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Adaptation of Norway spruce (Picea abies (L.) Karst.) to current and future climatic conditions

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Cover: Norway spruce needles and cones with frost damaged shoots.
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Abstract

Climate change urges our understanding of the capacity of Norway spruce (*Picea abies* (L.) Karst.) population to adapt and maintain, and even increase, their growth capacity at the level required to sustain a transition towards a biobased socio-economic model. Climate change is already anticipated to result in an increase of temperature. Although generally an increase in the average temperature is considered favourable for growth in the boreal climates, it will also consequence in more frequent temperature backlashes and drought. Outbreaks of pests and fungi are often associated with extreme events. Altogether, this exemplifies the need to investigate how Norway spruce may respond to those predicted changes.

Second generation material of eastern European origin, in relation to improved Swedish material, performs well in the current climate in southern Sweden, with later bud burst when grown in Sweden as compared to Swedish material. The second generation material is closer to Swedish material in timing of bud burst indicating a land race formation. At frost prone sites trees with late bud burst should be deployed as trees with early bud burst will increase the risk of spring frost related damages.

The impact of future climate change on 18 Swedish and Eastern European provenances showed that frost days in southern Sweden are likely to decrease, but as bud burst will occur earlier this is expected to lead to an increased occurrence of spring frost events. Furthermore, above normal temperatures during the latter part of quiescence phase can induce earlier bud burst and lower cold tolerance, hence increase the risk for frost damages in spring.

Drought can affect the height growth of trees both during as well as after a drought event. A higher genotype and environment interaction (G x E) was also observed to be high and significant in severely drought-damaged stands, thus drought may be the underlying factor for a stronger G x E and subsequently a change in the ranking of tree genotypes.

Keywords: Norway spruce, Frost damage, Drought, Bud burst, Seed shortage, Climate change, Growth

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Dedication

Till min familj och speciellt till min son, Darin

Somewhere, something incredible is waiting to be known
Carl Sagan

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. **Jenny Lundströmer**, Mats Berlin and Bo Karlsson (2020). Strategies for deployment of reproductive material under supply limitations – a case study of Norway spruce seed sources in Sweden. *Scandinavian Journal of Forest Research*, 35(8), pp. 495-505.

II. Tetiana Svystun, **Jenny Lundströmer**, Mats Berlin, Johan Westin and Anna Maria Jönsson (2020). Model analysis of temperature impact on the Norway spruce provenance specific bud burst and risk of frost damage (submitted to *Forest Ecology and Management*)

III. Haleh Hayatgheibi, **Jenny Lundströmer**, Mats Berlin, Matti Haapanen, Katri Kärkkäinen and Andreas Helmersson. Impact of drought stress on height growth of Norway spruce clonal trials in Sweden and Finland (Manuscript)

IV. **Jenny Lundströmer**, M Rosario García Gil and Johan Westin (2020). The effect of winter temperature on needle hardiness, bud burst and shoot growth pattern in Norway spruce (Manuscript)

The contribution of Jenny Lundströmer to the papers included in this thesis was as follows:

I. She was involved in data collection, conducted the analysis of the data, wrote the first draft of the manuscript and completed the paper in collaboration with the co-authors.

II. She conducted the analysis of the temperature data, had a main role in writing the first draft of the manuscript and completed the final manuscript in collaboration with the co-authors.

III. She conducted the analysis of the temperature data and had a main role in writing the first draft of the manuscript and completed the final manuscript in collaboration with the co-authors.

IV. She conducted the analysis of the data, had a main role in writing the first draft of the manuscript and completed the paper in collaboration with co-authors.

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Abbreviations

All abbreviations are explained when they first appear in the text.

1. Introduction

The world's land area consists of one third of forests, where almost a third is boreal forest that covers large parts of Fennoscandia, Russia, Canada and Alaska (Brandt *et al.*, 2013). The climate in the boreal forest is harsh with short summer periods for growth as well as long and cold winters with freezing temperatures (Burton *et al.*, 2010). Its dominant tree species are *Abies*, *Larix*, *Pinus*, *Picea*, *Populus*, *Salix*, *Betula*, and *Almus* (Burton *et al.*, 2010; Kneewhaw *et al.*, 2011; Shorohova *et al.*, 2011). Boreal forests´ ecological and economical importance has raised the awareness of a sustainable forestry management where conservation of biological and genetic diversity and sustainable exploitation of the natural resources is balanced (Carnus *et al.*, 2004; Lelu-Walter *et al.*, 2013).

In the Nordic and Baltic countries, the largest proportion of native trees are Norway spruce (*Picea abies* (L.) H. Karst.), Scots pine (*Pinus sylvestris* L.) and silver and downy birch (*Betula pendula* Roth and *B. pubescens* Ehrh.), with growing stocks of around 2800, 3500 and 1550 million m^3, respectively (Rytter *et al.*, 2016). Sweden is one of the five biggest exporter of tree products (e.g., paper, pulp and lumber) and more than 50% of the land area is covered by forests. The forestry sector is the most important net contributor to the economy in Sweden and the standing volume for productive forest land is more than 3000 million m^3. About 80% of the standing volume in Sweden are in stands with Norway spruce and Scots pine, while the rest are from a mixture of deciduous trees species and some non-native conifers (SLU, 2017).

Boreal forests are not an exception to climate change, and effects of climate change are already measurable (IPCC, 2013; ACIA, 2005). The annual mean temperature is expected to increase with 6 to

11°C by 2100 according to the scenario RCP 8.5, with an expected greater increase in temperature during winter than summer. The temperature sum is also expected to increase hence the vegetation period will be longer (IPCC, 2013).

More severe events are probably going to occur like spring frost and fires (Kilpeläinen *et al.,* 2010; Langvall, 2011). As well as increased risk for wind-induced damages and uprooting of trees (Peltola *et al.*, 2010). For Sweden to remain one of the biggest actors in forestry it is urgent to devote research resources to first understand the capacity of boreal tree populations to adapt to the new climatic conditions and, second, to develop sustainable management plans to maintain high quality and quantity of forest products.

1.1 Norway Spruce (*Picea abies*)

Norway spruce is widely distributed throughout Europe, from central up to northern parts of Europe, and over large areas to the east where it ends around the Ural Mountains (
Figure 1). The growing stock of Norway spruce in northern Europe (Sweden, Finland, Norway, Denmark and Lithuania) are around 2800 m^3 and more than 350 million seedlings are produced every year (Rytter *et al.*, 2016). In Sweden, the standard procedure that is predominately used is that Norway spruce forest stands are managed with thinning and clear-cutting, where regeneration is carried out mostly by planting improved seedlings. The stands are generally even aged and homogenous and thus are more susceptible to disturbance (Kuuluvainen and Siitonen, 2013; Venier *et al.*, 2014).

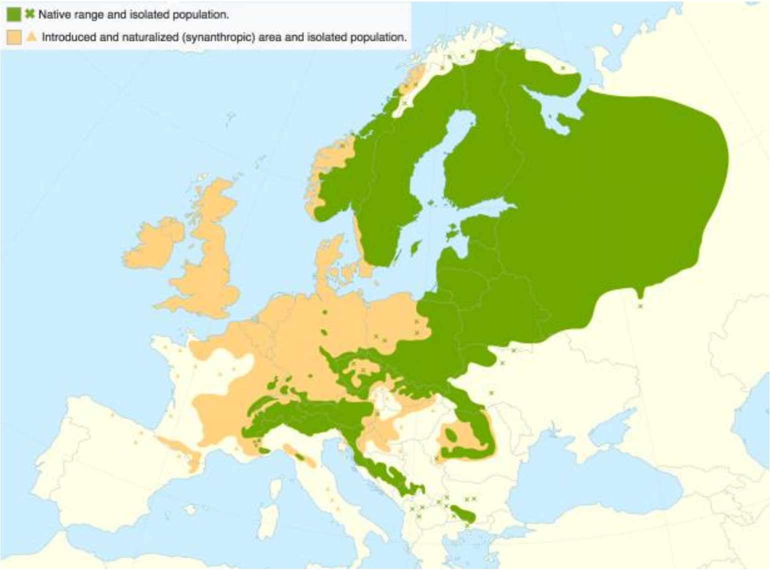

Figure 1 - Distribution map of Norway spruce (Caudullo *et al*., 2018) [CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/deed.en)]

1.2 The annual shoot growth cycle

The growth cycle of trees in Sweden consists of dormancy, quiescent and active periods (Perry 1971; Sarvas 1972; Sarvas, 1974; Fuchigami, 1982). Trees are in dormancy (resting) during winter, until the quiescent period starts where the trees can respond to environmental signals (i.e., dormancy is released). However, for the trees to be able to break dormancy chilling is needed, where the trees have to be exposed to a period of non-freezing temperature (Coville, 1920; Nienstaedt, 1967; Worrall & Mergen, 1967, Hänninen, 1990; Myking & Heide, 1995).

In spring, activity resumes in apical shoot meristems by cell divisions, cell differentiations and cell elongations, which results in a rapid enlargement of the buds, bud burst and shoot elongation. The exact time when bud burst and bud set occur in boreal trees varies between different provenances due to local adaption to seasonal changes in day length and temperature (Hänninen, 1990; Hänninen, 2016), as well as light quality (Clapham *et al*., 1998). For bud burst to take place a prolonged exposure to temperatures above a certain threshold is needed, and it is possible to use a model to estimate when bud burst occurs based on provenance specific temperature sum requirement (Hannerz, 1998). The model assumes that the dormancy completion takes place at a fixed date during spring, an assumption that has proven to be more accurate than models where dormancy completion depend on the accumulation of chilling. This in turn has led to hypothesis that something more than sufficient chilling is needed for dormancy completion (Häkkinen *et al.*, 1998; Häkkinen, 1999; Linkosalo, 2000; Linkosalo *et al.*, 2000).

In comparison with southern Sweden, the growing season in northern Sweden is generally shorter, including a relatively short spring and autumn transitions from winter conditions. As a consequence, northern provenances generally have a lower temperature sum requirement for bud burst compared with provenances from the south. Exposure to sufficient chilling is important in boreal trees species as bud burst may else be delayed due to an increased temperature sum requirement for bud burst (Man *et al.*, 2017; Hannerz *et al.*, 2003; Heide, 1993). Another aspect is photoperiod which also can delay or even advance bud burst. If the photoperiod is gradually shortened a delay in bud burst can be seen, while a gradually extended photoperiod results in earlier bud burst but only when the trees are exposed to sufficient chilling (Nienstaedt, 1967; Basler and Körner, 2014; Caffarra *et al.*, 2011; Partanen *et al.*, 1998).

From the start of bud burst, growth continues by visible shoot elongation during the summer to usually end in August. After completion of the visible shoot elongation, growth is less visible as the formation of buds occur until the end of the growth season and the trees enter dormancy to be able to survive the winter. Dormancy starts in late autumn and lasts until early next spring (Sarbas, 1974; Hannerz *et al.*, 2003; Hänninen, 2016). The term true dormancy is sometimes used when the buds are not able to burst at normal growth temperature in long days (Junttila *et al.*, 2003). In the study by Clapham *et al.* (1998) northern populations use the ratio of far-red to red light to decide if they enter dormancy, while southern populations do not. If the amount of far-red light decreases the northern population will stop growing.

High autumn temperatures (15-21ºC) can delay spring bud burst (Heide, 1974; Søgaard *et al.*, 2008). This effect appears to be greater on seedling from the south compared to the north (Søgaard *et al.*, 2008). In an experiment with Norway spruce in northern Sweden with whole tree chambers an increase in air temperature of 3-5 degrees above ambient temperatures resulted in bud elongation and initiation of shoot growth beginning two to three weeks earlier (Linkosalo, 2000; Slaney *et al.*, 2007). No visible bud burst was recorded before day 130, with or without elevated air temperature. Increasing temperatures will decrease the time required for bud burst because when trees are exposed to high temperatures the ontogenetic development of the bud toward bud burst following shoot elongation starts (Sarvas, 1972; Sarvas, 1974; Cannell & Smith, 1983; Hänninen, 1990).

1.3 Breeding of Norway spruce in Sweden and seed orchards

The breeding of Norway spruce trees in Sweden started in the 1940s (Werner & Danell, 1993) and has developed a lot since then. In the beginning, around 1000 plus-trees for 10 potential breeding zones were selected from mature and often naturally regenerated stands. The plus-trees were grafted and planted in clonal seed orchards. Progeny testing of plus-trees started in the 1970s and the base for breeding was later widened by an additional large selection of a second round of plus-trees, selected in younger, even aged and well-developed stands. Altogether the selected plus-trees formed the base for selection of trees, both progeny tested as well as untested trees, to the second generation of seed orchards. Around the same time, a large clonal testing program including 18,400 clones was established, along with 6100 selected plus-trees resulting in a total of 24500 trees that together conformed the long-term Swedish breeding populations (Karlsson & Rosvall, 1993). The establishment of the third round of seed orchards, entirely based on trees tested in field tests, started in the year 2000 and is expected to have a potential genetic gain of 25% in growth compared to unimproved trees (Remröd *et al.*, 2003; Rosvall *et al.*, 2001).

