertilization under low-light conditions (i.e., under the canopy), that both measures are effective under high-light conditions with underground competition (i.e., at the forest edge), while N fertilization is most effective where the seedlings have full light and no underground competition (i.e., in the clear-cut). This also agrees with the previous findings indicating that competition for water and nutrients is of relatively higher importance for Scots pine regeneration than competition for light, at least on nutrient poor soil with high permeability which is common in Scots pine forests of northern Sweden.

Conclusions

The results from this study support the previous findings that Scots pine seedlings suffer from belowground competition near mature trees. Despite internal competition among seedlings that increase as seedlings grow, we found an overall pattern that the seedlings grew best in clear-cut environments, followed by forest edge, and lastly under mature forest. We have here showed that the belowground competition along a forest edge may be alleviated by N fertilization and root isolation. Physical root isolation by steel frames and annual fertilization would be impractical to implement in practice; however, targeted microsite fertilization at planting locations in small gaps or clear-cut edges might be an option to improve regeneration of Scots pine in proximity to mature trees. Root isolation could potentially be achieved by deep soil scarification along forest edges that would interrupt root connection from mature trees. To avoid that the positive effect on seedling establishment is not counteracted by damage to the mature trees by root loss, the scarification should preferably be limited to cut off mature tree roots only in proximity to the planting position of the new seedling. Of course, this would have to be tested, preferably in a larger scale at more sites and in forest edges facing all directions. Overall, our results highlight that a transition to CCF forestry for northern European pine forests will necessitate substantial management innovation to alleviate these belowground resource constraints on seedlings in proximity to mature trees if aimed regeneration goals are to be maintained.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10342-023-01609-1.

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Author contributions AN contributed to the conception of the research question and design of the work, BH contributed with analysis and interpretation of data and results as well as scientific writing of the work, AN and MJG contributed with scientific writing and revising it critically for sound and intellectual content.

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Declarations

Conflict of interest AN is besides her affiliation to the Swedish University of Agricultural Sciences employed at Stora Enso, a forest industry company. MJG and BH declare no conflict of interest and have no commercial affiliations.

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With a warming climate, increases in drought periods and pests can reduce the regeneration success. Further consideration of site conditions may therefore be needed during planting. This thesis aims to better adapt boreal forest regeneration practices to local environments, with focus on regeneration of Scots pine (Papers I-IV), Norway spruce (Papers II & III) and silver birch (Paper II). The results emphasize that adapting regeneration practices to the site conditions at the time of planting is a key to success.

Bodil Häggström received her doctoral education in forest regeneration at the Department of Forest Genetics and Plant Physiology at the Swedish University of Agricultural Sciences (SLU). She received her Degree of Master of Geoscience from Stockholm University in 2019.

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