The starting point of a breeding program is the selection of plus-trees of improved quality for desirable traits such as growth, wood properties or disease resistance. To identify, weigh their relative importance and select the right traits adequately is a challenge in itself, which is accentuated by the difficulty of predicting the possible consequences of a climate change in the long term (Eriksson *et al.*, 2006; Prescher, 2007; Rosvall & Mullin, 2013).

In Sweden around 200 million spruce seedlings are deployed in the forest each year (Skogsstyrelsen, 2020). Improved seeds deliver higher genetic gain in growth, survival and wood quality traits compared to the unimproved seeds (Liziniewicz & Berlin, 2019; Haapanen, 2020). However, there is a shortage of improved seeds from Swedish seed orchards (Almqvist, 2014; Almqvist *et al.*, 2010). Norway spruce trees do not flower each year, instead, there is often a period of 5-7 years in between flowering years when seed production is scarce (Lindgren *et* al., 1977; Crain & Gregg, 2018). There have been several studies aiming to increase seed production during the flowering years (Almqvist, 2007; Crain & Cregg, 2018). Despite those efforts, an efficient treatment to initiate spruce flowering is still lacking and the factors controlling flowering in Norway spruce are not yet fully understood. In addition, during good flowering years, cones can be damaged by different pests and fungus that affect seed production (Almqvist & Rosenberg, 2016; Capador *et al.,* 2018). To be able to meet the demand, seeds from other countries have been imported, usually from Russia and Belarusian among other countries (Myking *et al.*, 2016).

In the south of Sweden, the imported trees sources have shown better growth but also a later bud burst in the spring compared to local seed sources (Danusevicius & Persson, 1998; Langlet, 1960; Persson & Persson, 1992). Since 2001, only around 54% of the seedlings that are deployed in the Swedish forest originate from Swedish seed orchards (Skogsstyrelsen, 2020). Around 27% originate from foreign stands and seed orchards, where most of them originate from Belarus, Poland, Lithuania, Finland, Latvia and Norway. From each of these countries more than 100 kg seeds between 2004-2018 were imported (Skogsstyrelsen, 2020). To import seeds from countries within EU is allowed (EU, 2000, 2008), whereas import of seeds from Belarus, outside the EU, was only allowed up to December 31, 2019 (EU, 2015). Belarus has been a big source of seeds and from 2004-2018 and more than 4000 kg have been imported (Skogsstyrelsen, 2020).

1.4 Future climate

The climate will change in the future with warmer days and longer vegetation periods, but this will also cause more temperature backlashes during spring which will increase the risk of tree frost damages (Langvall, 2011; Jönsson *et al*., 2004). A potential risk is also that wind-induced damage is going to increase which may bring more attacks by insects on the trees that have been uprooted (Jönsson *et al.*, 2007). Because of the higher temperature, a higher evaporation will occur and dry spells during summer may be prolonged (Ryan, 2011). As a sustainable production of biomass is needed in the future, the adaptability of existing populations needs to be assessed where not only traits of economic value has to be included but also breeding for biotic and abiotic stress-tolerance and vitality. To be able to understand the mechanistic and genetic basis of abiotic stress (such as drought and frost) tolerance in plants studies needs to be performed and different genetic material has to be tested in varying climates.

1.4.1 Frost

Spring frost events are usually site specific and occur when the sky is clear and no wind present (Langvall, 2000; Hammersmith, 2014). At these events the cold air accumulates, and the trees suffer from radiation frost damage, which usually causes mild to severe damage to all trees in active growth, but especially to seedlings where a short period of below zero temperatures can kill the newly sprouted shoots or even the whole plant (Auspurger, 2009; Jönsson & Bärring, 2004, 2011; Christersson & Fircks, 1988; Sakai & Larcher, 1987). Freeze damage occurs primarily in the membranes where the ice formation starts in the intercellular spaces (between the cells) at temperatures below 0ºC (Levitt, 1980; Steponkus, 1984; Thomashow, 1999). Then the water from inside the cells moves outside following a gradient of water potential, which will cause severe cellular dehydration (Wisniewski & Fuller, 1999). Membrane lesions can also be the result of frost damage (Steponkus *et al*., 1993; Uemura & Steponkus, 1999).

In the south of Sweden, a reduced risk of frost due to warmer climate may be counterbalanced by an increased risk of frost damage to newly sprouted buds caused by temperature backlashes during the spring, where the frequency of frost events will increase (Langvall, 2011; Jönsson *et al.*, 2004). If the frost damage to trees will decrease or increase depends on how warm it will become in the future but also how the provenance specific responses will be. Therefore, it will be important to assess different future scenarios to be able to select suitable seed sources for a decreased risk of frost damage. The risk of frost has to be implemented when choosing trees to deploy in the forest, if trees that are not able to correctly track the seasonal changes are deployed, a reduced or hampered growth can be the consequence.

To decrease the risk of frost, trees with later bud burst can be selected, especially on sites affected by high temperature fluctuations. In these sites, provenances from the Baltic regions and Belarus are a good choice because of their later bud burst. Although these provenances set the bud later, as compared to the Swedish provenances, the risk for autumn frost is low in the south of Sweden (Langlet, 1960; Skrøppa & Magnussen, 1993).

It is also possible to estimate the timing of bud burst and frost risk with phenological models driven by climate data (Augspurger, 2013). The best performing models are thermal time models that incorporate chilling and photoperiod, which is important to consider if the chilling is not fulfilled (Olsson & Jönsson, 2015; Linkosalo *et al.*, 2008; Linkosalo, 2006).

1.4.2 Warmer winters

The temperature will increase during winter as well as early spring which will most probably influence the timing of bud burst, depending on when the increase in temperature occurs, for how long and the amplitude. Information on how temperature and photoperiod affect the timing of rest and bud burst in Norway spruce will help to understand the impact of climate change in the future.

In several future scenarios the temperature will increase between 4ºC up to 11ºC (IPCC, 2013; World Bank, 2014), which in turn means that the winter in the Nordic countries will be even warmer. If plants are exposed to low but non-freezing temperatures the cold acclimation will be induced which is the processes where they gain cold tolerance. If for example Arabidopsis are exposed to low temperatures, an acclimation to cold periods or frost event will start and cease again when the temperature is higher (Thomashow, 1999; Heino & Palva, 2003). Warmer and fluctuating temperature during autumn, winter and spring will impact the maintenance of cold hardiness and increase the risk for spring frost damage (Schlyter *et al*., 2006; Chang *et al*., 2016). Longer nights and chilling temperatures that start in the autumn is a signal for the tree that winter is coming, and this will trigger growth cessation and dormancy processes as well as cold tolerance (Weiser, 1970; Christersson, 1978; Sakai & Larcher, 1987, Birgas *et al*., 2001; Li *et al*., 2004).

1.4.3 Drought

With higher temperatures in the future, a higher frequency of drought will occur. There are several reports about decrease of precipitation during summer which has caused moderate droughts, leading to reduced growth but also severe drought causing tree mortality (Girardin *et al*., 2008; Kurz *et al*., 2008; Allen *et al*., 2010; Kurz *et al*., 2013, Huang *et al*., 2018)). The snow will also melt earlier and an increase in evaporative demand in the North will increase the frequency of drought (Ryan, 2011). If the water availability in the summer decreases during long time periods, the water transportation from the soil to the needles will decrease and the water potential in the trees will also decrease. This will in turn increase the tension on the water column within the vascular system and with it the risk that it surpasses a critical value with xylem cavitation as a result. This leads to hydraulic and symplastic failure because of the air that comes into the conduits and in the end the death of the tree (Tyree and Sperry, 1988; Tyree and Zimmerman, 2002). Drought stress may also cause different responses for different trees, like a reduction of the annual increment or alternation of the chemical composition of the wood, but it depends on the species as well as the environment (Moran *et al*., 2017; Trujillo-Moya *et al*., 2018). Some trees are able to withstand drought periods better than others, but experiments have shown that Norway spruce is more sensitive to drought than Scots pine (Kellomäki *et al*., 2005; Kellomäki *et al*., 2008), and that it is really sensitive to drought events mainly at low elevations and southern exposed sites (Cermák *et al*. 2019, van der Maaten-Theunissen *et al*., 2013; Rosner *et al*., 2018). The severity and duration of drought stress will determine the survival of the tree and the response to drought both varies between different and within species (Street *et al.*, 2006; Wilkins *et al.*, 2009).

There are several periods of drought spells that have caused high mortality in Norway spruce during the years (Rybníček *et al.* 2010; Cermák *et al.* 2019; Nilsson & Örlander, 1995; Mäkinen *et al.*, 2001, Solberg, 2004). Usually, it is the drought that triggers other factors such as fungus or pest infections and this is the main cause behind the mortality. If the trees would have a higher drought tolerance then the mortality would decrease, which is why it is important to incorporate, in terms of drought tolerance, superior genotypes in tree breeding (Sonesson & Eriksson, 2003). However, most of the Norway spruce studies focus on traits like growth or wood quality traits (Chen *et al.*, 2014; Zhou *et al.*, 2019) and only a few have studied Norway spruce response to drought, like Sonesson & Eriksson, 2003 and Trujilo-Moya *et al.*, 2018.

To be able to measure the severity of drought several indexes have been developed like Keetch–Byram Drought Index (KBDI), Standardized Precipitation Index (SPI), Palmer Drought Severity Index (PDSI) and Soil Moisture Anomaly (SMA), but the Standardized Precipitation Evapotranspiration Index (SPEI) is one of the most widely used since it includes temperature as well as precipitation, and it is possible to calculate for one month up to 48 months. The codes for using the method are also freely available and easy to download (WMO & GWP, 2016). The SPEI drought index can be divided into seven categories (Table 1) ranges from extremely wet (EW) to extremely dry (ED) (Li *et al.*, 2015).

Table 1 – SPEI drought index categories adapted from Li *et al.*, 2015.

Moisture Category	**SPEI**
Extremely wet (EW)	2.00 and above
Very wet (VW)	1.50 to 1.99
Moderately wet (MW)	1.00 to 1.49
Near normal (NN)	−0.99 to 0.99
Moderately dry (MD)	−1.00 to −1.49
Severely dry (SD)	−1.50 to −1.99
Extremely dry (ED)	−2.00 and less

1.5 Adaption and assisted migration

Trees have long lifespans and because of this it takes a long time to adapt to environmental changes and therefore trees are vulnerable to climate change. However, after a single generation the offspring is already more adapted to the site than what is expected from the mean of the parents. The phenological traits such as bud burst and bud set are faster to adapt than growth (Skrøppa and Steffenrem, 2016). Research suggests that some part of the development depends on where the seed mature regardless of where the seeds are planted i.e., epigenetic effects, so if the seeds mature in warmer climate the trees will exhibit later bud burst (Kvaalen & Johnsen, 2008; Skrøppa et al., 2009).

In the future with faster climate change, the capacity of tree populations to genetically evolve to adapt fast enough will be challenged. This is where assisted migration will play an important role. Breeders can assist the transfer of trees with desirable properties to match the tree genetics with the environment to optimize tree performance (Koralewski et al., 2015; Williams & Dumroese, 2013).

1.6 Recommendation for deployment today

Skogforsk (The forestry research institute of Sweden) is responsible to deliver a recommendation on "*what to plant where*" in Sweden, and a tool, so-called Planters guide (Skogforsk, 2020), that is publicly available to optimize forest tree performance at each site, with the coordinates of the site for planting a list of recommended seed sources is available, where the option for the best possible gain in growth is made. The recommendation for Norway Spruce in Sweden is usually that trees are moved latitudinally northwards from the local origin to get a higher survival and growth (Kroon & Rosvall, 2004; Rosvall, 1982). In the south of Sweden, a longitudinal transfer is also recommended where seeds from the Baltic region are transferred to the south of Sweden for a higher growth, survival and also a later bud burst (Persson & Persson, 1992; Werner & Karlsson, 1982).

1.7 Quantitative genetics

Quantitative genetics is the study of polygenic traits, which means traits that are influenced by many gene loci and the environment. To be able to predict a family or individual genetic value the phenotypic variation is divided into genetic and environmental components (Lynch & Walsh, 1998). In breeding studies, the goal is to estimate the proportion of the genetic variance that is transmitted to the offspring, the breeding value (the additive variance), and heritability of the traits (the ratio between additive variance and the phenotypic variance) (White *et al.*, 2007; Floconer & Mackay, 1996). To be able to know if the estimates are robust several field tests at different sites need to be established (White *et al.*, 2007). Also, it is important to investigate the same trait in different environment to be able to understand the G x E interaction, where type-B genetic correlation (Burdon, 1977) is commonly used (Burdon *et al.*, 2019; Chen *et al.*, 2017; Berlin *et al.*, 2015). It is also possible to investigate the correlation between different traits in the same trial or across several trials, as well as the correlation for one trait during several years.

1.8 Spatial analysis

In forest field trials spatial analysis is commonly used to be able to reduce the error variance by improving the estimations of genetic parameters. It can detect continuous variation within blocks (patchy), global trends (gradient) and externally (nugget) across large agricultural or forest field trials (Chen *et al.*, 2018; White *et al.*, 2007, Dutkowski *et al.*, 2006, Gilmour *et al.*, 1997). There are different methods of spatial analysis that have been studied during the years like post-blocking (Gezan *et al.*, 2006; Ericsson, 1997), kriging (Zas, 2006; Hamann *et al.*, 2002) and nearest neighbour adjustment (Anekonda & Libby, 1996; Wright, 1978). However, one method recommended by Gilmour *et al.* (1997) is commonly used in forest breeding, where both the design features and the spatial component are fitted as first-order separable autoregressive model of residuals. This method has shown less bias in the estimation of genetic parameters (Dutkowski *et al.*, 2006; Dutkowski *et al.*, 2002), and therefore it was used for the spatial analysis in paper I, II and III.

2. Objectives

The overall aim with this thesis was to study adaptation and growth performance of Norway spruce and to provide insights about the performance of different plant populations grown under different climatic conditions. The climatic conditions considered in the study were mainly related to air temperature, specifically autumn, winter and spring temperatures, and water deficit. The performance was studied by assessment of traits related to plant survival, growth and frost damage.

The following specific objectives were addressed:

- To explore the performance of second generation material in Sweden in relation to improved material; and, to compare the performance of different seed sources (stands and seed orchards) in southern Sweden, using growth, survival, growth rhythm and frost damage (Paper I).

- To analyse how spring frost events together with bud burst will develop in the near and far future for genetic entities in southern Sweden in a changing temperature climate; and, to compare local climate conditions with gridded data (Paper II).

- To explore the impact of drought on growth performance, to estimate the genetic and phenotypic correlation between traits like annual height increment and final tree height; and to evaluate patterns of genotype-by-environment interaction for both annual height increments and the final height traits in Norway spruce growing in Sweden and Finland (Paper III).

- To study how an increase in temperature compared to ambient temperatures, during short periods in autumn, winter or spring or during the entire winter period will affect timing of bud burst, shoot growth patterns the following year and effect needle hardiness (Paper IV)

3. Materials and methods

3.1 Materials and field trials

Almost all of the trials addressed in this thesis are located in the south of Sweden (Figure 2) except for two trials in Finland for Paper III.

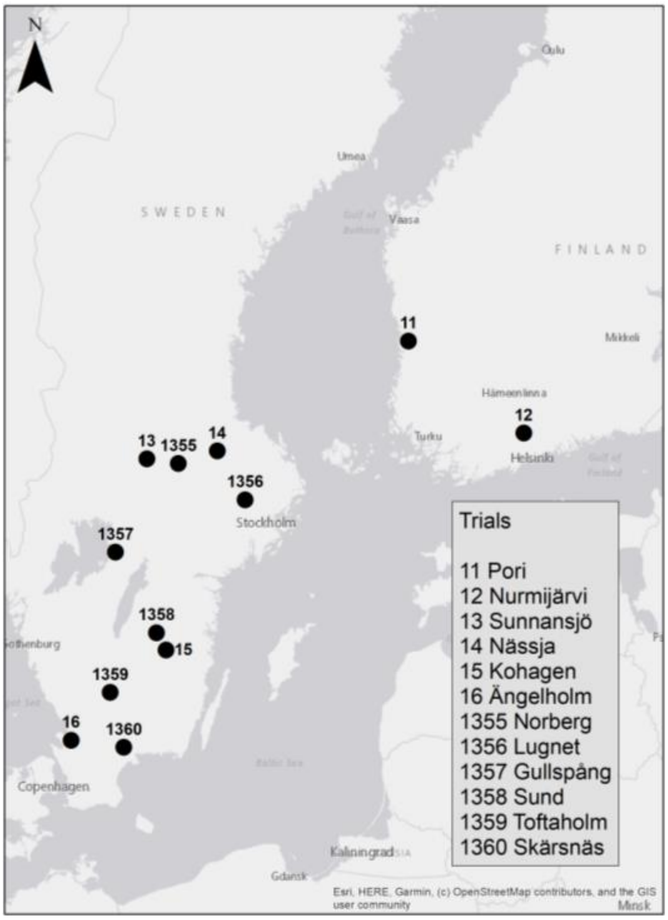

Figure 2 –Location of all trials used in Paper I, II and III.

In Paper I, six trials in southern Sweden were studied (1355 Norberg, 1356 Lugnet, 1357 Gullspång, 1358 Sund, 1359 Toftaholm and 1360 Skärsnäs, from here on only referred to as numbers), which were planted 2002. In Paper II, three of the six trials where the date of bud burst assessment was included were used, i.e., trials 1358, 1359 and 1360. All trials were planted with two-year seedlings and with randomized incomplete block design with single tree plots. The genetic material in the trial series consisted of 50 seed sources, where each seed source constitutes of a bulk seed collected from a number of trees or individuals in either a natural stand or in a seed orchard. The material was divided into five groups based on the origin of the seed. The groups, type of progenies and the number of seed sources within each group were as follows:
SweEast - Swedish stands of documented Eastern European origin, 20
SweS - indigenous Swedish stands, 6
EastS - indigenous Eastern European stands, 12
SweSO - Swedish seed orchards, 6
EastSO - Eastern European seed orchards, 6

All five groups of seed sources were used in Paper I while Paper II only involved SweS and EastS.

For the SweEast group, the seeds used are open-pollinated seeds from East European trees planted in Sweden (second generation material).

In Paper III, four field trials in Sweden (13-Sunnansjö, 14-Nässja, 15- Kohagen, 16-Ängelholm, from here on only referred to as the name) and two trials in Finland were used (11-Pori and 12-Nurmijärvi, from here on only referred to as the name) (

Figure 2). The trials Nässja and Sunnansjö were established 2013 with 57 full-sib families while Ängelholm and Kohagen were established 2014 with 84 and 85 full-sib families, respectively. The full-sib families originated from crosses between phenotypically selected plus trees in Sweden within the spruce breeding program. Pori was established in 2011 and Nurmijärvi in 2012 and comprised of second generation candidates phenotypically selected within open-pollinated families of 98 plus-trees in two young progeny trials in southern Finland. The Swedish trials were randomized incomplete block design using single-tree plot, while the Finnish were randomized complete block design using single-tree plot.

In Paper IV, ten clones of different origins were selected for the study among a larger number of clones available in the nursery at Ekebo. All clones had originally been propagated as rooted cuttings from seedlings in the year of 2006 originating from seedlings of either Romanian, Polish or Swedish origin or from seedlings of second generation west European origin growing in Sweden. Seedlings from three different seed sources from Sweden, Latvia and Estonia, respectively, were chosen as a reference material. Around 50 plants per variety were randomly distributed to eight different treatments.

3.2 Treatments

In Paper IV, the plant material consisting of clones and seedlings was divided into eight different treatments according to Figure 3. In all treatments three time slots (A, B and C) had been determined beforehand by which all plants were assessed, and needle samples were collected. Treatment 1 was considered to be a control treatment and the plants were thus kept in ambient temperatures conditions outdoor during the whole experiment. In treatment 2 and 3 the temperatures in the greenhouses were set at two different temperatures levels, 5 and 15 degrees, and the plants were kept there during the entire study period. In treatment 4-8 the plants were moved from ambient temperatures conditions outdoor into the greenhouses with temperature levels of 5 and 15 degrees (i.e. treatment 2 and 3) during four weeks within the time slots A, B or C. Afterwards they were moved back to ambient temperatures conditions outdoor.

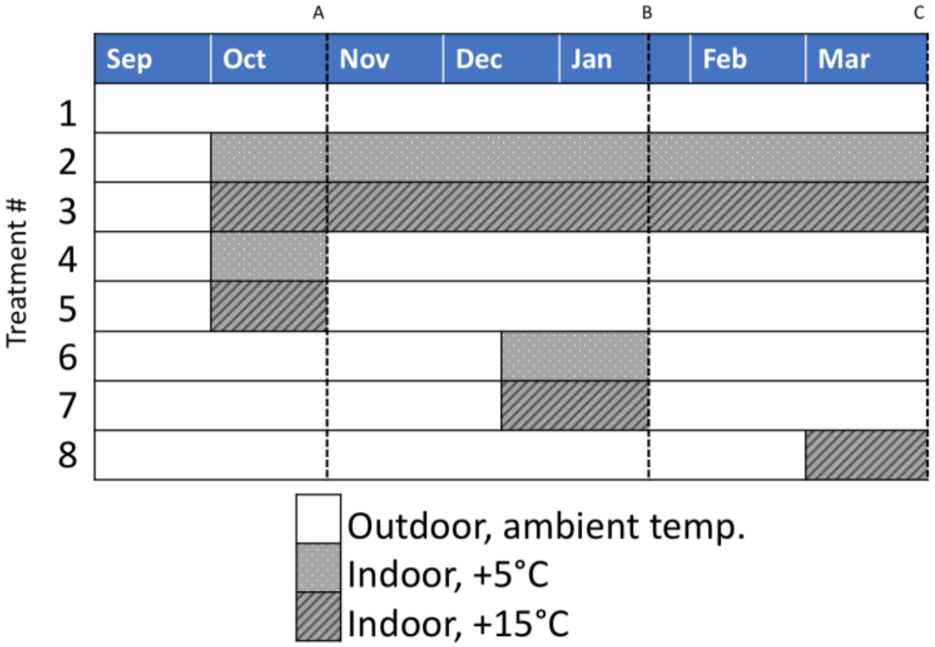

Figure 3– The eight different treatments included in Paper IV. Treatment 1 was outdoor during the whole experiment while the other treatments were indoor during some part of the experiment. At three different times (A, B and C) needles were collected.

3.3 Summary of traits studied

3.3.1 Height

The tree height (H) was measured in all the papers but at different ages depending on the study.

In the trials in Paper I and II the height was measured at age seven and 14 years, H7 and H14. For Paper III the height was measured at ages 3-6 in Sunnansjö and Nässja, at ages 2-5 in Kohagen and Ängelholm. In Pori at ages 6-8 and in Nurmijärvi at ages 5-7. For this study the height (Tot-Ht) each year was used but also the height increment growth (Ht) for the years 2017, 2018 and 2019 (Figure 4).

In Paper IV the height was measured at age 4.

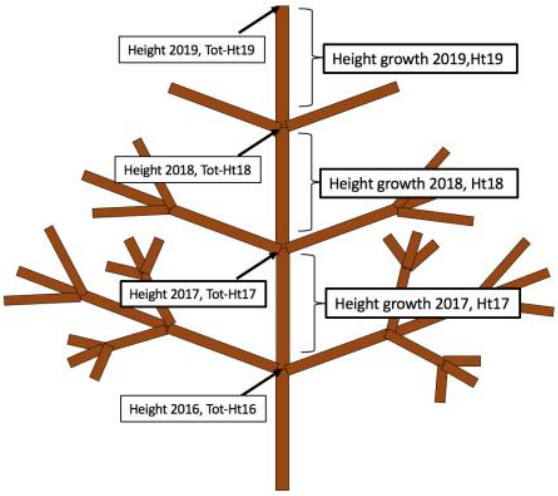

Figure 4 – An illustration of the height measurements and height growth from Paper III.

3.3.2 Diameter at breast height

Diameter at breast height (DBH) was measured at age 14 in the trials from Paper I and II.

3.3.3 Bud burst and Lignification

Bud burst (BB) was assessed at one timepoint in Paper I and II according to the so called Krutzsch scale (Krutzsch, 1973), where stage 0 is a resting bud, stage 3 was set as bud burst, and stage 8 is when new buds are sprouting and needles spreading. BB was measured at the age four in the trials from Paper I and II. In Paper III, BB was assessed as a binary trait 1/0 during several weeks.

Lignification (L) at age 5 were addressed in Paper I, where the percentage of the top shoot that was brown due to lignification was scored with score classes of 10 from 0-100.

3.3.4 Frost damage

In the trials in Paper I and II, frost injuries (F) were assessed in the spring at age four, which where after two years in the field. The trees were assessed on how severe the damage was on a scale from 0 (undamaged), 1 (at least 30% of the shoots were brown/dying), 2 (moderately damaged), and 3 (severely damaged) but was combined to a binary scale where trees scored 1-3 were set as damaged (1) and scored 0 were set as undamaged (0), to be able to calculate the percentage of trees damaged by frost.

In Paper IV freezing was performed on the needles at age 3 and frost damaged (FD) were assessed from 1 (healthy) to 4 (dead). Also, the physiological status (FS) of the needles before and after freezing was assessed at age 4 with chlorophyll fluorescence (Fv/Fm).

3.3.5 Tree survival ability

The survival was scored in the trials from Paper I and II at ages 4, 7 and 14, and in Paper IV at ages 3 and 4, where a binary scale was used 1/0 (alive/dead).

3.3.6 Shoot growth patterns

In the study in Paper IV different measurement on shoot growth was performed. The length of the annual top shoot (TS) and total height growth during the current year (HG) was measured at age 3 and 4. Also prolepsis (P) (the length of a late summer shoot with proleptic growth) and free growth (FG) (occurrence of late summer shoots with sylleptic growth) and the longest late summer lateral shoot were measured at age 3 and 4. The number of shoots that were longer than 8 cm, as a hypothetical proxy for sylleptic growth, was counted at age 3 and 4.

All traits addressed in this thesis and their age of assessment as well as the study and field trial in which they were measured are summarized in Table 2 and are defined on the next page.

Table 2 – Traits assessed and their abbreviation, the age of assessment and trial and paper for which they were assessed.

Trait	Abbreviation		Age of assessment	Paper/Trial
Tree height	H	mm	3-6, 7, 14	I,II,III,IV/1355-1360, 11-16
Diameter at breast height	DBH	mm	14	I,II/1355-1360
Bud burst	BB	0-8	4	I,II/1355-1360
Frost injuries	F	1/0	4	I,II/1355-1360
Lignification	L	%	5	I,II/1355-1360
Survival	S	1/0	4, 7, 14	I,II,IV/1355-1360
Bud burst	BB	1/0	3, 4	IV
Top shoot	TS	mm	3, 4	IV
Height growth	HG	mm	3, 4	IV
Prolepsis	P	mm	3, 4	IV
Free growth	FG	mm	3, 4	IV
No. of shoots	NoS	count	3, 4	IV
Longest lateral shoot	LS	mm	3, 4	IV
Frost damage	FD	1-4	3	IV
Frost status	FS	Fv/Fm	4	IV

3.4 Climate data

In Paper II climate data for the period 1989-2100 were extracted from three different data sets from CORDEX project with a spatial resolution of 0.11-degree latitude/longitude in a rotated pole grid representing the concentration pathway RCP8.5. To be able to compare different time periods the climate model data was split into three periods: 1989-2018 (reference period), 2021-2050 (near future) and 2071-2100 (far future).

The gridded observed temperature data for the period 1989-2018 was derived from the European gridded observational dataset (E-OBS version 20e), with a spatial resolution of 0.1-degree regular latitude/longitude grid (Haylock *et al.*, 2008; Cornes *et al.*, 2018) and used as observed temperature conditions for the trials in Paper II. This was because none of the trials had temperature loggers, but to be able to discuss the differences between gridded data and local data, minimum and maximum temperatures were extracted from loggers in 10 sites. Each site had two temperature loggers, one at 0.5m and one at 1.8m. The temperature loggers check the temperature once every half-hour and then an average mean and minimum temperature for each site was calculated. For the comparison of gridded observed temperature data with the logger temperature data, Cumulative Density Functions (CDFs) were created for January to June. The CDF were then rescaled to match each other, then ranked and plotted against relative temperature (mean or minimum) for easy visualisation. This method was developed for bias correction and provides a non-linear comparison of systematic differences between data sets (Brocca *et al.*, 2011; Drusch *et al.*, 2005).

3.5 Climate change impact assessment

In Paper II the temperature sum (TS) needed for bud burst was calculated as an accumulation of daily mean temperature above 5ºC with January 1st as starting day. This threshold value is according to Hannerz, 1999 the best for predicting the timing of bud burst in Norway spruce in Sweden.

For the analysis in Paper II the date of bud burst was needed and only some of the trees were in stage 3 (bud burst) when assessment in the field was performed. That is why the date of bud burst had to be calculated for all the other bud development stages. To do so the temperature sum requirement per stage for bud development was derived from the slope of the regression line of bud development stages 2-6 versus temperature sum (Hannerz, 1999). From the slope an average value of 40 growing degree days (GDD) per stage was derived, and this was added to the temperature sum of trees with lower bud burst stage than 3 and extracted from trees with higher bud burst stage than 3 so that all trees had a bud burst date.

A fulfilled chilling requirement is often important for the buds to burst and in Paper II the chilling days and number of chilling units were calculated to know that the trees had been exposed to sufficient chilling before January 1st. The number of chilling days (CD) was calculated as the number of days with a mean temperature below

+5°C (Cannell & Smith, 1983). The number of chilling units (CU) was calculated according to the triangular function by Sarvas, 1974.

Around 20-40 chilling days or chilling units is enough for Norway spruce provenances (Hannerz, 1998; Hannerz *et al.*, 2003; Hänninen, 1996), where northern Swedish provenances have lower chilling requirements than southern Swedish provenances and Belarus provenances has higher (Hannerz *et al.*, 2003).

In Paper II the site-specific frost risk, number of frost events and frost severity were calculated. The frost risk was calculated by the average number of frost days per year between 1989-2018 with thresholds -2ºC (to represent the temperature at which plant cells start to freeze (Jönsson *et al.*, 2004)) and 0 ºC for comparison. The number of frost events after bud burst was calculated for each provenance, and frost severity was calculated for each individual tree as the number of frost events between bud burst and frost damage, as well as the lowest minimum temperature.

To be able to visualise the result in Paper II, model simulations of the three different time periods (reference period, near future and far future) was performed and maps were created, where the impact of warmer climate conditions on each provenance was presented. In this thesis, only model simulations from two provenances, Ängelsfors2 and Minsk will be shown, representing Swedish and East European groups, respectively, but all the model simulations can be found in Paper II Appendix C.1§

3.6 Statistical analysis

3.6.1 Prior adjustments

Prior any analysis the data for all papers was assessed, and quality checked. In the trials addressed in Paper I and II a post-blocking procedure was performed to take into account the large-scale environmental variation (Ericsson, 1997). To linearize the binary variables (BB, F and L), normal scored transformation with mean zero and standard deviation one was performed (Gianola & Norton, 1981) in Paper I.

3.6.2 Spatial analysis

In Paper I, II and III, spatial analysis was used before analysis to adjust the data for within-trial environmental effects. A single trait spatial analysis based on a two-dimensional separable autoregressive (AR1) model was performed where first a model with only the experimental design feature and independent error were fitted. If the residuals were non-randomly distributed a second model was used. In this model the residual variances were separated into an independent component and a two dimensional spatially auto-correlated component (Dutkowski *et al.*, 2006; Dutkowski *et al.*, 2002; Gilmour, 1997)

3.6.3 Models used

In Paper I the statistical model used for single site analysis for each trial was:

$$Y_{ij} = \mu + G_i + FG_{ij} + E_{ij} \text{ (i)}$$

where Y_{ij} is the value of tree *ij*, μ is the average of the trial, *G* is the effect of the group (i=1,2,…5), *FG* is the effect of every seed source (*j*) in the group (*i*) and E is a random residual. All effects except the residual were considered to be fixed.

While the statistical model used for multi-site analysis of all the trials in Paper I was:

$$Y_{ijk} = \mu + G_i + FG_{ij} + T_k + T_k * FG_{ij} + T_k * G_i + E_{ijk} \text{ (ii)}$$

where Y_{ijk} is the value of tree *ijk*, μ is the average of the trial, *G* is the effect of the group (*i*), *FG* is the effect of every seed source (*j*) in the group (*i*), *T* is the effect of the trial (*k*), *T*FG* is the effect of every seed source (*j*) in the group (*i*) by environment (*T*), *T*G* is the effect of the group (*i*) by environment (*T*) and *E* is a random residual. *G* and *FG* were considered to be fixed, while the other variables were considered to be random.

In Paper IV the model used for the analysis of each trait was:

$$Y_{ij} = \mu + T_i + IT_{ij} + E_{ij} \ (iii)$$

where Y_{ij} is the value of plant ij, μ is the average of the study, T is the effect of treatment (i=1, 2, …8), IT if the effect of every identity (j) in the treatment (i) and E is a random residual. All effects except the residual were considered to be fixed.

In Paper IV the model used for the analysis of each trait was:

$$Y_{ij} = \mu + T_i + IT_{ij} + E_{ij} \ (iii)$$

where Y_{ij} is the value of plant ij, μ is the average of the study, T is the effect of treatment (i=1, 2, …8), IT if the effect of every identity (j) in the treatment (i) and E is a random residual. All effects except the residual were considered to be fixed.

To estimate additive, and non-additive genetic variance components in Paper III at each trial the following general linear mixed model for the trials with full-sib families was used:

$$y_s = xb + z_1u + z_1f + z_3c + e \ (iv)$$

where, $y_s$is the vector of adjusted observations of total height or height increment (HTV); b is a vector of fixed effects including site means, u is a vector of random additive genetic effects of individual genotypes; f is a vector of random effects of full-sib family; c is a vector of random effects of clones within full-sib families; and e is a vector of random residual terms. X, Z1, Z2, and Z3 are incidence matrices relating the observations in y to b, u, f, and c, respectively.

For the trials with half-sib families, the following general linear mixed model was used as:

$$y_s = xb + z_1u + z_3c + e \ (v)$$

where all variables are as described above except c, which here is a vector of random effects of clones within half-sib families.

3.6.4 Quantitative genetics

Additive genetic correlation between traits (type-A, r_A) and additive genetic correlation between pairs of sites (type-B, representative of GxE, r_B) were calculated as:

$$r_A = \frac{Cov_{(x,y)}}{\sqrt{\sigma_x^2 \times \sigma_y^2}} \quad \text{(vi)} \qquad\qquad r_B = \frac{Cov_{(x1,x2)}}{\sqrt{\sigma_{x1}^2 \times \sigma_{x2}^2}} \quad \text{(vii)}$$

3.6.5 Other statistical analysis used

For pair-wise comparison between groups/treatments TUKEY/Kramer (Proc Mixed, SAS Institute Inc, 2011) was used in study I and IV.

In Paper II two-way analysis of variance (ANOVA) in R (R core Team, 2020) was used to compare the absolute temperature sum requirements of the individual trees, the effects of field site, provenance and block. ANOVA was also used for the test of significance of difference in height between frost-damaged and non-damaged trees and between the groups of Swedish and East European provenances at an individual tree level.

To evaluate the relationship between frost damage and exposure to the lowest minimum temperature in Paper II during the frost susceptible period, the Pearson's correlation was used.

3.6.6 Statistical software

Statistical softwares used were ASReml 3.0 (Gilmour *et al.*, 2009), ASReml 4.0 (Gilmour *et al.*, 2015), R version 3.6.3 (R core Team, 2020) and SAS 9.4 (SAS Institute Inc, 2011).

3.7 Drought index

For Paper III a drought index was calculated to know the severity of the drought the years 2009-2019, but especially the year of 2018 when a severe drought occurred. Using the daily precipitation, maximum and minimum temperatures extracted from the closest station to the trials from climate databases (Sweden - https://www.smhi.se, Finland - (https://en.ilmatieteenlaitos.fi/), a monthly average was calculated for the temperatures and a monthly sum for the precipitation. Using the R package SPEI (Vicente-Serrano *et al*., 2014), the SPEI was calculated on monthly average for the months May to July and the average of the months each year represented the SPEI for that year.

4. Results and discussion

4.1 Comparing contemporary Norway spruce seed sources (Paper I)

The climate will change in the future with an increase in air temperature and longer vegetation periods (IPCC, 2013). Even if the temperature gets warmer during spring, the risk of more frequent temperature backlashes will increase and with it the risk of frost damage to newly sprouted shoots (Langvall 2011). To be able to counteract this risk, provenances with later bud burst need to be considered in the deployment strategies, especially at frost prone sites. However, the supply of improved seeds from seed orchards is limited. To be able to get a higher genetic gain compared to local trees, other seed sources need to be evaluated and the information on which seed sources to use needs to increase.

4.1.1 Second generation material

In the study in Paper I the objectives were to investigate if second generation material that already exists in Sweden (SweEast) could be used to meet the demand of seeds with higher genetic gain in growth, but also how it compares to seed orchard material from Sweden and Eastern Europe. The growth results showed that trees from SweEast were on average taller than trees from SweS, but trees from SweSO and EastSO were on average the tallest and widest (Table 3). Compared to SweS, the genetic gain (higher expected performance) in growth (H7 and DBH14) for SweSO was 11-14.6%, 9% for

EastSO, 6-7% for EastS and 5-7% for SweEast. All of the groups had higher genetic gain than SweS.

Table 3 - Least Square average of the traits Diameter at breast height (DBH) and Height (H7) and their standard errors (SE) with pairwise comparisons between all the groups (Different letters in the sig. columns indicate significant differences for the pairwise comparisons).

Group/Trait	DBH	SE	Sig.	H7	SE	Sig.
SweSO	73.02	4.79	A	203.52	22.19	A
EastSO	69.45	4.78	AB	200.20	22.19	AB
SweEast	68.34	4.75	B	192.52	22.14	AB
EastS	67.62	4.76	B	195.33	22.15	B
SweS	63.69	4.78	C	183.25	22.18	C

If we look at the bud burst during spring, a significant difference could be seen between the Swedish material (SweSO and SweS) compared to the East European material (EastSO and EastS) in all the trials, and the SweEast was closer in timing of bud burst to the Swedish material than the material from Eastern Europe (Paper I, Table 5). The Swedish material had progressed more in the bud burst at the time of assessment. On average the SweS had a bud burst score of 5, SweEast 4.7, SweSO 4.6, EastSO 3.4 and EastS 3.3. The bud burst showed that SweEast is much closer to SweS and SweSO than an average of EastS and SweS. This suggests that different variables might be involved other than pollen from trees surrounding the SweEast. The SweEast are from seeds collected from Swedish stands with East European origin, where the trees are open pollinated by the surrounding stands that are Swedish. The fact that the height in SweEast and EastS were not significantly different from each other indicates that the pollen should not have been from external sources. Even if the origin of the SweEast group and the East European material is not completely the same, the bud burst is expected to be similar for both groups. There can be several explanations as to why the SweEast are closer to the Swedish material in respect to bud burst but not growth. For example, if mortality would have been high, individual trees that were not adapted would probably be dead and influence from natural regeneration in the final stand would have been higher, but in our study the mortality of SweEast was low.

Another explanation could have been that seedlings from the surrounding indigenous stands could have been naturally regenerated within our trial, but these trees should have been shorter and removed by thinning or died by competition. Overall, what probably happened in our study was formation of land race, were the SweEast already after one generation had adapted to the Swedish climate more than expected with respect to bud burst. This effect has been reported by Skrøppa and Steffenrem (2016), where the environment of deployment of the seeds affects the trees phenological traits more than the growth traits (Skrøppa et al., 2009).

For the lignification, a similar pattern as for the bud burst was seen where the Swedish material had progressed significantly longer in growth cessation compared to East European material. This indicates that material with East European origin can suffer from more autumn frost, but this risk is low in the south of Sweden (Langlet, 1960; Skrøppa and Magnussen, 1993).

When compiling all the informatin from the study in Paper I the second generation material is a good choice in case of shortage of improved seeds, but it is important to note that the later bud burst the East European provenances show is not transmitted to the second generation in Sweden. Thus, seeds with East European origin is a better choice on frost prone sites, or material from Sweden that has later bud burst.

4.1.2 Genotype-by-environment (G x E)

To be able to detect the degree and pattern of genetic variation between the same trait in different environments several methods can been used (Skrøppa, 1984). Usually the type-B genetic correlation is used in breeding studies (Burdon, 1977), but to be able to use the method, a pedigree with all the information about the parents is preferred and also the material used has to be related (full-sib or half-sib).

For the material in Paper I, we did not have the complete pedigree and the material is not related. We only wanted to know how the different groups performed in the six different trials (the interactions) and to see if the traits are on average ranked the same in all the trials. To do so, a ranking from the least square means was performed on each trial for each trait (See Paper I Appendix A). Overall, the same group was ranked similar for all the traits in all the trials and only some small variations could be seen. It was not only the variation between the groups that was interesting, but the variation within the groups as well. To be able to visualise this, the seed sources were ranked in the same way as the groups (See Paper I, Appendix B). The variation was overall low and seed sources were ranked similar in all the trials, but there were some seed sources that ranked different compared to the others in the same group, indicating that some seed sources may behave differently in different sites. One explanation for this can be that the division of the groups are not perfect, for example some part of the East European material is from Poland while the rest is from Estonia, Latvia, Lithuania and Belarus. Another explanation can be that the northern trials are in one seed zone, while the southern trials are in another, and some of the trials are on frost prone sites (Berlin et al., 2015).

The study in Paper I indicates that it is important to select from the correct group, but it is also important to check the different seed sources within the group and select the best choice for your site. For this to work a deployment strategy needs to be implemented with information about the behaviour of different provenances in different sites. This will be more difficult in the future with the climate change and higher temperatures, which in turn increases the need for assisted migration, where trees with desirable properties are moved from one place to another (Koralewski et al., 2015; Williams & Dumroese, 2013).

4.2 Temperature impact on Norway spruce (Paper I, II and IV)

How temperature will affect Norway spruce in the future was assessed in Paper I, II and IV. In paper I, cold temperature during spring resulted in frost damage, while in Paper II model simulations of different Norway spruce provenances were performed and the impact of warmer springs with temperature backlashes was analysed. In Paper IV the impact of warmer temperatures during autumn, winter and spring was investigated.

4.2.1 Chilling and temperature sum

During the resting phase in winter the trees are in dormancy, and to break it they need to get sufficient chilling. The chilling requirements for the sites 1358, 1359 and 1360 were met by the beginning of December (Paper II), and therefore the trees were in quiescent in the beginning of the year. Also, in the model simulations, the chilling requirement will be met in the near and far future. This indicates that the trees from the study in Paper II will have sufficient chilling even in the future and will be able to bud burst during spring.

4.2.2 Climate change impact assessment

For the future climate change impact assessment, the RCP8.5 concentration pathway was used. This is the most extreme future scenario, which was used because we wanted to know what could happens in worst case scenario, but similar temperature changes are expected in the scenarios RCP4.5 and 6.0 for the near future.

Bud burst

During the reference period (1989-2018) the bud burst occurred in May and June, following a latitudinal gradient (Paper II, Fig. 9a). For the two provenances Ängelsfors2 and Minsk, a decrease of days to bud burst could be seen in the near and far future (Figure 5). For the near future, the bud burst will occur an average of 10 days earlier, whereas in the far future the bud burst will occur around 30 days earlier in southern Sweden. Along the western coast up to 60 days earlier bud burst will occur (Paper II, Appendix C). This is similar to the study from Olsson *et al*. (2017). With earlier bud burst and more frost events, an increased risk for frost damage during the spring will occur, especially for the south of Sweden.

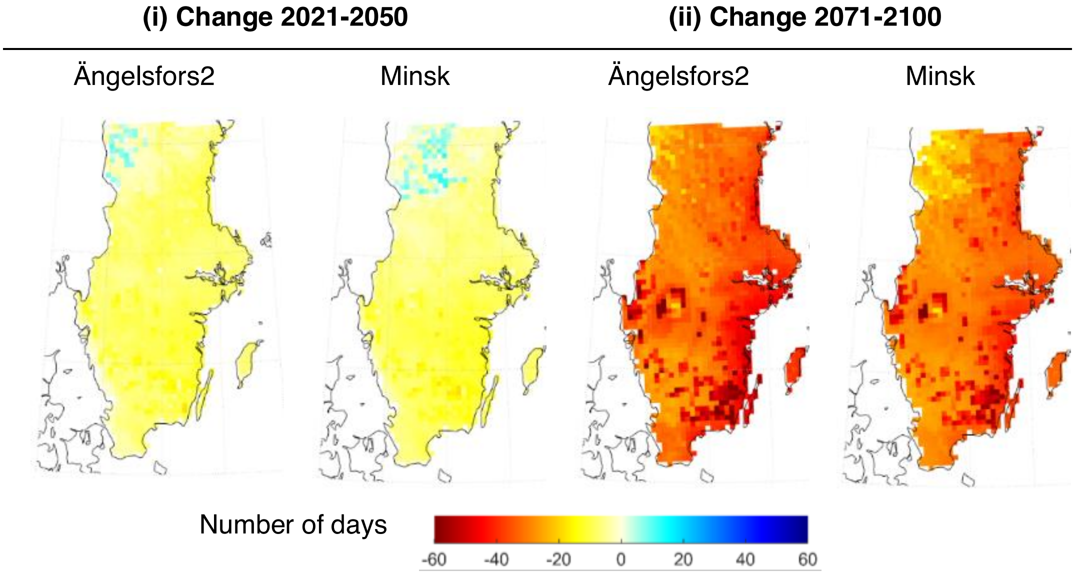

Figure 5 - The simulations are made for two contrasting Norway spruce provenances, using the climate model temperature data, for the differences (i) between 2021-2050 and 1989-2018, and (ii) between 2071-2100 and 1989-2018 for the number of days to bud burst.

Frost days and chilling days

During the reference period (1989-2018) an increase in number of frost days between January 1st and June 29th along the latitudinal gradient of Sweden could be seen (Paper II, Fig. 7), while a decrease could be seen for the near and far future (Figure 6). In the near future the decrease was around 5-20 frost days per year while it was 15-50 days for the far future.

For the reference period the number of chilling days increased from the south to north, while in the future the chilling days will reduce (Paper II, Figure 8a). The south of Sweden will experience a higher reduction than the northern parts. Chilling units varied more both during the reference and future periods (Paper II, Figure 8b), where decrease was indicated in the south and increase was indicated in the north.

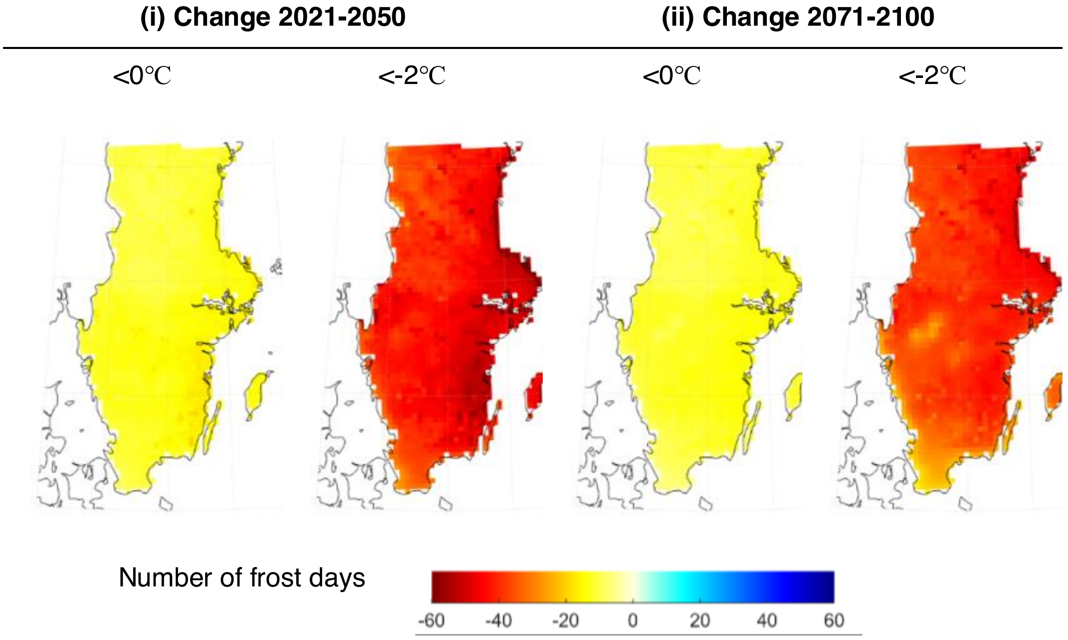

Figure 6 – The average number of frost days below 0°C and -2 °C per year. The calculations are made from January 1 till June 29, using climate model temperature data for the differences (i) between 2021-2050 and 1989-2018, and (ii) between 2071-2100 and 1989-2018.

Frost risk

The climate will change in the future and trees planted today will grow for around 60-90 years in the south of Sweden and encounter another climate than today. With a changing climate together with an increased risk of spring frost events, seed sources with frost avoidance and good performance in future climates need to be investigated. It is the growth rhythm that is important for Norway spruce and especially how the connection between bud burst and the risk of frost damage is affected by the climate change (Langvall, 2011).

In the study in Paper II, an investigation of the provenance specific timing of bud burst in relation to the risk of spring frost damage was performed. Together with the study of frost damage in Paper I, more information about how the spring frost can damage trees could be concluded.

During the spring of 2004, three trials suffered from spring frost damage: trial 1359 had 23% frost damage trees, 1357 had 6% and 1360 had 4% (Paper I). Studies has shown that earlier flushing trees will suffer from more frost damage (Hannerz, 1994; Jönsson &

Bärring, 2004; Prescher, 1982; Danusevicius & Persson, 1998) which was also confirmed by the studies in Paper I and II. In Paper II the average height of frost damaged trees was compared to non-damaged trees, were the non-damaged trees were taller on average. From Paper I, no significant differences were found between the different groups regarding spring frost damage, but the SweS had highest damage on average. When correlating bud burst to frost damage (Figure 7), an indication that seed sources that had come longer in bud burst during spring suffered more frost damage was perceived, a higher correlation was seen in trial 1359 than the other two, most probably due to the fact that the trial had on average more frost damage. In Paper II a correlation of exposure to lowest minimum temperature during frost susceptible period to occurrence of frost damage could be found, a higher correlation could be seen in trial 1359 than in trial1360. This shows the importance of selecting later flushing material for frost prone sites, since they will be more frost hardy in the spring. Also, provenances with lower temperature sums had on average higher percentage of frost damage because they were exposed to more frost events during the frost susceptible period.

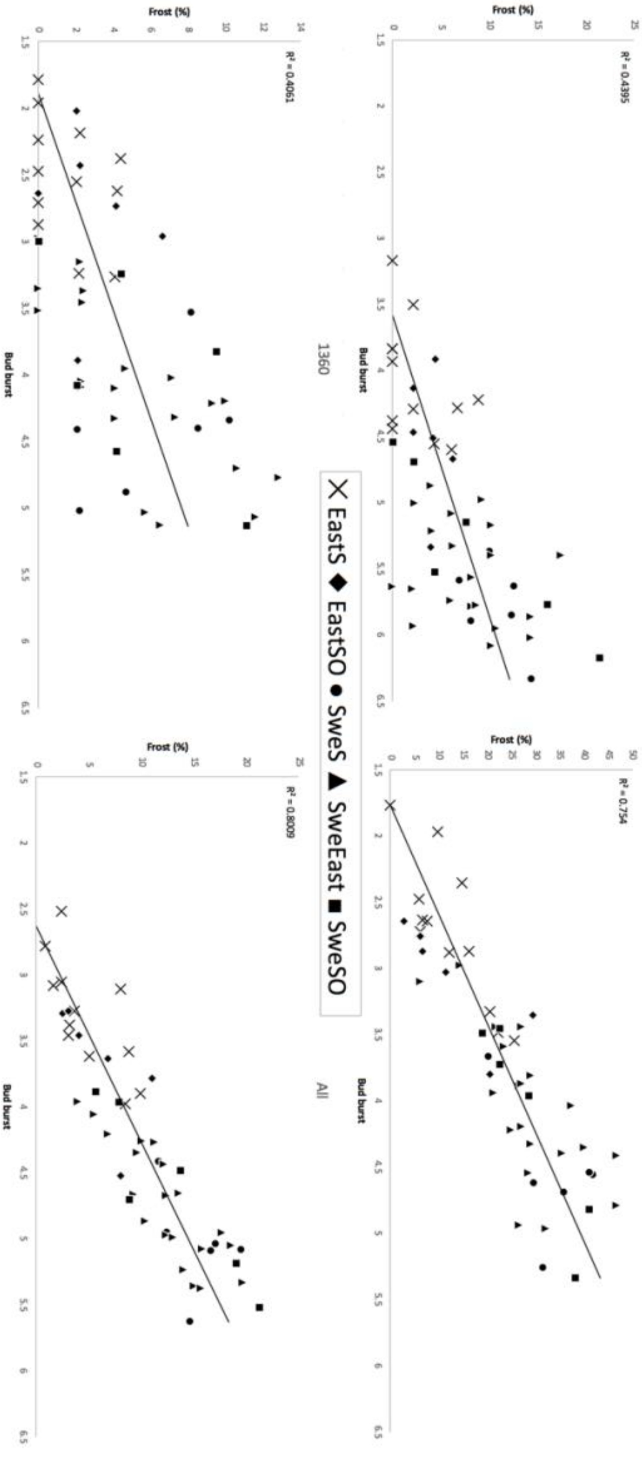

Figure 7– Bud burst versus frost damage for trials 1357 Gullspång, 1359 Toftaholm, 1360 Skärsnäs and these three together (all).

For the frost days at the sites 1358, 1359 and 1360 a decrease could be seen as the day of the year progressed and the accumulated temperature sum increased (Paper II, Fig.3). The trial 1359 had higher number of frost days and spring frost events compared to 1358 and 1360. For the period 1989-2018 the exposure to spring frost events was on average seven (Paper II, Fig. 9b), where northern provenances were exposed to more events compared to the southern provenances (Paper II, Appendix C). For the period of 2021-2050 and 2071-2100 an increase of spring frost events was indicated where for example the provenance Ängelsfors2 is expected to have more frost events in the future compared to Minsk (Figure 8). During the spring frost events, the north of Sweden had lower temperatures than the south of Sweden. In the future these events in the north of Sweden will have a higher minimum temperature and in the south of Sweden they will have a lower minimum temperature. Together with the earlier bud burst, all Norway spruce provenances studied will experience an increased risk of frost damage (Paper II, Appendix C).

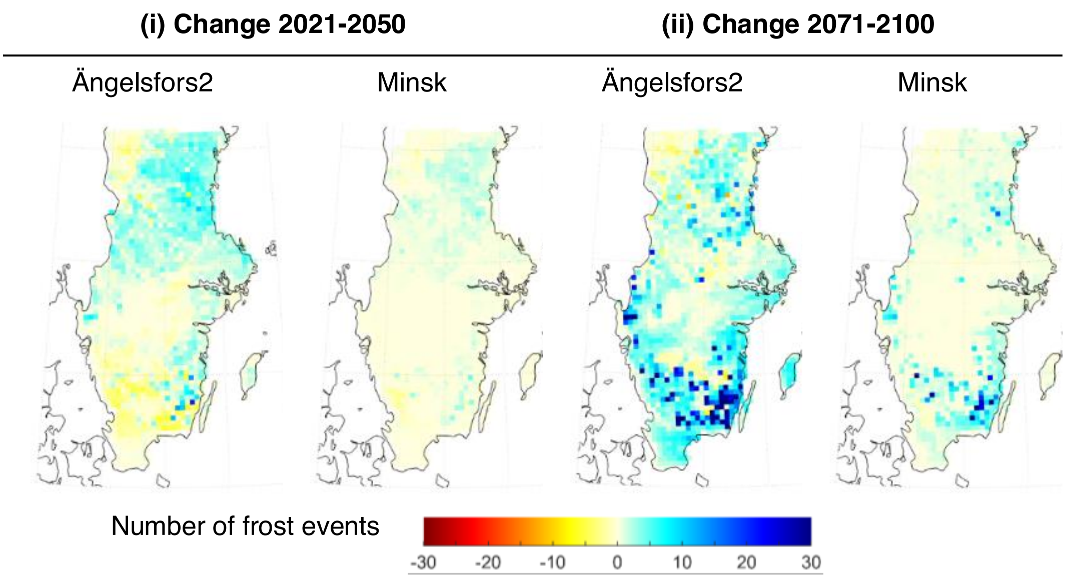

Figure 8 - The simulations are made for two contrasting Norway spruce provenances, using the climate model temperature data, for the differences (i) between 2021-2050 and 1989-2018, and (ii) between 2071-2100 and 1989-2018 for the cumulative number of spring frost events with the threshold of -2ºC calculated from the day of bud burst to June 29.

To conclude the finding about spring frost; (i) spring frost events are usually site specific and affect some sites more than others, (ii) earlier flushing trees will suffer from more spring frost damage, (iii) the spring frost events will probably increase. Overall, this indicates that some sites are more frost prone and will experience more frost events than other sites, but also that the south of Sweden will experience colder spring frost events in the future. This in turn will lead to more frost damage to the trees if they are not adapted for the site. That is why a deployment recommendation like Planters guide (Plantval) (Skogforsk, 2020) for frost prone sites and for sites that in the future will experience more frost events needs to be included in the recommendations that are used today to get information about which seed sources to use where. For a robust deployment strategy, the recommendation should be based on the near future due to the high uncertainties of future projections, but most of all because it is the seedlings that are most susceptible to frost damage, not the grown trees.

4.2.3 Gridded versus logger temperature data

In Paper II temperature data was not available, so gridded temperature data was used instead. One part of that study was to compare gridded temperature data and logger data for an indication if the gridded data is possible to use.

The results show that the gridded data is almost the same for the mean temperature at all sites studied, but for the minimum temperature an overestimation could be seen (Paper II, Appendix B), which indicates that gridded temperature data can be used if a good estimate of mean temperature is required. The overestimation of minimum temperature was greatest when comparing the temperature with the 0.5 m logger compared to the 1.8 m logger which can be seen in one example in Figure 9 but it was similar in the rest of the sites (Paper II, Appendix B). The gridded data gave higher minimum temperature on average compared to the logger data. In the study, results from January to June were shown because that is the period of interest, but the same trends could be seen from July to December. One explanation for the overestimation is that gridded data has other properties than temperature data, it in general has lower variability and fewer extremes (Director & Bornn, 2015), which has to be considered when using the data. The overestimation of minimum temperature was also indicated for the climate model data, were the number of frost days differed when calculating with climate model data (Paper II, Table C1) compared to E-OBS data (Paper II, Fig. 3a.). When interpreting the results from the models using minimum temperature from gridded data, some extra information has to be added, where for example the young and short seedlings experienced lower temperature than the model output and the frequency of frost events was even higher than calculated. All things considered, gridded data can be used, but depending on where the information will be used some extra effort needs to be put into analysis the results. For example, if the data is used for estimating the frost risk in deployment recommendation, there is a possibility that the actual frost risk is higher than estimated for smaller plants. This can be solved by weighing the risk for frost a little higher than estimated.

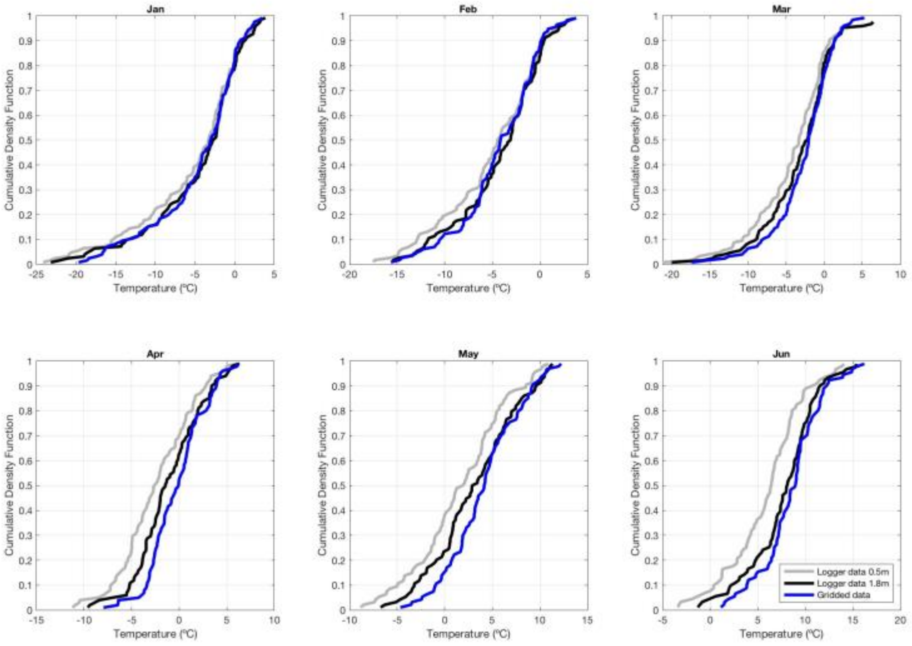

Figure 9 – Cumulative density function for minimum temperature for January to June at one of the sites in the study of gridded temperature data versus logger temperature data (One logger at 0.5 m and one at 1.8m).

4.2.4 The impact of warmer temperatures during winter

Bud burst

In Paper IV the warm temperature in March, +15°C (treatment 8), resulted in a significantly earlier bud burst compared to the other treatments, where 93% of the plants already had bud burst at day number 101 in 2011 and 100% had bud burst at that day in 2012. At the same time, in the year of 2011 only 28% from treatment 3 had bud burst and 8% from treatment 2, while the other treatments did not have any plants that had bud burst. In the year 2012, 78% of the plants from treatment 3 had bud burst, 52% from treatment 7 and 32% from treatment 2, while the other treatment did not have any plants that had bud burst (Paper IV, Figure 2 and 3). This is an indication that warmer temperature can indeed affect the bud burst so that it occurs earlier, especially if temperatures are warmer during the whole winter, but also if it is warmer during March (the beginning of spring). Other studies have shown that even if it is the temperature in spring that is the main driving force for bud burst, the timing can be significantly modified by the temperature conditions during bud set and bud maturation (Granhus *et al.*, 2009).

The earlier bud burst would also imply a higher risk of spring frost damages in frost prone sites (Hannerz, 1994; Jönsson & Bärring, 2004). In one of the years, the plants that had been indoors in December in +15ºC also had an earlier bud burst, indicating that warmer temperatures during winter may affect the bud burst, maybe since the plant remembers the warmer temperature and responds more easily to favourable temperature conditions. The results also show that intermittent warm temperatures in autumn and winter (+5/15°C in October or +5°C in December) do not induce earlier bud burst compared to the control. The bud burst for treatment 3 started first of all the treatments but trees from treatment 8 were faster at completing the bud burst. This may be an indication that it is the winter (i.e. February) or early spring temperatures, rather than autumn or winter temperatures per se, that are important for early bud burst. Some studies have shown that high temperatures in autumn can delay the bud burst (Heide, 1974, Søgaard *et al.*, 2008).

In the study in Paper IV information about the growth, needle hardiness and shoot growth patterns were also assessed to get information about how warmer climate will affect these traits.

Growth and shoot growth patterns

The initial height and length of the shoots were similar for all the treatments before the experiment and at least 90% of the trees were alive in the year of 2012 (Paper IV, Table 4).

The tallest plants on average were found in treatment 5, 4 and 1 (Table 4). The shortest plants on average were found in treatment 3, 8, 7 and 2, where each of them was significant different from all of the other treatments. Trees from treatment 1,4,5 and 6 had the longest top shoots and highest shoot height growth (Paper IV, Table 5). In 2011, treatment 2 had a height growth not significantly different from the top three but the height growth in 2012 was poor. A comparison between the different treatments and the control (treatment 1) show that the heat did not significantly increase the growth.

Warmer temperatures during October may induce shoot growth as indicated by the tendency for treatment 4 and 5 to have longer shoots compared to treatment 1, however such difference was not significant. One possible explanation for this could be that the apical meristems are still active in October and forming the next year bud, and the heat mostly affect bud development

The shortest height and height growth of the shoots and top shoot growth were from treatment 3 and 8 (Paper IV, Table 5), which suggests that warmer temperature during the entire winter and early in the spring may cause decreased growth. If trees are exposed to high temperatures and weak photosynthesis for a long time, the respiration will be high, and the low assimilation will deplete the stored reserves and gradually weaken the plants. Another explanation can be that the earlier bud burst causes more spring frost damage which result in decreased growth.

Table 4 – Average height (cm) in 2012 (H2) with standard errors (SE) (In sig. column: different letters indicate significant differences).

Treatment	H2 (cm)	n	SE	Sig.
1. Outdoor	146.2	79	2.0	AB
2. Indoor, +5°C	134.9	70	2.2	C
3. Indoor, +15°C	76.1	59	2.4	D
4. Oct. Indoor, +5°C	149.7	77	2.0	AB
5. Oct. Indoor, +15°C	152.1	73	2.2	A
6. Dec. Indoor, +5°C	141.9	78	2.0	BC
7. Dec. Indoor, +15°C	112.1	77	2.0	E
8. March Indoor, +15°C	86.0	75	2.2	F

The longest proleptic late summer shoots (P1 and P2) were found in treatment 2 but in 2012 also treatment 7 had long proleptic shoots (Paper IV, Table 6). In 2011, the longest sylleptic late summer shoots were found in treatment 8 (Paper IV, Table 6) but the year after the sylleptic growth was small and of little significant importance. One reason to why treatment 8 did not have sylleptic growth the second year could have been the natural frost damage that occurred during the spring that year and affected treatment 8 more than the others because it had come longer in the bud burst.

As sylleptic growth was mainly formed in treatment 8 it suggested that sylleptic growth, thus without an initial stage of bud scale formation, requires a high availability of assimilates. It is likely that type of shoot growth, how much and for how long is dependent on the availability of assimilates. When the apical shoot starts to elongate, and cell differentiation takes place assimilates are primarily needed there and thus further formation of proleptic/sylleptic growth ceases.

The average number of shoots longer than 8 cm (NoS1 and NoS2) and the longest on average lateral shoots (LS1 and LS2) in both of the years were greatest in treatment 2, but treatment 5 was non significantly different from treatment 2 in NoS2 and treatment 7 was non significantly different from treatment 2 in LS2 (Paper IV, Table 7). This indicates that trees in warmer climate have a prolonged growth of shoots. Another conclusion is that accounting the number of shoots is an indication of proleptic growth rather than sylleptic free growth.

Cold hardiness

If trees experience fluctuating temperatures during winter the cold hardiness can decrease and in our results plants that had been indoor in March (treatment 8) experienced most freeze damaged on average after the freezing test performed on needles collected in February and April (Paper IV, Table 9 and 10). Treatment 8 also had highest difference of Fv/Fm after the freezing performed on needles collected in April (Paper IV, Table 13). This is probably since these trees had earlier bud burst and started the growth earlier, which in turn makes the needles less cold tolerant (Danusevicius & Persson, 1998; Hannerz, 1994).

Needles collected in November from plants that had been indoor in +15ºC (treatment 3) experienced on average most frost damage (Paper IV, Table 8), indicating that warmer temperatures during autumn can affect the cold tolerance and the trees will not be able to withstand low temperatures. The needles collected in November and February from plants treated with +15°C in October (treatment 5) and outdoors (treatment 1) are the least damaged indicating that even a warmer temperature during October will not always result in more frost damage and that plants in their natural habitat are usually suited for frost during late autumn and winter.

For the chlorophyll fluorescence measurement on needles collected in November, the biggest difference in Fv/Fm before and after freezing could be seen for plants that had been indoor in +15°C (treatment 3) for all the freezing temperatures (Paper IV, Table 11, 12 and 13). However, treatment 1 and 2 were non-significantly different from treatment 3 under -30 ºC. In January, treatment 3 still had the highest difference, but it was not significantly different from treatment 7 in -30°C. This in turn indicates that plants in warmer temperature are not as cold tolerant as trees that have been in ambient temperature and that even a heat flash in December can decrease their cold tolerance.

One definition of dormancy is when no cell division occurs in meristematic tissues (Romberger 1963; Owens 1968). In our study, an indication that true dormancy occurred only in late November and

December was found. In southern Sweden it may not be critical in the current climate to be entirely in rest, however occasional backlashes may occur where low temperature may cause active meristems as apical buds to die.

4.3 The impact of drought (Paper III)

In Paper III the impact of a severe drought at the year of 2018 was investigated with six clonal field trials in Sweden and Finland. During the summer of 2018 the temperature was exceptionally high, and the precipitation was low, which resulted in forest decline and tree mortality. A study by Schuldt *et al.*, 2020 revealed that the event had a negative impact on the recovery of individual trees in 2019.

4.3.1 Drought index

For the study in Paper III the severity of the drought event 2018 needed to be calculated and compared to the years before and after the drought. For this, the SPEI was calculated for the period of 2009-2019 on monthly averages (Paper III, Figure 2). The trials Ängelholm and Kohagen had a severe drought in 2018, were Ängelholm went from an SPEI of around zero (near normal, NN) in 2016 and 2017 to -1.6 (Severely dry, SD) in 2018 (Figure 10). Kohagen had a less dramatic change from -0.9 (NN) in 2016 and -0.5 (NN) in 2017 to -1.8 (SD) in 2018. In the trials Sunnansjö, Nässja and Pori a moderate dry drought was indicated in 2018, while in Nurmijärvi it was near normal. The drought event in the year of 2018 was seen in all the sites, but it was especially dry for Ängelholm.

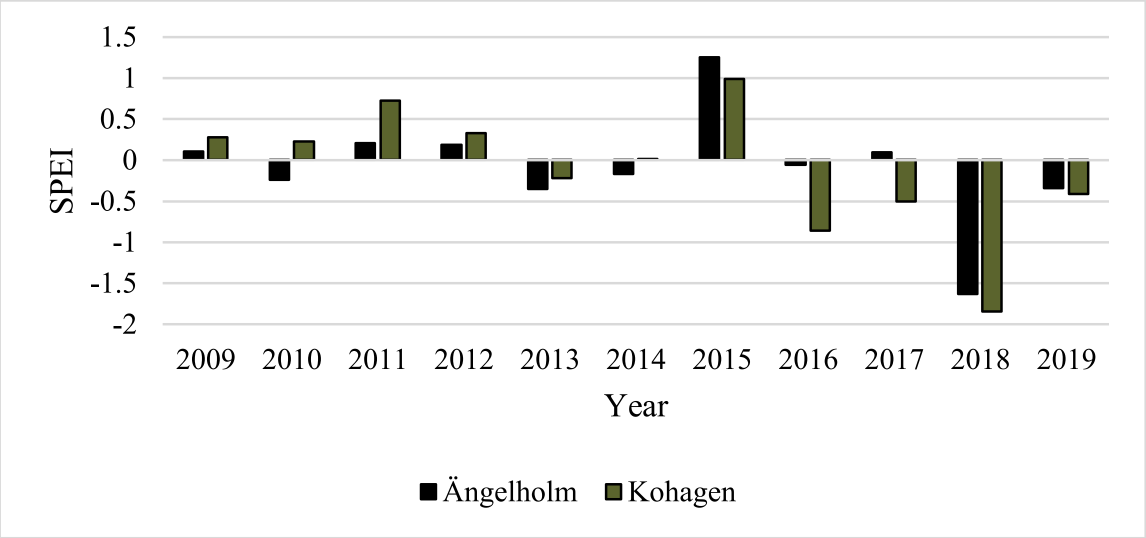

Figure 10 – The average of SPEI between the years 2009-2019 for 16 Ängelholm and 15 Kohagen for the months May to July.

4.3.2 Height increments

The highest rate of height increments among the Swedish trials was in Sunnansjö, while the others grew at a similar level with trees in Nässja as the slowest growing (Paper III, Figure 3). The height growth from 2017 to 2018 was very low or neglectable for Nässja, Kohagen and Ängelholm, while trees in Sunnansjö grew at a similar rate all the years. One explanation for this is that Sunnansjö is the only trial with higher slope and closer to a hillside and can therefore hypothetically take advantage of more mobile water (Hägglund & Lundmark, 1977) because it is usually the shortage of soil water that is the major growth-limiting factor for spruce trials (Lebourgeois, 2007).

In the Finnish trials, trees in Nurmijärvi grew much faster in 2019 than in 2018, while trees in Pori grew at a similar level both year 2018 and 2019 (Paper III, Figure 3). This might be due to the fact that Pori is located closer to the coast and this could have a negative effect on the site index of the stand (Hägglund & Lundmark, 1977).

4.3.3 Type-A correlation

In Paper III, the correlations between the annual height increment (Ht17, Ht18 and Ht19 in full-sib, and Ht18 and Ht19 in half-sib clonal trials) and total height for three-years, type-A additive genetic

(r_A) and phenotypic (r_P) correlation were estimated (Figure 12 and 12). Non-additive correlation was also estimated for the study, but not included in the thesis because it is the additive correlation that is used in the breeding program in Sweden. In general, the half-sib clonal trials had higher r_A compared to the full-sib clonal trials. The lowest r_A in all the trials was obtained for the correlation of Ht19 with all total-height traits. The lowest r_A in the full-sib clonal trials was 0.5 from Ht19 with Tot-Ht16, which was obtained in Sunnansjö, and it increased to about 0.75 with Tot-Ht19. Overall, both the r_A and the r_P correlations were generally lower in the year of 2019 (the year after the drought) for all the trials, which indicates that the drought had a negative impact on the genetic and phenotypic correlation of the growth the year after the drought with other growth traits. A study from Huang *et al*. (2018) observed similar effects, that trees can suffer from drought several years after an event. When comparing r_P and r_A, the phenotypic correlation was lower than the additive genetic correlation, which has been shown before (Fundova *et al*., 2019; Hayatgheibi *et al*., 2019).

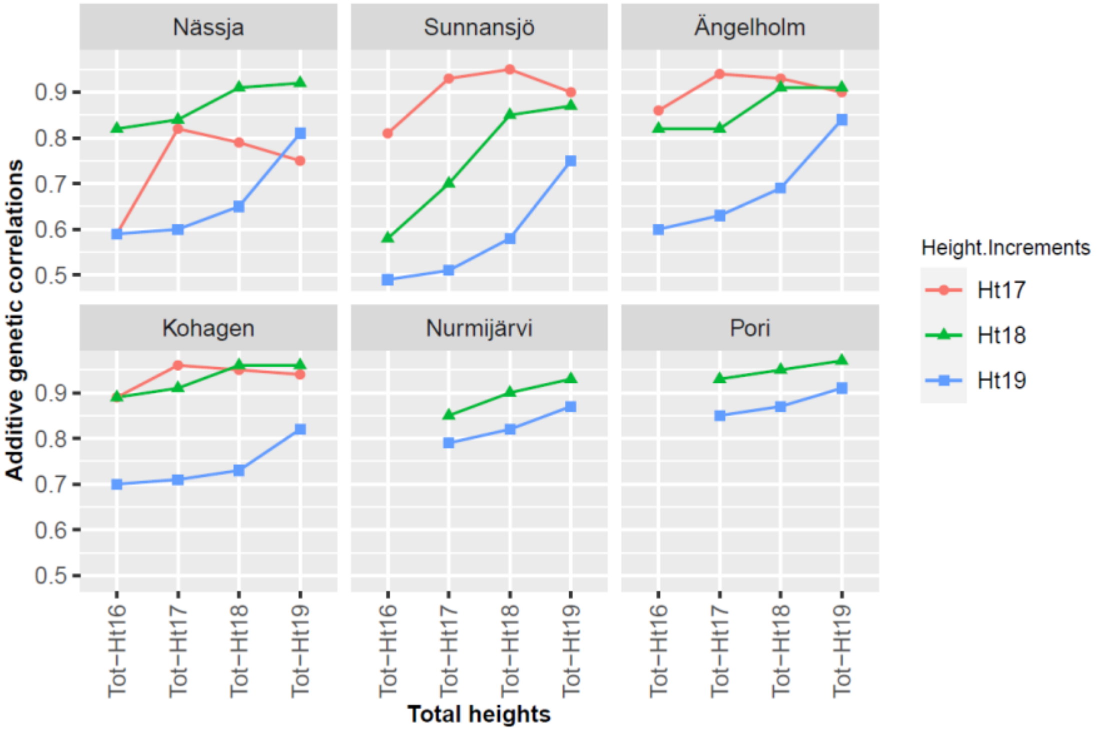

Figure 11 - Estimated type-A additive genetic correlation of three-years height increments measurements with total height in six trials.

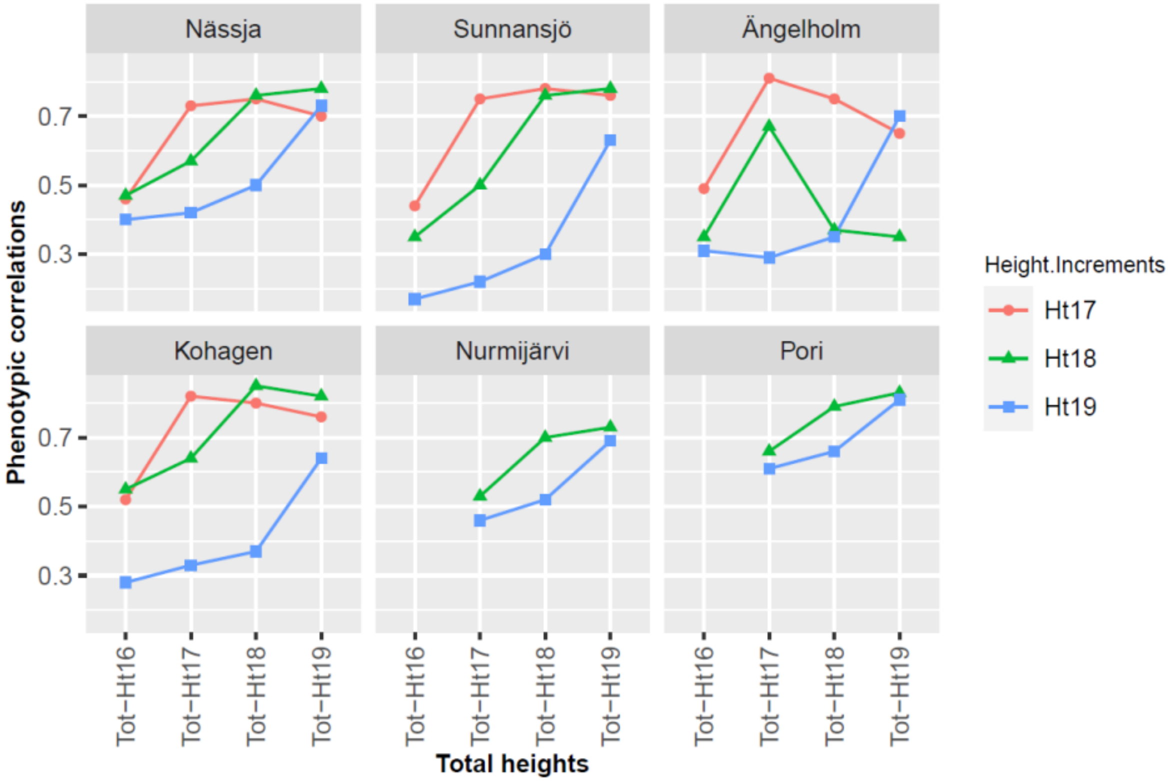

Figure 12 – Estimated phenotypic correlation of three-years height increments measurements with total height in six trials.

4.3.4 Type-B correlation

In the study in Paper III, the G x E correlation was estimated with type-B correlation (r_b), since we had full-sib and half-sib families and pedigrees. A value of r_b close to one indicates little G x E, while a low value indicates extensive G x E interaction. In general, type-B additive correlations for total-height traits were moderate in all trials, ranging from 0.52 to 0.86, while they were slightly lower for their corresponding annual height increments (Table 5). The lowest r_b was obtained for Ht18 in trial pairs Ängelholm-Kohagen, while such estimate was 0.71 in Nässja-Sunnansjö and 0.48 in Nurmijärvi-Pori. Moreover, r_b increased as trees became older in Nässja-Sunnansjö, while it decreased in other trial-pairs.

Results of G × E studies have revealed that G × E interaction is more significant for growth traits compared to other quantitative traits, such as wood quality (Wu & Matheson, 2005) which signifies genotype rankings may vary across trials.

The r_b values obtained for growth traits in our study are mostly in a similar range reported for growth of Norway spruce in other investigations (Berlin *et al.*, 2015; Berlin *et al.*, 2019).

Based on the observed SPEI results, trials Ängelholm-Kohagen have experienced a severe drought during 2018. This might be an underlying factor for the high and significant G x E obtained for the growth of 2018 at these trials.

Table 5 – Estimated type-B additive genetic correlations (r_b) with standard errors in parenthesis for height measurements in four full-sib and two half-sib clonal trials.

Trait	**Trial pairs**		
	Nässja Sunnansjö	Ängelholm Kohagen	Nurmijärvi Pori
	r_B	r_B	r_B
Ht17	0.69 (0.11)	0.59 (0.11)	-
Ht18	0.71 (0.11)	0.23 (0.13)	0.48 (0.11)
Ht19	0.79 (0.09)	0.35 (0.15)	0.44 (0.10)
Tot-Ht16	0.72 (0.11)	0.70 (0.08)	-
Tot-Ht17	0.78 (0.09)	0.67 (0.08)	0.66 (0.09)
Tot-Ht18	0.82 (0.08)	0.54 (0.10)	0.63 (0.10)
Tot-Ht19	0.86 (0.06)	0.52 (0.62)	0.62 (0.10)

5. Conclusions and future perspectives

In the studies underlying this thesis, we have analysed different provenances and clones to understand how the Norway spruce will behave in a changing climate with increasing temperatures, more frequent spring frost events and drier summers. We have also investigated alternatives in case of shortage of improved seeds. From these studies we can draw the following conclusions and future perspectives.

We recommend the deployment strategy of using East European material in the south of Sweden in case of shortage of improved seeds from Swedish seed orchards, and also indicate that second generation material is a good choice (Paper I). We have also seen that seeds from East European seed orchards have a similar growth performance compared to seeds from Swedish seed orchards, and therefore are a good option in the south of Sweden. This should be applicable for other Nordic countries since the imported material and the climate is similar. Several of these countries have native seed sources of desired provenances and would be able to use them in case of shortage of improved seeds.

The second generation material has similar growth as the East European stand material but is closer to the Swedish material in growth rhythm, like bud burst and lignification. This is an indication for development of land race with respect to phenological traits, where the place where the seed matures will affect these traits more than the growth traits. It should be noted that the difference in growth rhythm between second generation material and East European material may be in favour of the latter on frost prone sites.

In the future, more information about the climate and how different provenances of Norway spruce behave in different locations is needed. To be able to meet the demand of seedlings produced in the future, more sources of seeds need to be included and investigated. It will be important to include different genetic material in the seed orchards, and especially material that have later bud burst but still have an increased growth performance.

Both in Paper I and II a relationship between less damaged and late bud burst could be seen which other studies have shown before, so one way for the trees to avoid frost is to have a later bud burst.

We showed in Paper II that it is possible to use estimated provenance specific temperature sum requirements for bud burst to calculate the risk of spring frost events for an arbitrary site in southern Sweden. The start of the growing season as well as frost damage had an effect on tree growth, with some provenance specific differences.

In the model, gridded temperature was used and the comparison of daily minimum temperature between gridded and logger data indicated an overestimation by gridded data. This means that the risk of frost damaged can be even higher than calculated because the actual local minimum is lower.

For the model projection in the future with the RCP8.5 scenario, a decrease in the number of frost days together with earlier bud burst will increase the frequency and severity of frost events following bud burst. This model can be used in the future for seed orchard material and be a help in the selection of suitable seed material. In the trials used in the study, there are also seed orchard material planted that can be used in further modelling studies for information about how seed orchard material behaves in future climate. If the information from studies like that are included in the current system for deployment recommendation, an increase in growth and survival can be made.

Fluctuating temperatures during autumn, winter and spring can affect the bud burst and growth of Norway spruce, where an increase in temperature already from December but predominately from March appears to have a significant effect on the bud burst (Paper IV). More information is needed about when the trees are able to bud burst and at which temperatures. The results indicate that the trees studied are in a rest phase in November and December, or most likely during a shorter period than two months. Further studies are needed to, if possible, confirm when cell divisions in the buds is ongoing.

We suggest that it is relevant to study the effect and importance of a rest period and also to decide if it should be considered as a breeding goal *per se*. The study in Paper IV indicates that the trees utilize a large part of the off season for growth, even though it is not visible. In trees this can be regarded as an opportunity to achieve high growth performance but also as an increased risk and a potential to dieback of shoots and secondary diseases. For future breeding selections further studies of the rest period are recommended to avoid a potential unwanted increase of trees with short rest periods.

For future studies more information about how different clones behave in different temperatures could be investigated further, to get the pattern of G x E for the clones and include this information in further studies about the impact of warmer temperature on Norway spruce.

Drought can affect Norway spruce several years after a drought event, and in our study in Paper III the growth of the trees was assessed before, during and after a drought event. The drought in 2018 had a negative effect on the height increment of trees during the growing season of 2018. The lowest additive genetic and phenotypic correlations were obtained for correlations of Height in the year of 2019 with total-height traits in all clonal trials, which implies that the effect of the drought may negatively affect the height the year after the event.

We could also see that the drought could have been an underlying factor for very high and significant G x E, indicating that some genotypes have higher resistance to drought than others which could cause rank changes across sites.

The SPEI is a good representative of the drought but the availability of soil water is also important and should be included when assessing the effects from a drought event.

For future studies of drought more information about the effects some years after a severe drought would be interesting as well as more information about which trees are more resistant. This can also be included in the deployment strategies were trees with higher resistance are included in the future for higher chance of surviving in case of drought events.

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Populärvetenskaplig sammanfattning

Gran är en av Sveriges viktigaste trädslag som bidrar med mycket ekonomiskt, men också ekologiskt. Träet används vanligtvis till konstruktion, papper och virke bland annat. Gran som planteras idag måste överleva minst 60 år i fält för att man ska kunna avverka, vilket gör att den måste kunna anpassa sig. I framtiden kommer klimatet att ändras, där vintern blir varmare, fler bakslag av låga temperaturer under våren och torrare sommar. För att fortfarande kunna öka tillväxt, överlevnad och träets egenskaper så måste man undersöka hur granens egenskaper, så som höjd, diameter, skottskjutning, överlevnad och motståndskraft mot torka och frost påverkas av klimatförändringar.

Förädlingen av gran började redan på 40-talet där man valde ut bättre växande granar och planterar dem i fröplantage, vilket kan ge en högre tillväxt på upp till 25%. Det tar dock minst 20 år innan man kan börja ta frön från träden och gran är även känd för att blomma sällan. Även under bra blomsterår så kan granen angripas av pest eller svamp, vilket dödar kottarna som bär frön. Idag kommer endast runt 50% av fröplantorna som planteras i skogarna i Sverige från fröplantage, vilket gör att annat material måste tillkomma. För att fortfarande behålla tillväxten och ha hög överlevnad måste undersökning av annat material göras. Man måste även undersöka hur granen reagerar på olika klimatförändringar så som ökade temperaturer, frost och torka för att kunna välja ut de bäst lämpade träden att plantera i framtiden.

I studierna från denna avhandling har vi analyserat vilket material som kan användas ifall tillgång till förädlat frö inte räcker till. Resultatet var att det är möjligt att använda frön från svenska bestånd med östeuropeiskt ursprung och fortfarande få hög tillväxt, men man måste vara uppmärksam på att de beter sig mer som svenska träd än östeuropeiskt material när det gäller skottskjutning. Även frön från östeuropeiska förplantage och bestånd är möjliga att använda i södra Sverige.

Vi har även studerat hur olika granar med olika härkomst reagerar på framtidens klimat, där bland annat vårfrostskador, varmare temperaturer och torka har undersökts.

Granen kommer att ha tidigare skottskjutning i framtiden på grund av varmare temperaturer, vilket ökar risken för vårfrostskador eftersom frostnätterna efter skottskjutning kommer att öka. För att motverka detta behöver man välja granar med senare skottskjutning, speciellt på frostbenägna platser.

Torka under sommaren kan påverka granens tillväxt. En torka under sommaren 2018 visade på en negativ effekt på höjden under två efterföljande år. Vi såg även att vissa genotyper klarade torkan bättre än andra, vilket skulle kunna inkluderas i förädlingsprogrammet för att förbättra toleransen av vattenbrist.

Popular science summary

Norway spruce is one of Sweden most important species, both from economic and ecologic point of view. Its wood is usually used in construction, paper and wood. The spruces planted today have to survive for at least 60 years in the field before felling, and that is why they need to adapt to the environment of where they are planted. In the future, the climate will change with warmer winters, more backlashes of low temperatures during spring and dryer summers. In order to still increase growth, survival and the properties of the wood, the spruce characteristics like height, diameter, bud burst, survival and tolerance to drought and frost need to be investigated.

Norway spruce breeding started in the 1940s with the selection of better growing trees that were planted in seed orchards. Seeds from a seed orchard can get up to 25% higher growth compared to unimproved seeds, but it takes almost 20 years before seeds can be harvested and spruce have unregular flowering. Even at good flowering years the cones get infested with fungi or pests. Today only approximately 50% of the seedlings planted in Swedish forests are from seed orchards, which increases the importance of the study about high growth and survival in other material. It is not only these traits that are important but also how the climate change with increasing temperatures, frost and drought will impact the Norway spruce in the future. That is why an investigation for selection of the best trees to deploy in the futures needs to be done.

In this thesis, we have compared different material that can be used in case of shortage of improved seeds. The result was that it is possible to use seeds from Swedish stands with East European origin and still get high growth and survival, but just to have in mind that they behave more like the Swedish trees with respect to bud burst. It is also possible to use seeds from East European seed orchards and stands in the south of Sweden.

We have also investigated how different Norway spruce provenances and clones react to the future climate, like spring frost damage, warmer temperature and drought.

Trees will experience earlier bud burst in the future due to warmer temperatures, which in turn will increase the risk of spring frost damage because of more spring frost events after bud burst. To counteract this, trees with later bud burst need to be planted especially on frost prone sites.

Drought events during summer can affect Norway spruce growth. A drought event in 2018 revealed a negative effect on height during two consecutive years. We also observed that certain genotypes were able to respond better than others to drought, which could be selected as parents in a breeding program to improve tolerance to water deficit.

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The future climate is going to change, and trees have to adapt to survive. Along with the climate change, pests and fungal infections are likely to increase which may compromise Norway spruce (*Picea abies* (L.) Karts.) seed supply. In this thesis, different seed sources have been investigated as an alternative to improved seeds in case of seed shortage and assessments of how Norway spruce from different origins adapts to warmer temperatures, drought events and risk for spring frost were made.

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